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Avian responses to fire regimes in montane dry sclerophyll forests of south-eastern Australia

by

Michael John Macquarie Franklin

Supervisors

Ross A. Bradstock, Richard E. Major, Owen F. Price

A thesis submitted in fulfilment of the requirements for the award of the degree

Doctor of Philosophy

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Abstract

Wildfires are becoming larger and more frequent in forests under climate change, with corresponding increases in area burnt recently and at high-severity. Australian fire regimes are changing rapidly, but the implications for fauna are poorly understood. The first of two overarching aims of this research was to increase understanding of the mechanisms and processes that underpin avian responses to fire regimes in montane dry sclerophyll forests of south-eastern Australia. The second was to investigate the implications of altered fire regimes for birds through evaluation of their responses where fire activity is currently high.

Across multiple landscapes of the Greater Blue Mountains, 75 sites with different combinations of time since fire, fire frequency and fire severity were established on ridges. Two research chapters were allocated to bird survey methodology, and three were focused on avian responses to fire regimes.

Three frameworks were used to produce a robust bird survey method using acoustic recorders. The optimal method used 200-min of manually processed recordings per site, and may also be applied in other research and monitoring in dry sclerophyll forest. The frameworks can be used globally by ecologists to produce context-specific survey methods.

Avian mobility was investigated as a mechanism that may influence species capacity to access resources in fire-prone landscapes. The occurrence of groups of nomadic, migratory (both relatively mobile) and exclusively sedentary (less mobile) species in relation to fire frequency and long unburnt forest was estimated using a Bayesian multispecies occupancy model. Many species and migrants as a group responded positively to the presence of long unburnt forest in the landscape. Fire frequency was less influential on birds. Relative mobility was linked to occupation of preferred habitat in pyric landscapes.

Avian responses to the extent of historical high-severity fires were investigated through time since fire using Bayesian latent variable models. Positive or negative responses to high-severity fire among species did not change over time since fire, suggesting persistent effects of such fires on habitat. The extent to which avian responses to short-term effects of high-severity fire on habitat persist, including whether additional time since fire moderates any negative responses, was unknown. Other species were unlikely to occur where time since fire was short.

The relative strength of direct (mortality, emigration) and indirect (canopy structure) effects of time since fire on birds were investigated using Bayesian mediation models. Direct effects of time since fire had little effect on birds after five years. However, ongoing regeneration of canopy structure (determined from LiDAR data) had strong positive influences on species richness and occurrence.

Of all species investigated in relation to fire, 25% were averse to at least one component of fire regimes at a level representative of increased fire activity under climate change. Most of these species required habitat at mid-range or longer time since fire. Consequently, the resilience of many species will be challenged in fire-prone landscapes. To support avian diversity, a management approach that incorporates vegetation structure in the identification and retention of substantial, suitably distributed forest with longer fire-ages is recommended.

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The Dharug, Wiradjuri and Darkinung peoples are the traditional owners of the lands on which this research was conducted, and I pay my respects to their elders past and present.

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Thesis Certification

I, Michael John Macquarie Franklin, declare that this thesis, submitted in fulfilment of the requirements for the conferral of the degree Doctor of Philosophy, from the University of Wollongong, is wholly my original work unless otherwise referenced or acknowledged. This document has not been submitted for qualifications at any other academic institution.

Michael John Macquarie Franklin

18th July 2022

Statement on Thesis Style

This thesis has been prepared in journal article compilation format. The main body of research is presented in Chapters 2-6, and each of these has been published in or submitted to scientific peer-reviewed journals. In collaboration with co-authors, I led the conceptualisation, investigation, methodology and writing for all of these research articles. Standardised formatting has been applied to all articles for consistency throughout the thesis. The content of Chapters 2-5 is identical to their published versions, apart from minor alterations that were required to present an integrated thesis, such as renumbering chapter sections, figures and appendices. Because Chapters 2-6 are stand-alone research articles, there is some unavoidable repetition in sections describing the study area and bird survey methods. Chapter 1 is a general introduction containing a literature review followed by the research aims and thesis structure. Chapter 7 is a general conclusion and synthesis of the findings of the preceding chapters.

Publications and Author Contributions

Chapter 2 was published on the 4 March 2020 as an article titled ‘Establishing the adequacy of recorded acoustic surveys of forest bird assemblages’ in the journal *Avian Conservation and Ecology* (https://doi.org/10.5751/ACE-01521-150108).

Relative author contributions were Michael J. M. Franklin[1] (80%), Richard E. Major[2] (7.5%), Michael Bedward[1] (7.5%) & Ross A. Bradstock[1] (5%).

Chapter 3 was published on 15 March 2021 as an article titled ‘How much survey effort is required to assess bird assemblages in fire-prone eucalypt forests using acoustic recorders?’ in the journal *Wildlife Research* (https://doi.org/10.1071/WR20099).

Relative author contributions were Michael J. M. Franklin[1] (90%), Richard E. Major[2] (7.5%) & Ross A. Bradstock[1] (2.5%).

Chapter 4 was published on 7 July 2021 as an article titled ‘Relative avian mobility linked to use of fire-affected resources in forested landscapes’ in the journal *Forest Ecology and Management* (https://doi.org/10.1016/j.foreco.2021.119484).

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Chapter 5 was published on 8 April 2022 as an article titled ‘Forest avifauna exhibit enduring responses to historical high-severity wildfires’ in the journal *Biological Conservation* (https://doi.org/10.1016/j.biocon.2022.109545).

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Chapter 6 was submitted on 9 July 2022 as an article titled ‘Canopy structure mediates the effects of time since fire on arboreal birds’ to the journal *Biological Conservation*.

Relative author contributions were Michael J. M. Franklin[1] (90%), Richard E. Major[2] (5%) & Ross A. Bradstock[1] (5%).

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Associated works

Franklin, M, Major, R & Bradstock, R 2019, 'Survey of montane forest birds using acoustic recorders', *Australasian Ornithological Conference,* Darwin (Oral Presentation).

Franklin, M, Major, R, Bedward, M & Bradstock, R 2022, 'Movement strategies and avian responses to forest fire history', *Australasian Ornithological Conference,* Auckland (Oral Presentation).

List of Abbreviations

% = percent
° = degrees
C = Celsius
DSF = dry sclerophyll forest
g = grams
GBMWHA = Greater Blue Mountains World Heritage Area
ha = hectares
km = kilometres
LiDAR = Light Detection and Ranging
LOO = leave-one-out cross-validation
m = metres
MCMC = Markov Chain Monte Carlo
min = minute
mm = millimetres
NDVI = Normalised Difference Vegetation Index
sp. = species
SPOT = Satellite Pour l'Observation de la Terre

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Chapter 1. General Introduction

1.1 Climate change, fire regimes and forest birds

Wildfire is a natural, yet potentially powerful agent of disturbance in forests globally, such that a single fire may impact much of the biota at the landscape scale. Further to the effects of any one fire, biological communities respond to fire regimes, which represent dynamic combinations of fire frequency, intensity, season of occurrence, and the spatial extent of fires at a given location through time (Gill 1975, Bond & Keeley 2005). Over the coming decades, climate change is predicted to continue to drive increases in fire activity in forested landscapes worldwide (de Groot et al. 2013, Dupuy et al. 2020), including those located in south-eastern Australia (Bradstock et al. 2009, Dowdy et al. 2019). These predictions have already manifested at continental scales, as evidenced in the 2019-2020 mega-fires in eastern Australia (Abram et al. 2021), which burnt extraordinary amounts of natural vegetation at high-severity (Collins et al. 2021). These fires impacted substantial proportions of the distributions of many vertebrate species, including those with threatened status before the fires (Ward et al. 2020). A consequence of larger, more frequent fires is that the total amount of recently-burnt forest in a region is increased (Fairman et al. 2016), which has non-trivial implications for fauna that require older habitat. For example, particular bird species are more likely to occur where time since fire is longer in foothill-gully forest systems (Robinson et al. 2014), so there is potential for significant reductions in suitable habitat for those species.

Recent advances have been made in understanding avian responses to time since fire (Gosper et al. 2019a), and components of fire regimes such as fire frequency (Kelly et al. 2017), in particular Australian systems. However, the implications of changing fire regimes for dry sclerophyll forest birds in terms of their habitat requirements, response mechanisms, and the effects of fire on ecological processes, are currently not well understood. In south-eastern Australia, extensive dry sclerophyll forest communities support the spread of wildfires through the montane terrain of the Great Dividing Range. These floristically and structurally diverse communities are subject to widely varying fire regimes (Keith 2004), and are important habitats for birds (Smith et al. 2019).

The responses of individual bird species to different fire regimes vary across habitats and are influenced by the effects of fire on vegetation, as well as environmental and climatic factors (Bradstock et al. 2005, Kelly et al. 2017, Valentine et al. 2012, Woinarski & Legge 2013, Woinarski & Recher 1997). Potential habitat for some species may reflect narrow combinations of these variables (Hutto & Patterson 2016). Our understanding of the most suitable fire history patterns for the maintenance of avian diversity is incomplete or absent for many regions and ecosystems (Kelly et al. 2015). Understanding the response of birds at the species level in their various habitats is necessary to maintain populations across species distributions (Connell et al. 2017, Driscoll et al. 2010). For example, the tropical savannas of northern Australia have experienced increases in the frequency of intense, late-dry season fires, to which 43 of 44 savanna bird species responded by showing range contractions in distribution modelling (Reside et al. 2012). Deeper insights can be obtained by combining information about species distributions in areas within landscapes that represent existing fire regimes, with what is known about species traits and life histories (e.g., Gosper et al. 2019a). Because the responses of many bird species to fire are context-dependent, gaining and integrating understanding about species response mechanisms is important for fire management that aims to reduce the risk of extinction of any species (Driscoll et al. 2010). Identification of favourable fire regimes for different functional groups of bird species is an important area for future research (Kelly et al. 2017), but insights will be reliant on a sound understanding of the fire-response mechanisms of the focal species (Driscoll et al. 2010).

1.2 Avian responses to time since fire

The responses of birds to time since fire vary by species and according to context, ranging from preferences for burnt habitat immediately following fire to long unburnt vegetation. In avian assemblages, abundance and/or richness at the species or functional group level in relation to time since fire may be explained by variation in the availability of resources required by species as the vegetation regenerates and matures (Gosper et al. 2019a). However, the capacity of a species to move within and beyond fire-affected landscapes, both in immediate response to fire, or shortly after to locations where vegetation is at suitable successional stage, influences the distribution and population viability of a species (Nimmo et al. 2019). Vegetation succession is related to time since fire, so the latter has to be considered, incorporated, or controlled for in any landscape-scale study of the responses of animals to fire regimes.

To maximise biodiversity, fire management and planning for natural landscapes has often aimed to maintain a mosaic of patches with contrasting fire histories, but this approach potentially lacks specificity and may achieve sub-optimal results (Bradstock et al. 2005, Taylor et al. 2012). For example, the responses of many of the avifauna of semi-arid, multi-stemmed (mallee) eucalypt ecosystems have shown that a higher proportion of older vegetation, rather than an even spatial distribution of a range of fire-age classes, would better support avian diversity (Connell et al. 2017, Taylor et al. 2012, Taylor et al. 2013). Greater species richness (Taylor et al. 2012), relative abundance (Kelly et al. 2015), and probability of occurrence of many species, including a number of threatened species (Connell et al. 2017), were associated with longer time since fire. In addition to requiring long-unburnt vegetation, a number of species were also restricted in their distributions to areas with particular climate and vegetation characteristics (Connell et al. 2017). More needs to be known about the requirements of montane dry sclerophyll forest birds for habitat at particular fire-ages. Plant reproductive mechanisms and time to maturity were used to establish a fire return interval of 7-30 years to guide the fire management of dry sclerophyll forests with shrubby understories in south-eastern Australia (Bradstock & Kenny 2003, Kenny et al. 2004). The following subsections are structured broadly in relation to this interval, as short (< 7 years), mid-range (7-30 years) and long (> 30 years) time since fire.

1.2.1 Short time since fire

The responses of birds to recent fire in eucalypt forests can vary widely among species and are associated with the direct effects of wildfire, and the effects of fire on required resources. Direct effects include mortality and emigration (Whelan et al. 2002), which may contribute to rapid population declines if large fires burn substantial proportions of species distributions, particularly if those fires are severe (Legge et al. 2021, Jolly et al. 2022). Wildfires alter the availability of habitat resources used by birds, including vegetation structure (Karna et al. 2020, Doherty et al. 2022), hollows for nesting (Haslem et al. 2012), and food (Valentine et al. 2014). The absence of understorey vegetation immediately after fire in dry eucalypt forests can result in an influx of bird species that use open areas for foraging. However, regeneration of the vegetation commences promptly, and bird species present pre-fire, but absent post-fire, may return to burnt areas within two or three years (Woinarski & Recher 1997). The early stage of vegetation regeneration proceeds rapidly, so post-fire specialists can be lacking in eucalypt forest bird assemblages (Lindenmayer et al. 2008). In New South Wales coastal forest, rapid eucalypt resprouting may have been responsible for the recovery of most species and bird assemblages in a range of habitats two years following fire (Lindenmayer et al. 2008). Total bird abundance in a range of habitats further south, including dry sclerophyll forest, had recovered to pre-fire numbers by three years after fire, but the degree of recovery at the species level was varied (Loyn 1997). For example, numbers of honeyeaters were very low immediately following fire, which was probably a function of their high mobility and capacity to track resources at regional scales. In diverse foothill forests dominated by eucalypts that resprout post-fire, some bird species were more likely to occur where time since fire was short, while the probability of occurrence in recently burnt habitat was reduced for other species (Kelly et al. 2017).

Post-fire recovery of birds can be more rapid in structurally complex vegetation, e.g., layered forest, compared with simpler forms such as heath, perhaps because under equivalent fire conditions, there is potential for proportionally more habitat structure to be lost from simpler forms (Barton et al. 2014). Nevertheless, some understorey species can persist in a burnt area by varying the way they use habitat shortly after fire, although their populations are still vulnerable when fire is frequent. The Splendid Fairy-wren (*Malurus splendens*), Western Thornbill (*Acanthiza inornata*) and Yellow-rumped Thornbill (*Acanthiza chrysorrhoea*) may resume breeding in the season following fire in burnt heathland (Brooker & Rowley 1991). In unburnt heath, Splendid Fairy-wrens used plants that either resprout or regenerate exclusively from seed following fire in equal proportions for nesting, but were totally reliant on resprouting plants for nest substrate in the first breeding season after fire. These birds also adapted by positioning their nests at different heights in the vegetation strata compared with pre-fire nest locations. Breeding was delayed for particular species, which was attributed to reduced levels of food and nesting materials. Other species did not breed in the heath for at least two years.

1.2.2 Mid-range time since fire

The responses of species, guilds, and assemblages to short time since fire are often not the same a decade or more after fire, although persistent effects of fire on habitat can result in sustained negative responses from birds. In the year after fire in mixed eucalypt/White Cypress Pine (*Callitris glaucophylla*) forest in western NSW, there were more species and individuals in areas that had not been burnt by wildfire (Turner 1992). When the same areas were surveyed again eight years after the fire, there were many more species and individuals in the burnt forest than in the unburnt areas. The additional species in the burnt areas were mainly foliage, understorey, and ground foraging insectivorous species. In alpine areas, the post-fire recovery of vegetation, including trees such as the Snowgum (*Eucalyptus pauciflora niphophila*), takes longer than many of their low altitude counterparts owing to different regeneration mechanisms (Green 2013). Shifts in the structure of bird assemblages were observed in response to time since the last hazard reduction burn in eucalypt woodland of South Australia. In addition to sites last burnt at least 20 years ago having more birds overall, assemblages in recently burnt sites had increased proportions of large, generalist species, but these effects were lessened if some long-unburnt woodland was accessible (Prowse et al. 2017). Ten years after wildfire in the Snowy Mountains of south-east Australia, the Snowgum canopy had not regrown, which negatively impacted species that would forage in that space, especially granivores. Nectivorous birds were also less common, which corresponded with reduced availability of flowers from the obligate seeding *Grevillia victoriae* (Green 2013).

1.2.3 Long time since fire

Birds continue to respond to time since fire up to and beyond 100 years in particular Australian ecosystems. In south-east Australian eucalypt forests, the majority of species that responded to time since fire of between 0-70 years, including the Rose Robin (*Petroica rosea*), Yellow-faced Honeyeater (*Lichenostomus chrysops*) and Golden Whistler (*Pachycephala pectoralis*), were more abundant in long-unburnt areas (Kelly et al. 2017). The responses of individual species in sites representing a 100-year gradient of time since fire differed in two types of regional mallee eucalypt community (Watson et al. 2012a). Only four of 16 species that responded significantly to time since fire did so in both vegetation communities, but the shape of the response curve was the same in each community for only two species, which were both honeyeaters. Despite the variation in the linear and non-linear patterns of species responses, habitat with a time since fire of at least 20 years was optimal for most species in the region. Similarly, in obligate-seeding Australian eucalypt woodland, most bird species were more abundant, and assemblages were richer, with increasing time since fire (Gosper et al. 2019a). Species responses to different aspects of fire regimes, such as time since fire, may vary along rainfall and temperature gradients (Kelly et al. 2017). For example, in south-east Australian eucalypt forests, the probability of occurrence of the Australian King Parrot (*Alisterus scapularis*) peaked in areas with longer time since fire, but only where summer temperatures were at the low end of the regional range (Kelly et al. 2017).

1.3 Avian responses to fire severity: from single to multiple fires

The severity of a wildfire can be considered as representing the effects of fire intensity through incineration or change in vegetation in a location (Keeley 2009). Large wildfires burn through landscapes at different levels of intensity because of factors such as variation in topography or changing weather conditions, so the effects of a fire in terms of burn severity are spatially heterogeneous (Bradstock 2008). Fire severity may be determined using a range of approaches. The difference in Normalised Difference Vegetation Index (NDVI) values for pre and post fire satellite images, with associated validation using measurements obtained in the field, may be used to infer fire severity (e.g., Hammill & Bradstock 2006). Fire type (wildfires, prescribed burns) may be used as a surrogate for fire severity, but effects on birds may be difficult to detect owing to the coarseness of the measure and rapid regeneration of fire-adapted vegetation following either type of fire (Kelly et al. 2017). Amazonian forest birds responded to the density of live trees after fire, which was used as a proxy for fire severity (Barlow & Peres 2004).

Much of what is known about the effects of fire severity on birds is based on the period shortly after fire. Immediately following fire, the general differences in bird assemblages in areas with varying levels of burn severity, including unburnt areas, may be only minor in some habitats. In tropical savanna, bird species richness and total abundance were alike in burnt and unburnt areas shortly after an extensive high-severity fire, although particular species were more common in either burnt or unburnt areas (Legge et al. 2008). Similarly, no differences in bird diversity were detected between unburnt, mildly burnt and severely burnt sites in the weeks following a fire in African savanna (Mills 2004). Both of these studies were conducted in areas subject to high fire frequency, with the lack of difference in bird diversity amongst severity treatments in African savanna attributed to the rapid rate of recovery of the vegetation (Mills 2004). Likewise, bird assemblages were similar in patches of North American montane conifer forest that were either unburnt, or very recently burnt to different levels of severity (Tingley et al. 2016). Over the ensuing 10 years, the bird assemblages associated with the original levels of fire severity differentiated, rather than becoming more similar. This may be at least partly explained by the fact that the responses of the vegetation to different fire severities resulted in divergence of plant communities over the period (Tingley et al. 2016).

Short-term responses of bird species and assemblages to increasing levels of fire severity can be negative in particular south-east Australian habitats. Eastern Bristlebirds (*Dasyornis brachypterus*) were less abundant post-fire in coastal habitat burnt at high severity, which was probably due to the complete loss of the required dense shrub layer (Bain et al. 2008). In a range of habitats in the same region, avian species richness measured one year after wildfire declined with increasing fire severity and fire frequency (Lindenmayer et al. 2008). In montane forests, where the dominant trees were obligate-seeding eucalypts, the effects of fire severity on birds varied considerably among species, however increases in the extent of severely burnt area negatively affected the majority of species (Lindenmayer et al. 2014). In mixed eucalypt forest subject to frequent fire, bird species richness 2-3 years after the most recent fire was 29% greater in sites where only the understorey was burnt, compared with those burnt at a high level of severity (Robinson et al. 2014). This was not the case in other parts of the study area where the fire return interval was longer, but in these areas the composition of assemblages and the occurrence of 11 species differed between sites burnt at low and high-severity in the last fire.

Particular species are associated with the early post-fire habitat state because of their life history traits, but the level of fire severity influences their occurrence. In eucalypt forests, species such as the Flame Robin (*Petroica phoenicia*), Buff-rumped Thornbill (*Acanthiza reguloides*) and Eastern Whipbird (*Psophodes olivaceus*) may be present in higher numbers 2-3 years after fire in sites where the tree canopy has been either scorched or burnt (Robinson et al. 2014). Flame Robins are early post-fire colonisers and may be more abundant shortly after fire (Kelly et al. 2017), because they favour open areas created by fire (Lindenmayer et al. 2014, Stokes 1975). Numbers of the Superb Lyrebird (*Menura novaehollandiae*) were greater in areas of eucalypt woodland and open forest where the understorey had been recently removed by a low-intensity hazard reduction burn (Doty et al. 2015). This was presumably because foraging was more efficient in the absence of low-level vegetation structure. In other parts of the world, species such as the Black-backed Woodpecker (*Picoides arcticus*) depend on food resources in the form of wood-boring beetles that disperse into recently burnt forest. The post-fire colonisation and persistence of this species was maximal in Californian forest that had burnt recently, and highest levels of colonisation occurred in severely burnt areas (Tingley et al. 2018).

1.3.1 Avian guilds and fire severity

When a fire regime shifts towards increasing amounts of high-severity fire, populations of bird species may be threatened, and some of these species may have guild or functional group membership in common. Severe fires are becoming more frequent in the tropical savannas of northern Australia, and the species that are potentially vulnerable are those 1) that use the ground, understorey, or tree hollows, 2) that are frugivorous or granivorous, 3) with poor dispersal capacity, and/or 4) with long lifespans and low reproductive rates (Noske 1992, Woinarski & Legge 2013). These attributes are among those that can make species susceptible to high-severity fires in diverse ecosystems. Of all guilds assessed in Sumatran tropical rainforest, understorey insectivores were the only group to be negatively affected by increasing fire severity (Adeney et al. 2006). Bird abundance and species richness in most foraging guilds in Amazonian forest, including insectivorous guilds that forage on the ground or at low levels in the vegetation, were relatively low at the highest level of fire severity (Barlow & Peres 2004). In North American conifer forests, the richness of tree and primary cavity-nesting bird guilds declined as both patches burnt at high-severity increased in size, and the distance to areas burnt at lower severity increased (Steel et al. 2021).

1.3.2 Recurrent high-severity fire

To support avian diversity, and forest ecosystem function more broadly, greater understanding is required about how dry sclerophyll forest bird assemblages are affected by repeated high-severity wildfires over time. The amount and distribution of area burnt at different levels of severity within the spatial extent of wildfires has been shown to have a strong influence on birds (Lindenmayer et al. 2014, Steel et al. 2021). Furthermore, the frequency of fire and variation in the severity of the most recent fire interact to influence birds (e.g., Robinson et al. 2014). However, to date investigations into the effects of fire regimes on birds have not accounted for the severity levels of each of the fires occurring through multiple consecutive decades. Mapping the severity of the entire extent of major wildfires at fine spatial scales (e.g., Chafer et al. 2004, Hammill & Bradstock 2006, Hammill et al. 2010, Hammill Stone 2014) has provided unprecedented opportunities for investigation of the cumulative or longer-term effects of fire severity on components of ecosystems. Attributes of avian habitat such as the density of live trees, distribution of tree hollows, and the amount of coarse woody debris are affected by frequent fires and are likely to be important for particular bird species (Kelly et al. 2017, Woinarski & Recher 1997). It is unclear about the extent to which frequent, severe fires may diminish these aspects of avian habitat (Prior et al. 2016).

1.4 Avian responses to fire frequency

Populations of many bird species may have the capacity to persist and recover from refugia within, or external to, the boundary of large wildfires (e.g., Robinson et al. 2014). However, the return interval of such fires in a location may have important consequences for the biota (Bradstock 2008), including the occurrence of forest birds (Kelly et al. 2017). Fires that occur frequently in a location have the potential to disrupt population processes of species that are residents for at least part of the annual cycle (Biodiversity Conservation Act 2016 (NSW), s.4). Following wildfire, the vegetation structure and resources used by forest birds take time to regenerate to resemble their pre-fire state. Changes in the structure and composition of the vegetation may occur if subsequent fires burn these areas before plants are able to reach maturity (Bradstock 2008). The effects of climate change on fire regimes can result in altered forest composition that represents an increase in the proportion of plants that can tolerate increased fire activity (Bradstock 2010, Fairman et al. 2016). This in turn could detrimentally affect bird species that have strong associations with negatively impacted plants.

Detailed, longitudinal studies of the population biology of particular species in frequently burnt habitat shed light on local extinction risk for those species (Woinarski & Recher 1997). In heathy woodland habitat, an area threshold under which isolated populations of the Splendid Fairy-wren (*Malurus splendens*) would no longer be viable when exposed to frequent fire (probability of fire 0.2 per annum) was predicted to be 2,000 ha (Brooker & Brooker 1994). The modelling was based on data from an 18-year study, during which the behaviour and population dynamics of the wrens were studied in detail in relation to rainfall, nest parasitism, nest predation, and a fire regime including multiple fire events (Rowley & Brooker 1987, Brooker & Rowley 1991, Russell & Rowley 1993). Population parameters were at lower levels in the post-fire years, with recovery aided by factors such as availability of unburnt areas.

In eucalypt forest bird assemblages, the responses of species to fire frequency vary according to their habitat requirements and foraging behaviours. In a range of eucalypt forests of south-eastern Australia, the insectivorous Eastern Yellow Robin (*Eopsaltria australis*) and White-browed Scrubwren (*Sericornis frontalis*), and the omnivorous Silvereye (*Zosterops lateralis*) were more common when fire frequency was low (Kelly et al. 2017). Many common bird species that make up assemblages in eucalypt forest with a history of anthropogenic disturbance may be generally resilient to frequent low-intensity fires that only burn the forest understory, as long as the fires are small in extent. In Victorian foothill eucalypt forests, of the 27 bird species assessed in relation to variation in the frequency of low-intensity hazard reduction fires, only four species responded significantly, and they were all insectivores (Loyn & McNabb 2015). The inter-fire intervals of the replicated burnt patch treatments for this long-term (27 year) experiment were three years and 10 years. The insectivorous Brown Thornbill (*Acanthiza pusilla*) and Scarlet Robin (*Petroica boodang*) forage in the shrub layer and on the ground respectively and were less abundant in the frequently burnt sites. Australian Magpies (*Cracticus tibicen*) also forage on open ground but were more common in frequently burnt patches, as was the Rufous Whistler (*Pachycephala rufiventris*), which feeds in the tree canopy (Loyn & McNabb 2015).

1.4.1 Avian guilds and fire frequency

Fire occurs frequently in particular northern and western Australian ecosystems, and several studies of the effects of fire frequency on biota have revealed some consistent themes in terms of avian responses at the guild level. Frequent fire can detrimentally affect frugivores, granivores, insectivores and ground and hollow nesting species, because of a corresponding reduction in food resources and/or habitat (Valentine et al. 2012, Woinarski & Legge 2013, Yates et al. 2008). In particular, species that are negatively impacted by frequent fire may have requirements for suitably distributed unburnt vegetation, fire-sensitive vegetation and/or diversity of grasses (Woinarski & Legge 2013). For example, granivores and frugivores were not detected in semi-arid Western Australian shrublands with a time since fire of less than 44 years (Davis et al. 2016). Species with poor dispersal ability and small home ranges are also vulnerable to frequent fire in these and other types of fire-affected ecosystems (Yates et al. 2008, Nimmo et al. 2019). It remains to be seen whether relatively low mobility is an attribute that may expose bird species to negative impacts of high fire frequency in montane dry sclerophyll forests . Conversely, more needs to be known about the capacity of highly-mobile species to access distant, unburnt habitat in forested landscapes, as fire frequency increases under climate change.

1.5 Consideration of scale in bird-fire research

Birds are highly mobile organisms, and the apparent responses of birds to fire depend on the spatial scale at which predictor variables are expressed (Kelly et al. 2017) and bird responses are measured (Burgess & Maron 2016). Accordingly, study sites, or the areas within which fire history is quantified in relation to the location where bird assemblages are surveyed, need to be large enough so that there is a match between species home ranges/space use and the ecological effects of fire on the habitat. The responses of vertebrates, including birds, to fire frequency were stronger within a region than they were when considered across multiple regions (Kelly et al. 2017). This may be expected, because over larger areas there is greater variation in other environmental factors that also influence bird distributions (Kelly et al. 2017). Furthermore, birds respond to the effects of fire on attributes of habitat that exhibit high local variability, such as the average diameter of trees, or leaf litter depth (Kelly et al. 2017). The responses of foraging guilds to fire regimes and environmental attributes may also vary depending on whether bird responses are evaluated and expressed at the site or landscape scale. For example, at the landscape scale, the extent of habitat with time since fire of > 10 years had the strongest influence on richness of insectivores, frugivores and canopy species, but range in elevation was the best predictor of richness of these guilds at the patch scale (Burgess & Maron 2016).

1.6 Recorded acoustic bird survey methods for fire-prone forests

An appreciation of the completeness of survey data is of vital importance when evaluating a range of approaches to fire management for the maintenance of avian diversity (Driscoll et al. 2010, Watson 2017). Well-understood, reliable survey methods are required to assess patterns of avian occurrence in fire-affected landscapes. The use of acoustic recorders to survey birds in natural areas has recently increased owing to a range of advantages over surveys conducted by human observers (Shonfield & Bayne 2017, Darras et al. 2019). Acoustic recorders can be left unattended to sample over time, so they are well-suited to survey birds in remote, forested landscapes, because time spent in the field is much reduced. Additionally, any potential for temporal confounding is reduced if a number of recorders are simultaneously deployed in multiple sites. Once collected in the field, acoustic recordings need to be processed to extract the species data. While the development of methods for automated processing of recorded data is advancing (Priyadarshani et al. 2018), the technical barriers to reliable identification of all species present in recordings have not yet been satisfactorily overcome (Darras et al. 2019). Manual processing that involves listening and viewing bird calls in a spectrogram by an analyst has the capacity to deliver relatively accurate results (Venier et al. 2017). However, there is scope to increase the rigour and efficiency of manual processing through the development and testing of explicit protocols in the system under investigation. More needs to be known about how methods using acoustic recorders perform in dry sclerophyll forest habitat, and how results compare with those obtained from traditional bird survey methods.

1.7 Research aims and thesis structure

Over decades, successive wildfires burn through dry sclerophyll forest landscapes at different levels of severity and frequency to produce spatial patterns representing different fire histories in the habitat used by birds. Following a wildfire, succession of the vegetation is a function of time since fire superimposed on the antecedent fire regime, and there is corresponding variation in the availability of resources used by birds. In these ways, fire regimes shape the structure and composition of vegetation, and birds respond in time and space to their fire-affected habitats (Bradstock et al. 2005, Woinarski & Legge 2013). While some of these relationships are understood, many of the linkages and underlying response mechanisms are unknown. The use of passive sensors to collect field data, and increased availability of spatial habitat and fire history information have provided opportunities to increase understanding of the responses of birds to fire regimes over large areas. This research project has two overall aims. The first is to increase understanding of the mechanisms and processes responsible for diurnal bird responses to fire regimes in montane dry sclerophyll forests of south-eastern Australia. Secondly, to better comprehend the implications of changing fire regimes for these birds, species responses to current fire regimes representing high fire activity are investigated. The specific aims are:

To systematically develop a reliable and efficient method of surveying forest birds using passive acoustic recorders, so that results can be used to assess avian responses to fire regimes **(Chapter 2)**

Using passive acoustic reorders to survey birds in remote natural landscapes has several advantages over traditional observer-based methods. However, there has been a lack of testing and validation of methods using these devices in terms of field deployment protocols, sound file processing, species detectability and sampling completeness. In **Chapter 2**, two frameworks were established and applied for the dual purpose of developing, testing, and validating an acoustic survey method for dry sclerophyll forest birds, and to provide structured approaches that other ecologists can use to produce their own context-specific method. The first framework involved the use of a Bayesian multispecies occupancy model to obtain species detection probabilities for a traditional observer-based method and an acoustic protocol conducted in the same sites with equal sampling effort, as a basis for comparison of the methods. The second framework compared a set of candidate acoustic survey protocols on the basis of sampling completeness, or the proportion of total species detected.

To determine the amount of survey effort required to assess bird assemblages in fire-prone eucalypt forests using acoustic recorders **(Chapter 3)**

Chapter 3 is an extension of the testing and validation of the focal acoustic bird survey method from the preceding chapter. Here, a third framework was instituted, through application of a results-based stopping rule to recorded acoustic subsamples at the desktop, to establish when to cease sampling each site. The resulting numbers of subsamples per site were averaged over all sites. This mean level of sampling effort was then used as a guide in the development of a candidate set of fixed-effort acoustic survey protocols for evaluation, on the basis of survey completeness and strategic field deployment considerations. Through the separate processes undertaken in Chapters 2 and 3, an optimal method of surveying dry sclerophyll forest bird assemblages using acoustic recorders that is robust and has well-understood capacity and limits was produced. The optimal method was used to obtain bird species data for the research in Chapters 4-6.

To investigate whether avian patterns of occurrence in relation to fire frequency and long unburnt forest in the landscape were similar in functional movement groups of sedentary, migratory, and nomadic species **(Chapter 4)**.

Mobility is a mechanism that may support avian persistence as forest fire activity continues to increase under climate change, because relatively mobile species may locate and access suitable habitat and widely-distributed resources more effectively. While the capacity and propensity to move varies among species, little is known about the consistency of fire responses among species at the movement group level. In **Chapter 4**, species were allocated to movement groups according to whether they were exclusively sedentary (less mobile), migratory or nomadic (both relatively mobile), and their responses to fire frequency and long unburnt forest were investigated. Fire frequency was quantified as the number of fires over a longer period than most previous studies, which allowed for greater contrast in levels of fire frequency and increased the potential to make inferences in relation to future fire regimes. Field sites representing fire history combinations were established across an 80-km latitudinal gradient on the high parts of the Great Dividing Range, south-eastern Australia. Bird data was analysed using a Bayesian multispecies occupancy model, from which estimates of the probability of occurrence of species and movement groups in relation to fire history were obtained.

To establish whether avian responses to historical high-severity fire differ in forests at short time since fire compared with mid-range time since fire **(Chapter 5)**

The effects of high and low-severity wildfire on forest habitat are not the same, and the resulting differences persist well into the first decade following fire. However, very little is known about whether avian responses to these differences extend beyond that time, including whether increased time since fire mitigates any negative avian responses to high-severity fire. **Chapter 5** investigated avian responses to historical high-severity fire, time since fire, and their interaction using Bayesian latent variable models. Only a few broadly similar studies have been conducted, but this study differed from those in important ways, and is the first of its kind done in the southern hemisphere. Most work in this domain has assessed the effects of individual fires and fire history on birds in the years shortly after fire, whereas this chapter also investigated the extent to which avian responses to fire history persist over time since the last fire. This investigation accounted for the contributions of the severity of a chronological series of fires to the extent of historical high-severity fire over large forest patches, which was unprecedented. Spatial fire severity layers for major fire years that had been derived from satellite imagery as differences between pre and post-fire values of spectral vegetation indices, were used to determine patterns of historical high-severity fires in landscapes.

To determine the extent to which canopy structure mediates the effects of time since fire on the richness and occurrence of canopy bird species **(Chapter 6)**

Studies of the responses of birds to fire regimes often include both habitat structure and fire regime variables in statistical models, and then assess the extent to which birds respond to fire and/or habitat. However, aspects of fire history such as time since fire are proxies for a range of understudied processes that vary spatially in fire-prone forests. In **Chapter 6**, some of these processes are addressed explicitly, by investigating avian responses to direct (emigration, mortality) and indirect effects (habitat structure) of time since fire. Bayesian mediation models are a form of structural equation model that were used to partition the direct and indirect effects of time since fire on birds, with canopy cover as the mediating variable. Canopy cover estimates were derived from airborne LiDAR (Light Detection and Ranging) point clouds.

Chapter 2. Establishing the adequacy of recorded acoustic surveys of forest bird assemblages

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Acoustic recorder deployment, Blue Mountains National Park

2.1 Abstract

The use of programmable acoustic recorders to survey forest birds is increasing owing to a range of advantages over surveys conducted by human observers. Users of these devices require a methodological framework for designing and testing a proposed survey protocol in context, to be assured that it has the capacity to efficiently meet the requirements of their study. We aimed to demonstrate how a potential acoustic survey protocol may be effectively tested by comparison with either (1) an observer-based method using species detection probabilities, or (2) the survey completeness levels among a set of other candidate acoustic protocols. Surveys using acoustic recordings (manually processed) and standardised area searches were conducted over the same period in dry sclerophyll forests of south-eastern Australia. A multispecies occupancy modelling framework was used to obtain estimates of the probability of detecting individual species for both standardised searches and an acoustic protocol representing similar temporal sampling effort. Detection probabilities for 73% of species recorded using these methods were greater with the acoustic protocol than standardised searches, which established its adequacy for particular research questions. The survey methods resulted in a similar pattern of detection probabilities for foraging stratum guilds, although members of the canopy/subcanopy guild were less likely to be detected using both methods. Survey completeness (species detected/total species) was adopted as an alternative framework for acoustic protocol evaluation. The complete acoustic data set was (1) used with the incidence-based coverage estimator (ICE) to obtain the total number of species, and (2) subsampled to produce a candidate set of potentially useful survey protocols. Completeness levels ranged from 62% to 73% in the set, which provided options for subsequent protocol selection. Other ecologists may adopt one of the frameworks to establish the adequacy of their own acoustic survey protocol to suit their research question and available resources.

2.2 Introduction

Birds can be considered indicators of ecosystem integrity (Wimmer et al. 2010), so understanding their fine-scale distributions increases knowledge about species habitat requirements, capacity to tolerate disturbance and wider community resilience. Reliable and efficient methods to measure bird diversity are necessary to provide understanding of the effects of changing global climate and increasing anthropogenic pressures on forest ecosystems. Cost-effective methods are required because governments worldwide have reduced their financial support for the management of protected areas, which makes monitoring and maintaining biodiversity more difficult to achieve (Watson et al. 2014). Incorporation of remotely-deployed sensors into methods to capture species data in large natural areas is increasing as technology develops and becomes more available (Shonfield & Bayne 2017), while the cost of replicated surveys conducted by an observer in such areas remains high (Darras et al. 2019). In general, birds are aurally conspicuous, which renders them excellent subjects for the development of acoustic methods using devices left unattended to record in the field (Shonfield & Bayne 2017). However, to expand the capacity of acoustic recorders to survey forest bird assemblages, frameworks representing structured approaches are required for the development and testing of efficient methods that incorporate the high accuracy of manual processing of recorded sound files.

There are several advantages to using acoustic recording methods to survey birds. A minimum of two short visits to a site are required to deploy and later collect a recorder, so there is scope in study designs to reduce the number of trips to sites and time spent in the field overall. For large studies (e.g., Furnas & Callas 2015), a set of recorders may be progressively re-located until many sites have been surveyed. Field personnel responsible for deployment of acoustic recorders do not require specialised ornithological skills (Hobson et al. 2002), which provides more staffing options for field data collection. When combined with potential for saving time in the field, the capacity to program an acoustic recorder to capture an extended temporal sample means that recorders can be efficiently deployed in remote areas, where access may not be straightforward (Shonfield & Bayne 2017). Furthermore, a researcher may incorporate the flexibility of being able to draw post-hoc samples from long duration recordings into a study design. It is possible to derive several different avian response variables from acoustic recordings (Darras et al. 2019). In addition to species richness (e.g., Wimmer et al. 2013), abundance or density can be estimated using data collected with a single recorder (e.g., Van Wilgenburg et al. 2017, Sebastián-González et al. 2018, Bombaci & Pejchar 2019).

Once deployed, an acoustic recorder can collect large amounts of data over time while unattended at a location, but the resulting sound recordings need to be processed to extract the species data. While automated processing methods are available, manual processing of sound files is currently the most reliable and accurate option when the aim is to detect all species present in recordings (Wimmer et al. 2013, Shonfield & Bayne 2017, Venier et al. 2017). Manual processing involves systematically opening sound files in software that enables the analyst to listen to bird calls whilst viewing them represented in a spectrogram of frequency over time. Species detected in this way can be recorded for each sampling unit. Accounting for all recorded species while manually processing recordings can be time consuming, because, for example, short sections of complex sound files of the dawn chorus or diverse sites may need to be replayed, perhaps alternately with reference calls. However, the time is spent conveniently at the desktop and the permanent record of a survey in the form of a sound file provides a means to obtain high accuracy in the detection of species (Shonfield & Bayne 2017). Reductions in processing time can be achieved if the analyst is able to make instantaneous visual appraisals of vocalisations on simpler spectrograms, without complementary audio (Truskinger et al. 2013).

Manual processing of large quantities of recorded acoustic data can yield comprehensive assessments of bird assemblages, but the level of resources required typically render this approach unfeasible and/or too costly (Balestrieri et al. 2017). Studies seeking to use manually processed recordings to survey forest bird assemblages require an efficient and proven method, that is tailored to the requirements of the study. The development of such a method would ideally take place within a robust framework that is flexible enough to accommodate a wide range of forest types and research aims. In this paper, we demonstrate and evaluate two frameworks that other researchers may consider for use as alternative approaches to producing their own acoustic survey method to efficiently collect and process field data, or retrospectively sub-sample large amounts of recorded acoustic data.

Given records of species detected in acoustic recordings obtained in a set of sites, with replicate sampling for each site, hierarchical multispecies occupancy modelling can be used to simultaneously estimate probabilities of species occurrence and detection (Darras et al. 2019). This approach attempts to account for imperfect detection, i.e., the chance that a species occupied a site during a survey visit, but was not detected. Probability of detection can vary widely among the bird species comprising an assemblage and can be influenced by numerous factors including, bird appearance and behaviour, site attributes and the survey method used (Iknayan et al. 2014). Validation of potentially useful survey protocols using acoustic recordings can be achieved by running them in parallel with an established method conducted by an observer and comparing the results (Wimmer et al. 2013, Darras et al. 2018a). We used occupancy modelling to estimate and compare the probability of detection of individual species and guilds between a potentially useful acoustic protocol and an observer-based method (e.g., Furnas & McGrann 2018).

An alternative framework for developing an adequate acoustic method involves assessment of the survey completeness levels of a set of candidate acoustic protocols for collecting acoustic data in the field. Survey completeness can be expressed as the number of species detected, divided by the estimated total number of species present (Watson 2017). The completeness levels of the set of candidate protocols may, for example, lie in the range of 70-90%, with a final method selected to suit the aims of a study (Watson 2010, Callaghan et al. 2017). High-level sampling completeness (e.g., 90%) may be required for detailed studies of species ecology, perhaps moderate completeness (e.g., 80%) when species numbers are required, and modest completeness (e.g., 70%) can be adequate when assemblages are to be compared in relative terms (Watson 2010). To apply this approach, a set of candidate protocols can be devised that reflect different temporal arrangements of samples and levels of total sampling effort. The number of species detected in a site using each of these protocols can then be represented as a percentage of the total number of species (e.g., Wimmer et al. 2013).

Forests worldwide are exposed to changing climate, increases in direct human disturbances, and flow-on effects, such as altered fire regimes (e.g., Bradstock et al. 2014). Some of these forested areas are large, remote and difficult to access. For these reasons, they are often important reservoirs of global biological diversity. Focused acoustic recording methods are highly suited to survey bird assemblages in these areas. The present study was conducted in an area subject to these threats and with these attributes. The Greater Blue Mountains World Heritage Area is a one million hectare, mainly forested, contiguous protected area in south-eastern Australia. The overarching aim of the study was to demonstrate and assess two frameworks that other ecologists could use to establish the adequacy of their own recorded acoustic survey protocol, using manually processed data. Specifically, we aimed to demonstrate how a potential acoustic protocol may be effectively tested by comparison with either: 1) an observer-based method using species detection probabilities, or 2) the survey completeness levels among a set of other candidate acoustic protocols.

2.3 Methods

2.3.1 Study sites

Ten replicate dry sclerophyll forest sites were established on the tops and upper slopes of sandstone ridges, in the central Blue Mountains, south-eastern Australia (Fig. 2.1). The landscape of the study area consists of a regular pattern of ridges interspersed with gullies, at elevations grading from 500 m in the east to 850 m in the west. All sites had a shrubby understory and were last burnt by a wildfire in early 2002 (Office of Environment & Heritage NSW 2016). Commonly-occurring tree species included Scribbly Gum (*Eucalyptus sclerophylla*), Sydney Peppermint (*E. piperita*), Red Bloodwood (*Corymbia gummifera*) and Sydney Red Gum (*Angophora costata*), which formed a canopy of 15-25 m in height with 30-70% foliage cover. Shrubs included species of *Banksia*, *Leptospermum*, *Persoonia*, *Isopogon*, *Petrophile*, *Epacris* and *Lambertia*. Area searches and acoustic recording were conducted during mid-2017.

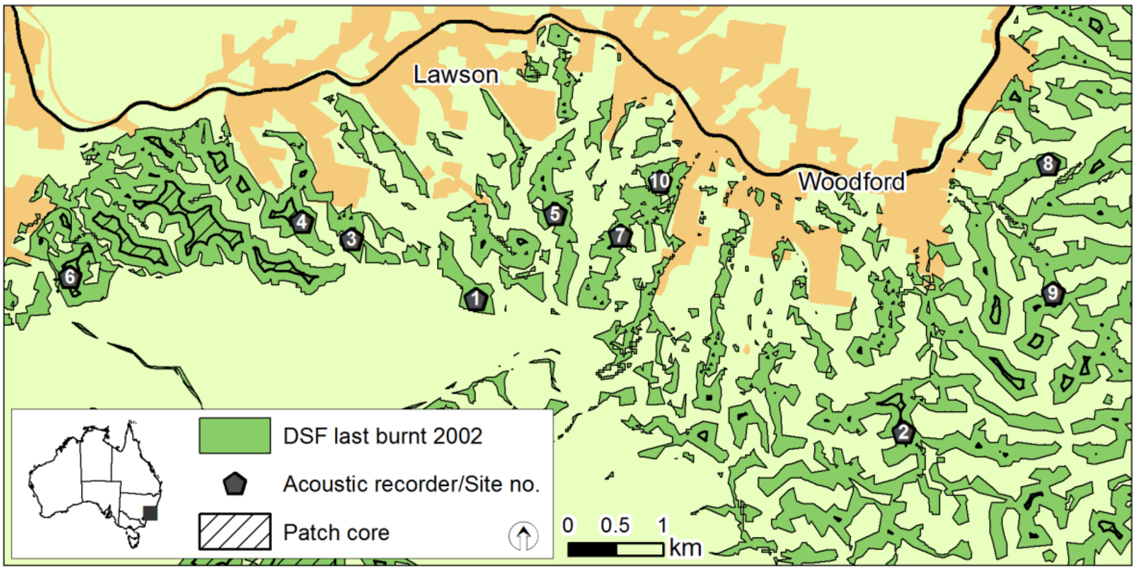

Fig. 2.1. The study was conducted in natural landscapes of the central Blue Mountains. Acoustic recording and area search methods were carried out in 10 dry sclerophyll forest (DSF) sites to survey bird assemblages. In each site, an acoustic recorder was randomly located in the forest patch core area, which excluded a 100 m wide buffer zone internal to the site boundary. Other native vegetation and urban areas are indicated by pale green and orange shading respectively.

2.3.2 Bird surveys

2.3.2.1 Standardised area search

For the study, records of species present in sampling periods were obtained using both an observer-based method and acoustic recording. For the former, we used the standardised search (Watson 2003), which is built upon a 2-ha/20-min area search method that has been commonly used in Australian forests (Loyn 1986, Watson 2004). The 2-ha/20-min area search is also the most valuable survey method in Birdlife Australia's Atlas of Australian Birds and Birdata projects (https://birdata.birdlife.org.au/survey-techniques). In each site, individual birds seen, heard or both seen and heard were recorded in timed 20-min periods, while the observer actively searched a 2-ha area within the site (Loyn 1986). The 2-ha areas were typically 100 x 200 m rectangles, but the shapes were allowed to vary to remain within the dry forest sites. All searches were conducted by the same observer (MF), who was experienced with the visual and aural detection of species occurring in the region.

Successive 20-min/2-ha searches were conducted for three hours following dawn, for as many days as were required to satisfy a results-based stopping rule, that was applied to survey forest sites equivalently (Watson 2003). The stopping rule was to cease sampling in a site when three consecutive 20-min searches yielded no new species (Watson 2004). The number of 20-min samples required before the stopping rule was triggered ranged from seven to 15 among sites, resulting in an average of 9.8 periods/site. The starting point for the first search of each day was randomly selected, with subsequent 2-ha searches continuing directly on into new parts of the site, with the aim of actively searching throughout the site (Watson 2003). Sites were large enough to accommodate this approach, with the smallest being 14 ha. All samples used in this study were taken on days of no rain and no more than very light wind.

2.3.2.2 Acoustic recording

Acoustic recorders (Song Meter SM4, Wildlife Acoustics, Massachusetts, United States) were deployed to record on days immediately preceding or following standardised searches in each site. Recordings were not made on the same days as standardised searches in a site to eliminate the possibility of the presence of a moving observer affecting the behaviour of vocal birds (Digby et al. 2013, Klingbeil & Willig 2015, Darras et al. 2018*a*). Recorders were randomly located on ridge tops but were excluded from a 100 m wide buffer zone internal to the site boundary (Holmes et al. 2014, Fig. 2.1). The assumption was that this functioned to limit, but not exclude, the recording of individuals calling from outside the site (Hingston et al. 2018). Increasing the buffer width was not possible owing to the consistent narrowness of ridges and associated ridge-top forest amongst sites (Fig. 2.1).

Because birds have higher detection probability in acoustic recordings from the first three hours post dawn (Wimmer et al. 2013), Song Meters were configured to record continuously for this period until five days of clear-weather recordings had been captured in each site. In this way, a complete data set consisting of a total of 900 min/site of stereo recordings (16-bit wav files) was obtained. Recorders were set to use a sample rate of 24,000 Hz, with no filtering, and the default gain of 16 dB (Venier et al. 2017, Hingston et al. 2018). Microphones had a signal to noise ratio of 80 dB (Darras et al. 2018*a*). Microphone sensitivity can decline to varying degrees with increasing time in the field (Turgeon et al. 2017), but testing following deployment showed that all microphones remained within the sensitivity range stated by the manufacturer when this type of microphone is new. Sound recorders were attached to a tree of no more than 110 mm diameter, at 2 m above the ground, with a cable lock (Depraetere et al. 2012, Darras et al. 2018*a*). Limiting tree diameter in this way meant that at least one of the two microphones on opposite edges of the recorder was unobstructed in a horizontal plane.

To identify bird species from recorded calls, acoustic recordings were systematically analysed in processing software (Kaleidoscope Pro, Wildlife Acoustics, Massachusetts, United States). All recordings were manually processed by viewing spectrograms and replaying and listening to calls to identify species, with repetition as required (Hingston et al. 2018). This was carried out by a single person (MF) and involved recording all species that were present in 20-min sampling periods. This sample duration had been used previously for point counts and acoustic recordings (Darras et al. 2018*b*) and was selected to match that of standardised searches, to maximise comparability. Several other measures were applied to ensure accurate identification of species. Firstly, collections of recorded bird calls were referred to while processing (Van Gessell & Kane 2002, Buckingham & Jackson 2007). Secondly, a reference library of calls was developed from the data itself and used for ongoing verification of species identification (Wimmer et al. 2013). Finally, where there was any uncertainty about the species responsible for vocalisations, calls were given a unique code during processing, and additional expert opinion was sought (Celis-Murillo et al. 2012, see Acknowledgements).

2.3.3 Multispecies occupancy modelling framework

2.3.3.1 A potential acoustic survey protocol

The complete acoustic data set was subsampled to devise a potentially useful acoustic survey protocol, for comparison with standardised searches using occupancy modelling. The acoustic protocol that we used consisted of five 20-min periods immediately following dawn for two consecutive, clear-weather days. This protocol was designed to match with standardised searches in terms of length of sample period (20-min), average number of samples per site survey (10 x 20-min) and the number of consecutive days over which a survey was conducted (two). This short site survey period reduced the overall duration of the study, which meant that the multispecies occupancy modelling assumption of a closed population was more likely to have been met (Iknayan et al. 2014).

2.3.3.2 Probability of detecting species and guilds

We used a Bayesian approach to model the number of detections $y_{i,j,m}$ of species j in site i under survey method m as a Binomial variable:

$$y_{i,j,m} \sim \text{Binomial}(N_{i,m},\ z_{i,j}p_{j,m}) \qquad \text{Equation 2.1}$$

Where $N_{i,m}$ is the number of replicate samples of site i performed with survey method m; $z_{,i,j} \in \{0,1\}$ is the true, unknown occupancy of the site by species j; and $p_{j,m}$ is the probability of detection for this species using method m. This treats the detectability of a species using a given survey method as invariant across sites and replicate samples.

We modelled occupancy as a function of a species-site intercept drawn from a Normal distribution with a species-specific mean, plus a site intercept drawn from a standard Normal distribution. The site intercept allows for the possibility of general site effects that might increase or reduce the probability of occupancy across all species.

$$z_{i,j} \sim \text{Bernoulli}(\psi_{i,j}) \qquad \text{Equation 2.2}$$

$$\text{logit}(\psi_{i,j}) = \alpha_{z_{i,j}} + \beta_i$$

$$\alpha_{z_{i,j}} \sim \text{Normal}(\alpha_{z_j}, 1)$$

$$\alpha_{z_j} \sim \text{Normal}(0, \sigma_z)$$

$$\beta_i \sim \text{Normal}(0,1)$$

The probability of detection for species j using survey method m was represented in a similar way, with a species-method intercept drawn from a Normal distribution with a species-specific mean. Standard deviations of one were used for the Normal priors on the alpha and beta parameters. Northrup & Gerber (2018) warn against large prior standard deviations which can bias a logistic model towards extreme probability values. The overall prior standard deviation for the linear predictor of occupancy above is approximately 1.4, which accords with the value recommended by Northrup and Gerber.

$$\text{logit}(p_{j,m}) = \alpha_{p_{j,m}} \qquad \text{Equation 2.3}$$

$$\alpha_{p_{j,m}} \sim \text{Normal}(\alpha_{p_j}, 1)$$

$$\alpha_{p_j} \sim \text{Normal}(0, \sigma_p)$$

To complete the model, we defined Exponential prior distributions for the two standard deviation terms (McElreath 2016, Simpson et al. 2017):

$$\sigma_z \sim \text{Exp}(1) \qquad \text{Equation 2.4}$$

$$\sigma_p \sim \text{Exp}(1)$$

The model was fitted using Markov Chain Monte Carlo (MCMC) with JAGS version 4.3.0 (Plummer 2003) via the runjags package (Denwood 2016) in R (R Core Team 2019). We ran four chains with a burn-in period of 4,000 iterations followed by a sampling period of 40,000 iterations with a thinning rate of 20. Model convergence was checked using the Gelman-Rubin statistic (Gelman & Rubin 1992) after which the separate chains were combined into a single matrix of 8,000 samples.

For each species, we summarised the probability of detection under each of the two survey methods by calculating the interquartile range and central 90% of posterior distributions. We assessed the degree to which the acoustic protocol was better at detecting each species than standardised searches by calculating the proportion of posterior probabilities that were greater for the acoustic method. To assess whether there was any potential survey method bias in the probability of detecting species at different levels within the vertical forest strata, posterior probabilities of detection for species under each survey method were aggregated according to foraging stratum guild.

2.3.4 Survey completeness framework

Survey completeness, or the number of species detected as a percentage of the total number of species (Watson 2017), was adopted as a metric to evaluate and compare a set of potential acoustic survey protocols. Initially, estimates of the total number of species for each site were obtained using the incidence-based coverage estimator (ICE), which uses information about infrequently detected species to estimate unobserved species (Chazdon et al. 1998, Chao et al. 2000). These estimates (Appendix A.1) were based on the complete acoustic data set for each site and were calculated in R using the SpadeR package (Chao et al. 2016). ICE has been shown to out-perform other established estimators of species richness in terms of accuracy, precision and level of bias when recorded acoustic samples have been used (La & Nudds 2016, see also Chazdon et al. 1998). Then, a set of candidate acoustic survey protocols, which reflected a range of different temporal configurations of sampling days and 20-min periods, were developed by sub-sampling the complete acoustic data set. The completeness levels of each of these protocols was calculated for each of the 10 sites and then averaged.

2.4 Results

Overall, 57 species were recorded, including seven species that were observed only once (Appendix A.2). Of these seven species, only visual observation was made of the Satin Flycatcher (*Myiagra cyanoleuca*) and the White-throated Gerygone (*Gerygone olivacea*). The other five species were either seen and heard, or heard only. The Eastern Spinebill (*Acanthorhynchus tenuirostris*) was the most frequently detected species in both acoustic recordings and standardised searches. Other common species included the Pied Currawong (*Strepera graculina*), Brown Thornbill (*Acanthiza pusilla*) and Crimson Rosella (*Platycercus elegans*). Three nocturnal species were recorded, but they were omitted from data analysis, because they were not targeted by our methods (Appendix A.2).

Each of the first five acoustic sampling periods following dawn resulted in the detection of a mean of approximately 11 species, with numbers of species declining in subsequent 20-min periods, for the complete acoustic data set (Fig. 2.2a). Similarly, the rate at which new species were detected diminished after the first five sampling periods (Fig. 2.2b). Accordingly, later subsampling of the complete acoustic data set to produce candidate survey protocols was restricted to samples from the first five sampling periods following dawn.

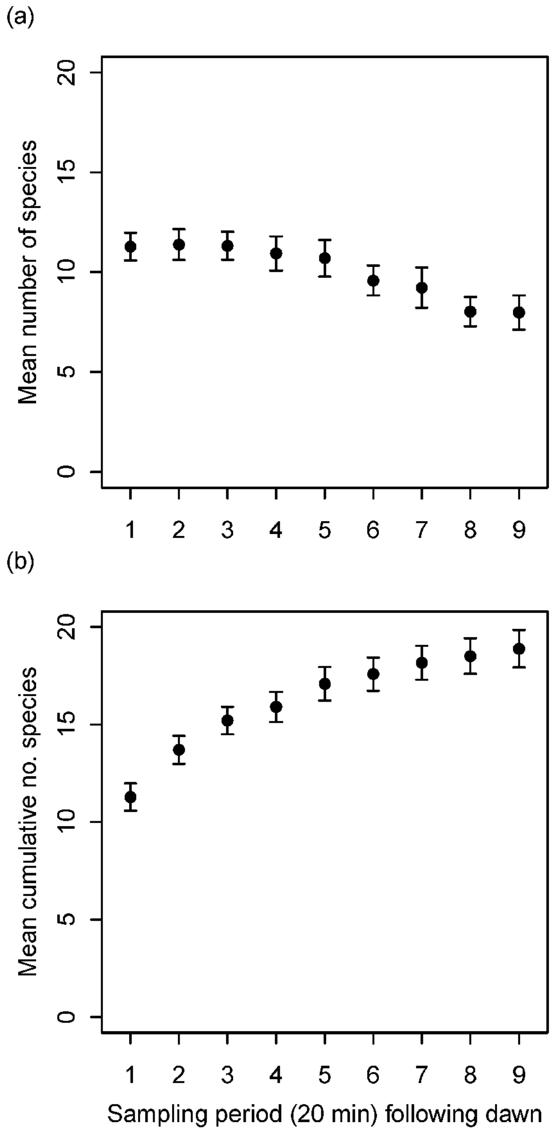

Fig. 2.2. The mean (a) and mean cumulative (b) number of bird species detected in acoustic recordings in each 20-min sampling period for three hours immediately following dawn (bars 95% CI). Means were calculated using data from five days sampling in each of 10 sites.

2.4.1 Multispecies occupancy modelling

Detection probabilities obtained for species according to the acoustic protocol and standardised searches were spread across the entire range from zero to one (Fig. 2.3). When the probability of detecting a particular species using our acoustic protocol was ~ 25% or greater, the probability of detection was almost always much greater than for standardised searches. This is evidenced by the complete separation of the central 90% of posterior distributions, which was the case for almost half of all species detected by these methods. The detection probabilities according to the two methods were relatively similar for species with low detectability. Exceptions were the Jacky Winter (*Microeca fascinans*), Rose Robin (*Petroica rosea*) and Eastern Yellow Robin (*Eopsaltria australis*), which were more readily detected in standardised searches (Fig. 2.3). For 73% of species detected by these methods, at least 69% of posterior detection probabilities were greater for the acoustic protocol than standardised searches (Table 2.1).

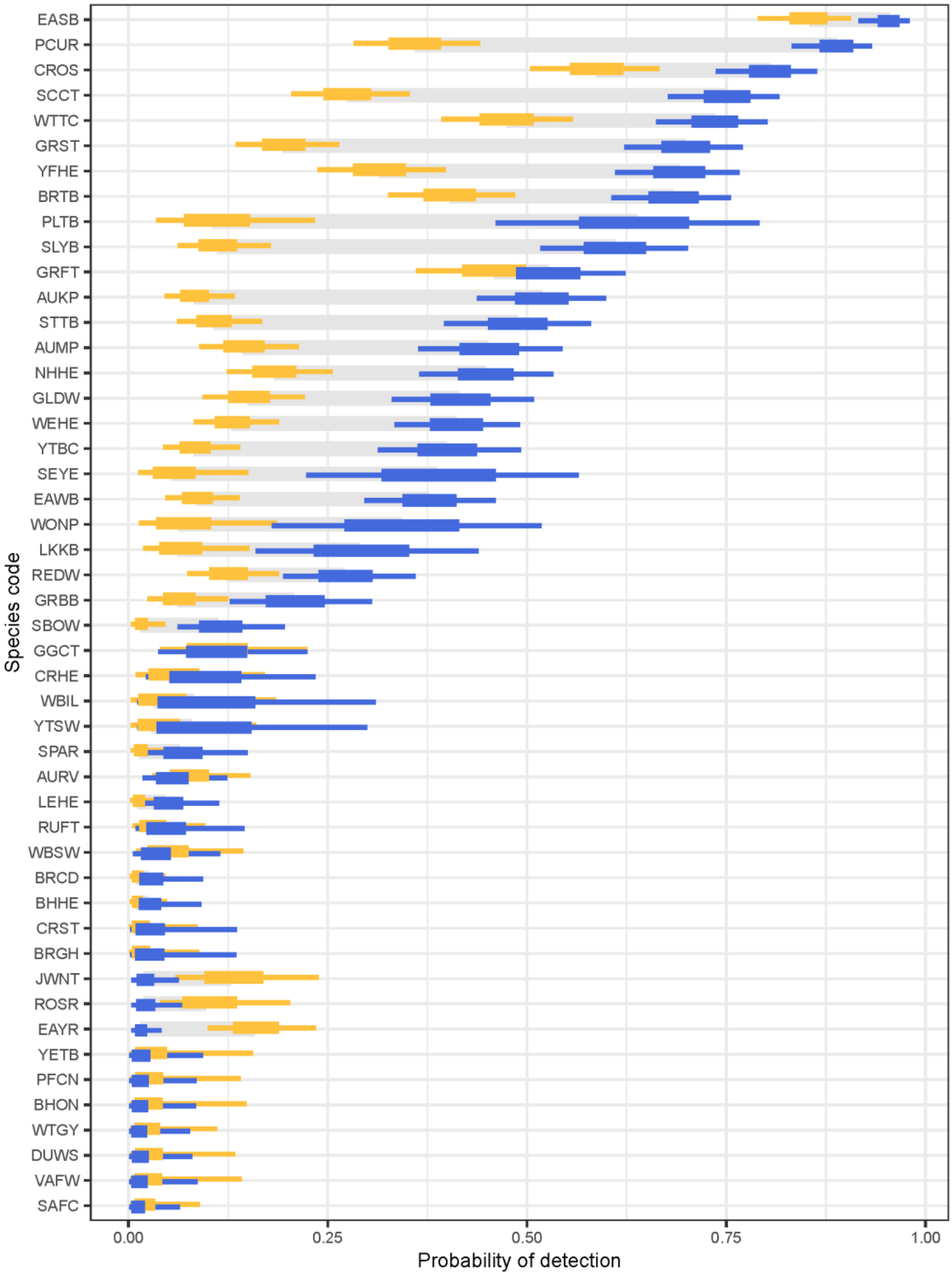

Fig. 2.3. The probability of detection of bird species for the acoustic survey protocol (blue) and standardised searches (gold). Bars represent the interquartile range and central 90% of posterior distributions. Species common and scientific names are provided against species codes in Table 2.1.

Table 2.1. Species detected using the acoustic survey protocol and/or standardised searches (n = 48) are listed with their corresponding species codes. The proportion of times that posterior detection probabilities were greater for the acoustic protocol compared to standardised searches is provided for each species (Acoustic pd > SS pd). Species membership of foraging stratum guild categories are shown (Higgins 1999, Higgins & Davies 1996, Higgins & Peter 2002, Higgins et al. 2001, Higgins et al. 2006, Marchant & Higgins 1994).

Scientific name	Common name	Sp. code	Acoustic pd > SS pd	Foraging stratum†
Alisterus scapularis	Australian King-Parrot	AUKP	1.00	All
Cracticus tibicen	Australian Magpie	AUMP	1.00	G/U
Acanthiza pusilla	Brown Thornbill	BRTB	1.00	All
Platycercus elegans	Crimson Rosella	CROS	1.00	C/S
Acanthorhynchus tenuirostris	Eastern Spinebill	EASB	1.00	All
Psophodes olivaceus	Eastern Whipbird	EAWB	1.00	G/U
Pachycephala pectoralis	Golden Whistler	GLDW	1.00	All
Colluricincla harmonica	Grey Shrike-thrush	GRST	1.00	All
Dacelo novaeguineae	Laughing Kookaburra	LKKB	1.00	All
Phylidonyris novaehollandiae	New Holland Honeyeater	NHHE	1.00	All
Strepera graculina	Pied Currawong	PCUR	1.00	All
Pycnoptilus floccosus	Pilotbird	PLTB	1.00	G/U
Ptilonorhynchus violaceus	Satin Bowerbird	SBOW	1.00	All
Zosterops lateralis	Silvereye	SEYE	1.00	All
Acanthiza lineata	Striated Thornbill	STTB	1.00	C/S
Cacatua galerita	Sulphur-crested Cockatoo	SCCT	1.00	All
Menura novaehollandiae	Superb Lyrebird	SLYB	1.00	G/U
Lichenostomus leucotis	White-eared Honeyeater	WEHE	1.00	All
Cormobates leucophaea	White-throated Treecreeper	WTTC	1.00	All
Leucosarcia melanoleuca	Wonga Pigeon	WONP	1.00	G/U
Lichenostomus chrysops	Yellow-faced Honeyeater	YFHE	1.00	All
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	YTBC	1.00	All
Cracticus torquatus	Grey Butcherbird	GRBB	0.99	All
Anthochaera carunculata	Red Wattlebird	REDW	0.99	All
Pardalotus punctatus	Spotted Pardalote	SPAR	0.97	C/S
Meliphaga lewinii	Lewin's Honeyeater	LEHE	0.95	All
Macropygia amboinensis	Brown Cuckoo-Dove	BRCD	0.84	All
Melithreptus brevirostris	Brown-headed Honeyeater	BHHE	0.84	All

Sericornis citreogularis	Yellow-throated Scrubwren	YTSW	0.84	G/U
Smicrornis brevirostris	Weebill	WBIL	0.82	C/S
Rhipidura albiscapa	Grey Fantail	GRFT	0.79	All
Phylidonyris pyrrhopterus	Crescent Honeyeater	CRHE	0.77	All
Accipiter fasciatus	Brown Goshawk	BRGH	0.71	A/G
Falcunculus frontatus	Crested Shrike-tit	CRST	0.71	All
Rhipidura rufifrons	Rufous Fantail	RUFT	0.69	All
Callocephalon fimbriatum	Gang-Gang Cockatoo	GGCT	0.49	C/S
Sericornis frontalis	White-browed Scrubwren	WBSW	0.33	G/U
Gerygone olivacea	White-throated Gerygone	WTGY	0.3	C/S
Corvus coronoides	Australian Raven	AURV	0.29	G/U
Myiagra cyanoleuca	Satin Flycatcher	SAFC	0.29	C/S
Lichmera indistincta	Brown Honeyeater	BHON	0.28	All
Artamus cyanopterus	Dusky Woodswallow	DUWS	0.28	All
Falco peregrinus	Peregrine Falcon	PFCN	0.28	A/G
Malurus lamberti	Variegated Fairy-wren	VAFW	0.28	G/U
Acanthiza nana	Yellow Thornbill	YETB	0.27	C/S
Petroica rosea	Rose Robin	ROSR	0.02	All
Eopsaltria australis	Eastern Yellow Robin	EAYR	0	All
Microeca fascinans	Jacky Winter	JWNT	0	All

† Guild category abbreviations: All (all strata), G/U (ground/understorey), C/S (canopy/subcanopy), A/G (aerial/ground).

The survey methods resulted in a similar pattern of detection probabilities for species that forage at all levels in the forest strata and those that mainly feed in the ground/understorey layers (Fig. 2.4). In both cases, the acoustic protocol resulted in generally higher detection probabilities than standardised searches for these groups. Median detection probabilities resulting from both survey methods for canopy/subcanopy species were low. Results are approximate because the foraging stratum guilds differ in number of species (Fig. 2.4).

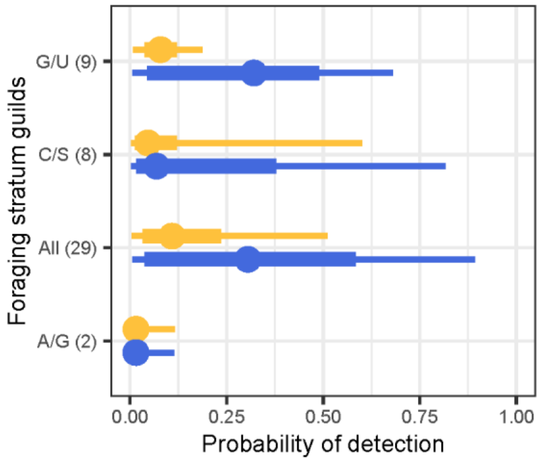

Fig. 2.4. The probability of detection of species members of foraging stratum guilds for the acoustic survey protocol (blue) and standardised searches (gold). The median value is shown as a circle in the bars, which represent the interquartile range and central 90% of posterior distributions. The number of species belonging to each guild category are shown in brackets. Guild category abbreviations are: All (all strata), G/U (ground/understorey), C/S (canopy/subcanopy), and A/G (aerial/ground). Species membership of foraging stratum guilds are provided in Table 2.1.

2.4.2 Survey completeness

The survey method used to obtain the complete acoustic data set detected on average 88% of the estimated total number of species per site (Table 2.2). The completeness levels of the acoustic survey protocols that were developed by sub-sampling the complete data set increased steadily as more samples were added, but gains in completeness were small for large increases in sampling effort. For example, attainment of 73% completeness required an additional 50% of the effort required to obtain 69% completeness (Table 2.2). For the pairs of protocols using six or eight samples, more species were detected on average with the protocol versions that used fewer samples on more days.

Table 2.2. Survey completeness levels for methods using acoustic recordings. In the first row, the method used to acquire the complete acoustic data set is shown. The complete data set was sub-sampled to produce the following candidate set of nine potentially useful survey protocols for evaluation.

Days	20-min samples†	Days x samples	Total survey time (min)	Species/ total species‡	Survey
5	9	45	900	88%	Complete data
2	3	6	120	62%	Protocol 1
3	2	6	120	64%	Protocol 2
2	4	8	160	64%	Protocol 3
4	2	8	160	68%	Protocol 4
2	5	10	200	69%	Protocol 5
5	2	10	200	69%	Protocol 6
3	4	12	240	71%	Protocol 7
4	3	12	240	72%	Protocol 8
5	3	15	300	73%	Protocol 9

†Consecutive periods commencing at dawn.

‡Species detected as a percentage of the total number of species was calculated for n = 10 sites, and then averaged.

2.5 Discussion

We have demonstrated how two different approaches to developing an efficient and reliable acoustic survey protocol may be applied for studies intending to use passive acoustic recording to survey forest birds. Multispecies occupancy modelling and the assessment of survey completeness are two different frameworks, but they each have strengths and advantages that may better suit particular research aims. We have provided examples of the application of both frameworks in the context of dry sclerophyll forests of south-eastern Australia, but either may be used as a template in many other global forest types. Furthermore, both frameworks are flexible, for example, a point count method could be substituted for area searches to compare species or guild detection probabilities with those obtained using a potential acoustic protocol.

2.5.1 Multispecies occupancy modelling

Detection probabilities for 73% of species recorded using these methods were greater with the acoustic survey protocol than the standardised search (Table 2.1). Many of these species had a relatively high probability of detection (Fig. 2.3), so the acoustic protocol was a better survey method for those species that are more readily detected in these forests. In mainly forested habitats of California, surveys using acoustic recordings also resulted in higher average detection probabilities than point counts conducted by an observer (Furnas & McGrann 2018). Detection probability for species that were recorded only once, or a few times, were typically low, regardless of survey method (Fig. 2.3, Appendix A.2).

There are several factors that would have influenced the variation in species detection probabilities between the methods. It is likely that the capacity to replay and review more complex sound files through manual processing contributed to the higher detection probabilities obtained with the acoustic protocol (Shonfield & Bayne 2017). The acoustic protocol was restricted to the first five 20-min samples following dawn, which was when more species were detected by their call per sample (Fig. 2.2). However, standardised searches were conducted up to 180 min following dawn, and so included a less productive period, which may partly explain some of the lower detection probabilities obtained by this method. Some of the differences in results obtained by standardised searches and the acoustic protocol were probably due to the fact that these methods sampled different parts of each site. The capacity to detect bird calls over distance is not the same for human observers and acoustic recorders, which was likely to have contributed to variation in results (Van Wilgenburg et al. 2017, Yip et al. 2017). Records of species heard calling outside the 2-ha area during standardised searches were excluded from analysis, but acoustic recorders would have been sampling an area larger than 2-ha for species that have the capacity to transmit their calls over relatively long distances. However, the inclusion of such species in the standardised search dataset had a negligible effect on detection probabilities (Appendix A.3). Nevertheless, we recommend that if possible, recorders are located several hundred meters inside site boundaries.

The capacity of the observer to sight birds resulted in standardised searches being superior to the acoustic protocol in detecting three species from the family *Petroicidae*. The Rose Robin, Jacky Winter and Eastern Yellow Robin were either only detected visually or were seen but seldom heard in the study. In Tasmanian forest, the Dusky Robin (*Melanodryas vittata*) was at times only seen by the observer and was one of the few species heard and seen by the observer in 100 m radius point counts that was not detected by the acoustic recorder (Hingston et al. 2018). In the same study, the Flame Robin (*Petroica phoenicea*) had also been recorded as only seen, and it was found that the human observer was better than acoustic recorders at detecting their calls. There can be considerable seasonal and diurnal variation in the extent to which the Eastern Yellow Robin and Jacky Winter vocalise (Keast 1994). For example, peak vocalisations may occur at the start of the breeding season, and/or during the pre-dawn period, neither of which were sampled in our surveys. Future work using autonomous recording units should include sampling in periods of peak vocalisation of all species of interest when establishing the timing of deployments and recording schedules.

Detection probabilities of foraging stratum guilds were generally greater for the acoustic protocol than standardised searches. There was one exception with the acoustic protocol, in that the median probability of detecting species that mainly forage in the forest canopy or subcanopy was ~ 25% less than that of species that use lower strata, or those that use all strata. Recorders were placed at 2 m above the ground, so species that use the upper strata of the forest may have been more difficult to detect simply because they were further away from the recorder than species using the lower strata. This result could also be due to the characteristics of the typical calls made by the species in this particular canopy/subcanopy guild (Table 2.1). Further investigation of potential bias against canopy species in recorded acoustic surveys would be useful.

The 20-min area search has been widely used as a bird survey method in Australia (Watson 2004), so we used 20-min for acoustic samples, to best compare the methods. Twenty-min periods have also been used effectively in other research that compared aspects of observer-based and acoustic recording methods (Darras et al. 2018*b*). However, experimentation with reducing the length of acoustic samples while varying the temporal arrangement of samples could be a worthwhile area for further investigation, because increased survey efficiency might be achieved (e.g., La & Nudds 2016, Cook & Hartley 2018).

2.5.2 Survey completeness

The survey completeness framework relies upon robust estimates of the total number of species. Some estimators of total species, such as ICE (Chazdon et al. 1998, Chao et al. 2000), have been shown to provide reliable estimates with limited numbers of samples (La & Nudds 2016).

However, extensive sampling in a subset of sites prior to conducting the main study should be carried out, not only to test methods (Watson 2017), but also to enable the behaviour of the selected estimator to be assessed in a particular forest community. In the present study, the complete acoustic data set was obtained by processing 900 min/site of recordings and resulted in an average of 88% survey completeness. This level of completeness may be close to the upper limit of what is achievable in some habitats, regardless of effort (Watson 2010). For example, on Barro Colorado Island, 192 hours of sampling a diverse bird assemblage resulted in 91% completeness, but adding 210 hours of results obtained by complementary methods gave less than a 1% increase in completeness (Watson 2010).

Gains in completeness were small and accrued at a reduced rate as sampling effort was incrementally increased in the set of candidate acoustic survey protocols (Table 2.2). The level of survey completeness among the candidate set of protocols commenced at 62%, requiring six 20-min samples. An identical level of completeness was obtained for the same amount of total sampling time in woodland and open forest, but in that study, shorter (1-min) recorded acoustic samples were taken randomly over five days from the post-dawn period (Wimmer et al. 2013). The highest level of survey completeness among the acoustic protocols was 73%, which required 300 min of recordings. This represents a large amount of survey effort, given that ~78% of 194 reviewed avian studies conducted between 2004-2016, sampled for a total of 240 min or less per site survey (Watson 2017). At 73%, the completeness level of this protocol is modest, but it is only 15% less than that obtained for the complete data set, for a third of the effort (Table 2.2).

In the survey completeness framework, a protocol selected for use should represent the most efficient way of attaining the required level of completeness, which will be established by the aims of a study. For example, the acoustic protocol we devised that used the first five 20-min samples following dawn for two days had an average survey completeness of 69%. This protocol detected all the common species recorded in the study, as well as several rare species (Appendix A.2). The nine species from the complete acoustic data set that were not detected by this protocol were recorded in very few sampling periods overall: 1/450 (one species), 2/450 (four species), 3/450 (two species), 4/450 (one species), and 13/450 (one species). Using results for the more common species can be sufficient to evaluate the effects of temporal or spatial environmental variation on assemblages (Lennon et al. 2004, Callaghan et al. 2017). Furthermore, investigation of the reasons why commonly occurring species are absent from an area is an effective approach to understanding drivers of species richness patterns (Lennon et al. 2004).

2.6 Conclusion

Researchers and natural area managers require cost-effective tools to monitor and assess diversity under increasing climatic and anthropogenic pressures on natural systems (Watson et al. 2014). Using acoustic recordings to survey forest birds offers several advantages over observer-based methods (Darras et al. 2019), but frameworks that users can adopt to design their own context-specific acoustic protocol have had limited application. We have demonstrated how two different frameworks can be applied to test and confirm the adequacy of potential survey protocols.

With the multispecies occupancy modelling framework, the acoustic protocol resulted in higher detection probabilities than standardised searches for most species, which established its adequacy for particular research questions. This framework enables the researcher to make decisions about how useful a protocol would be for individual species or guilds. The use of our occupancy modelling framework means that at least initially, a single acoustic protocol can be tested, which minimises the volume of acoustic sound files that need to be manually processed. With the completeness framework, it was not necessary to conduct observer-based surveys, but manual processing of a substantial quantity of recordings was carried out to enable reliable estimation of the total number of species present. The range of average completeness levels resulting from the candidate set of acoustic protocols provided a basis for the selection of a protocol that could suit a given study aim. Ultimately, the decision to adopt one of the frameworks over the other will be based on the nature of the proposed project and the available resources.

2.7 Data accessibility

Data and R code used in occupancy modelling are available online at https://github.com/mfrnkln/birdsurvey1.

2.8 Acknowledgements

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Chapter 3. How much survey effort is required to assess bird assemblages in fire-prone eucalypt forests using acoustic recorders?

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Dry sclerophyll forest, Blue Mountains National Park

3.1 Abstract

Forest fire activity is expected to increase in many parts of the globe over the course of the 21st century, with corresponding potential for heightened levels of proximate and ultimate threats to avian diversity. Landscape-scale investigations of the responses of birds in locations where current extreme fire regimes represent those expected in the future provide opportunities to identify potentially vulnerable species in advance. Autonomous acoustic recorders are well suited to survey birds in the typically large and remote natural areas with low accessibility required for these types of studies, because they offer cost-effective and relatively safe options for obtaining reliable data. The present study aimed to optimise survey using acoustic recorders to achieve a satisfactory assessment of montane dry sclerophyll forest bird assemblages using these devices. Survey completeness, or the number of species detected as a percentage of total species, was used as a metric to gauge survey suitability. Acoustic recorders were deployed in 10 ridge-top forest sites in the Blue Mountains, south-eastern Australia. Extensive field recordings were processed by an analyst, with species detected by their calls recorded in a series of 20-min samples. A results-based approach, incorporating a stopping rule that established when to conclude sampling at a site, was applied to the data. The results guided the target survey completeness and sampling effort levels assigned to a set of fixed effort survey methods, which were subsequently evaluated. The optimal survey method involved using recordings from five 20-min samples immediately following dawn for 2 days, achieving an average survey completeness level of 69%. The optimal survey method can obtain results that are suitable for many types of studies involving assessments of bird assemblages, because the method can detect all common and moderately common species in assemblages, plus a fair proportion of rare species. The present study has systematically developed an effective method of using autonomous acoustic recorders to research and monitor montane bird assemblages in fire-prone dry sclerophyll forests. This methodological approach may also be applied in systems subject to altered patterns of flood, storm or other extreme weather under climate change.

3.2 Introduction

Over the 21st century, fire activity is predicted to increase in global forests at mid-high latitudes under climate change (Moritz et al. 2012), including larger, more frequent fires in dry sclerophyll forests of south-eastern Australia (Bradstock 2010). As part of these processes, unprecedented wildfire events can be expected in the region, such as the extensive fires of the 2019–20 fire season (Boer et al. 2020, Nolan et al. 2020). In all probability, these broad-scale changes to fire regimes will affect fauna that occupy fire-prone natural areas. Although birds are relatively mobile organisms, individuals of many species will be directly impacted by fire events and/or experience post-fire reductions in the quantity and distribution of suitable habitat (Fox 1978, Nimmo et al. 2019). In the medium to long term, bird populations may struggle to remain viable, regardless of their current conservation status. A valuable approach to understanding the exposure of birds to the threats posed by changing fire regimes is to investigate species distributions in relation to varied extant fire histories in forested landscapes (Driscoll et al. 2010). The naturally vegetated study areas required for such investigations are typically large, remote and potentially difficult to access. In this context, methods using autonomous acoustic recorders to survey birds can be better suited than traditional observer-based methods (Darras et al. 2019). Systematic development and testing of recorded acoustic survey methods are necessary to provide cost-effective options for the assessment of the threats of increased levels of forest fire activity to avian diversity.

Recorded acoustic surveys can be configured to match the temporal and spatial designs of established observer-based methods, and they have the capacity to detect species at least as effectively as surveys conducted by an observer (Shonfield & Bayne 2017, Darras et al. 2018a; Franklin et al. 2020). Landscape-scale studies of the effects of fire regimes on bird assemblages have used timed point counts of 5–15-min duration (Lindenmayer et al. 2014, Robinson et al. 2014, Sitters et al. 2014a) or 20-min searches of 2–3-ha areas (Loyn 1997, Loyn & McNabb 2015, Gosper et al. 2019a), conducted by observers. Similarly, other types of bird studies using autonomous acoustic recorders have used replicate samples between 1 min (Wimmer et al. 2013) and 20 min (Darras et al. 2018b) in length.

Recorders can sample at any time of the day or night in remote, difficult-to-access locations, which can be an advantage over observer-based methods in terms of costs and logistics involved in using field personnel for the task, particularly for large studies (Darras et al. 2019). On a single-day visit to a remote study area, selectively undertaken during favourable weather, multiple recorders can be deployed during a convenient period of the day. This flexibility has the potential to enhance fieldwork safety, as well as reducing overall travelling time and time spent in the field (Shonfield & Bayne 2017). Use of autonomous recorders has further safety benefits when bird data is required during the bushfire season in fire-prone forests (October–March in New South Wales). In situ recorders can continue to sample during periods when fire weather and fuel condition combinations would expose field personnel to increased risk of wildfire. Relatively inexpensive recorders are available (Darras et al. 2019) to ameliorate the risk of loss owing to fire. This advantage will become increasingly relevant over the coming decades as weather conducive to the occurrence and spread of wildfire occurs more frequently in south-eastern Australia, with a corresponding increase in the length of the official fire season (Clarke et al. 2011).

The capacity of weatherproof acoustic recorders to capture extensive temporal samples, with comparatively little additional cost once deployed, is an important advantage the technology has over observer-based methods. Long deployments provide large datasets that can be subsampled later at the desktop in a variety of ways (La & Nudds 2016). Recorders can be programmed to record during periods of peak daily vocalisation by the target species and sampling can be extended through seasonal or longer cycles to the limits of power supply and data storage capacity, both of which can be extended in various ways (Darras et al. 2019). Recorders can be expensive to purchase, but they are reusable, so the initial cost can be set against several studies. With multiple recorders, study sites can be surveyed at the same time, thereby temporally standardising those samples (Darras et al. 2019).

Acoustic recordings obtained in the field need to be processed to determine the species present. The two main approaches to processing recordings are to use: (1) automated methods, which can involve specifying a set of defining calls for a target species, then initiating an automated search of recorded data for matches; and (2) manual processing, involving real-time listening and/or viewing of recordings in a spectrogram (frequency over time). Automated processing is an area of active research, and promising techniques have emerged (Priyadarshani et al. 2018), but there are several reasons why manual processing currently performs more reliably for determining assemblage composition. Automated detection of all species in recordings is currently limited by data complexity introduced by factors such as overlapping calls, irregular or incomplete calls, extent of species song repertoires, distance between bird and recorder, effects of terrain or vegetation structure on call transmission, and background noise levels (Catchpole & Slater 2008, Darras et al. 2019). Because of limitations such as these, manual processing can take less time than automated methods to generate a set of results for a small group of species (Joshi et al. 2017).

Manual processing of recordings by an analyst can be very accurate (e.g., Knight et al. 2017), but the quantity of data to be processed per site survey is moderated by the need to use replicate sites at the treatment level, and is restricted by overall study resources. A consequence of limited sampling effort is that bird surveys are incomplete, but the extent to which sites and species might be under- or over-sampled is often unknown (Watson 2017). If sampling of a site must be limited to practical levels, then an understanding of resulting completeness (species detected as a proportion of the total number of species) is desirable (Watson 2017).

Different levels of survey completeness can suit different types of research questions. Once the requirements of a study are defined, an acoustic survey method can be developed and tailored to meet the desired level of completeness (Watson 2017). Site surveys achieving modest completeness, for example 70% (Callaghan et al. 2017), typically detect the common and moderately common species, which can suffice for evaluating effects of environmental differences on aspects of assemblages (Lennon et al. 2004, Callaghan et al. 2017), including assemblages of breeding birds (Pearman & Weber 2007). It is necessary to specifically investigate and monitor common or moderately common species responses to extreme fire regimes at broad scales, because for example, common species that are associated with diminishing long-unburnt habitat can also be vulnerable to habitat loss through regional land-use change (Gosper et al. 2019b).

General frameworks are available for ecologists to use to develop reliable acoustic protocols to survey bird assemblages. For example, given equal sampling effort, a prospective acoustic protocol can be compared with an established observer-based method on the basis of species detection probability, using occupancy modelling (Franklin et al. 2020). In the present study, we used a results-based sampling method to determine survey effort requirements as a step in the process of developing an optimal acoustic survey protocol that maximised sampling efficiency. Results-based methods use a priori rules, such as ‘stop the survey when three consecutive samples yield no new species’, which can be applied to survey forest sites equivalently (Watson 2003, Watson 2004). Theoretically, the application of such rules accounts for the fact that more sampling effort may need to be expended to detect a representative proportion of assemblages in locations with greater habitat complexity, compared with areas with relatively open structure (Watson 2003).

In terrestrial ecosystems such as the dry sclerophyll forests of south-eastern Australia, wildfire is a dominant, periodic disturbance. Increasing fire activity is expected in these forests over the

21st century (Bradstock 2010). Similarly, the occurrence and magnitude of floods, tropical storms and other extreme weather events are changing (and in some regions increasing) under climate change (Hughes 2003). The effects of altered frequency and intensity of these system-wide disturbance events on birds is uncertain in many cases. Therefore, it is imperative that efficient, reliable methods of monitoring avian diversity are available to ecologists and natural area managers. Because of the advantages they represent, autonomous acoustic recorders have much potential for application in this context. Survey methods using acoustic recordings need to be developed and/or tested with the target species in the study habitat, because sound transmission properties vary among habitats, and species exhibit geographical variation in their calls (Catchpole & Slater 2008). The focus of the present study was the use of acoustic recorders to survey birds in fire-prone forests. Our objective was to determine the amount of survey effort required to achieve a satisfactory assessment of dry sclerophyll forest bird assemblages using acoustic recorders.

3.3 Methods

3.3.1 Study area

The study was conducted in the mid-Blue Mountains (338450S, 1508260E), within the Greater Blue Mountains World Heritage Area, New South Wales. Mean maximum temperatures range from 23.48C in January to 9.68C in July, with 1404 mm average annual rainfall (Katoomba Station, Bureau of Meteorology 2021). Each of the 10 sites was located on top of a different ridge in the study area. The vegetation community in each replicate site was dry sclerophyll forest with a shrubby understorey (Keith 2004), that had not been burnt since 2002 (Office of Environment & Heritage NSW 2016). Site boundaries were defined at changes in vegetation community and were between 14 and 46 ha (mean 26 ha). Particular sclerophyllous shrubs that occur in the understorey of dry forests in the region flower in the cooler months and are an important food resource for honeyeaters (*Meliphagidae*, Pyke 1988, Franklin et al. 2014). During the present study (late autumn–early winter 2017), honeyeaters were observed foraging on inflorescences of the following understorey species in the sites: *Banksia spinulosa*; *B. ericifolia*; and *Epacris pulchella*.

3.3.2 Recorded acoustic bird surveys

A Song Meter SM4 acoustic recorder (Wildlife Acoustics, Maynard, MA, USA) was deployed in each site by attaching it to a small tree with a cable lock at 2 m above the ground (Depraetere et al. 2012, Darras et al. 2018a). Recorders were randomly located in the central parts of the dry sclerophyll forest sites, which excluded the area within 100 m of the site boundary (Holmes et al. 2014). Site boundaries represented a change in vegetation community, so maintaining a distance between the recorder and the boundary was expected to reduce the recording of birds calling from different habitats (Hingston et al. 2018). Devices were programmed to record for the first 3 hours immediately following dawn, because that is when eucalypt forest and woodland species may vocalise more frequently (Wimmer et al. 2013). A set of four recorders were used in the study. Recorders were collected from the field after 5 days of clear weather data had been recorded, and then redeployed until all sites had been surveyed. See Franklin et al. (2020) for further details of recorder deployment and configuration.

Acoustic recordings were manually processed by MF to identify species present in 20-min samples (Darras et al. 2018b) by listening to calls and viewing spectrograms (call frequency over time) using Kaleidoscope Pro software (Wildlife Acoustics, Maynard, MA, USA). The resulting complete dataset consisted of nine 20-min samples on each of 5 days in all 10 sites, totalling 450 20-min samples for the study. Three steps were taken to ensure that species were accurately identified from their recorded calls: (1) sets of published bird calls (Van Gessel & Kane 2002, Buckingham & Jackson 2007) were used for comparison while processing recordings; (2) a library of calls was developed by harvesting representative calls from the recordings, which was also used as a reference during processing; and (3) other people with expertise in species calls (see Acknowledgements) were consulted for assistance with identification of calls that could not be assigned to a species with complete confidence during the main processing (Darras et al. 2019, Franklin et al. 2020).

3.3.3 Data analysis

Recorded acoustic survey methods were compared based on their average survey completeness levels (Watson 2004), which required estimates of the total number of species in each site. We define a survey as a set number of 20-min samples obtained from a site using an explicit temporal specification. Extensive acoustic recordings were processed for each site to (1) enable robust estimates of the total number of species in each site, and (2) provide options for different temporal sampling configurations in the development of an optimal survey method. The incidence-based coverage estimator (ICE, Chazdon et al. 1998, Chao et al. 2000) was used with the complete dataset to obtain estimates of the total number of species in each site (La & Nudds 2016) using the SpadeR package in R (Chao et al. 2016, R Core Team 2019, see Franklin et al. 2020 for estimates). To establish overall completeness levels for the different survey methods, the number of species detected in each site was divided by the estimate of the total number of species for that site, and then averaged over the 10 sites for each method. Species accumulation curves for sites based on the complete dataset were produced using EstimateS (Version 9, R. K. Colwell, unpubl. data), with the order of 20-min samples randomised 100 times for each curve (Colwell & Coddington 1994).

To establish a satisfactory level of survey completeness, we used a results-based method incorporating a rule established a priori, that when met, signified the conclusion of subsampling of the complete dataset for each site. This method included 20-min samples until three consecutive 20-min samples yielded no new species in each site (Watson 2004) – we refer to this as the ‘three-sample stopping rule method’. This and subsequent subsampling methods were restricted to the first five 20-min samples immediately following dawn, because in montane dry sclerophyll forests of the region, more species may be expected to be detected in recordings during that period (Franklin et al. 2020).

Next, we optimised subsampling of the complete dataset with the aim of increasing average survey completeness, by developing different fixed-effort methods with total sampling effort closely matched to the three-sample stopping rule method (9.1 20-min samples, Table 3.1). The candidate fixed-effort methods applied at the site level reflected different configurations of sampling days (d) and 20-min samples (p), commencing at dawn. A random method of selecting 20-min samples was applied to subsample the complete dataset (Wimmer et al. 2013). This involved random selection of 10 20-min samples from the pool of 25 20-min samples taken over 5 days. The other two methods that were devised and tested were 5d2p (5 days × two 20-min samples) and 2d5p (2 days × five 20-min samples), with each requiring 10 20-min samples in total (Franklin et al. 2020). The optimal fixed-effort method was selected following evaluation of the results (Table 3.1). The proportion of 20-min samples in which each species was detected (incidence rate) was calculated for the different survey methods (Appendix B.1) and used in the evaluation process.

3.4 Results

There were 47 diurnal species detected in the complete dataset, which consisted of a total of 9,000 min of post-dawn recordings obtained in replicate montane dry sclerophyll forest sites (Appendix B.1). Four of the 10 most frequently detected species were honeyeaters (*Meliphagidae*). Other common birds included the Pied Currawong (*Strepera graculina*), Brown Thornbill (*Acanthiza pusilla*), Crimson Rosella (*Platycercus elegans*), White-throated Treecreeper (*Cormobates leucophaea*), Sulphur-crested Cockatoo (*Cacatua galerita*) and Grey Shrike-thrush (*Colluricincla harmonica*). The Gang-gang Cockatoo (*Callocephalon fimbriatum*) was detected in recordings and is listed as a vulnerable species under the NSW Biodiversity Conservation Act 2016. After a rapid initial increase, the rate of accumulation of species had declined to different degrees among sites after 45 20-min samples (Fig. 3.1). Final numbers of species in sites ranged between 20 and 34. Species recorded in the complete dataset accounted for 88% of estimated total species per site on average (Franklin et al. 2020).

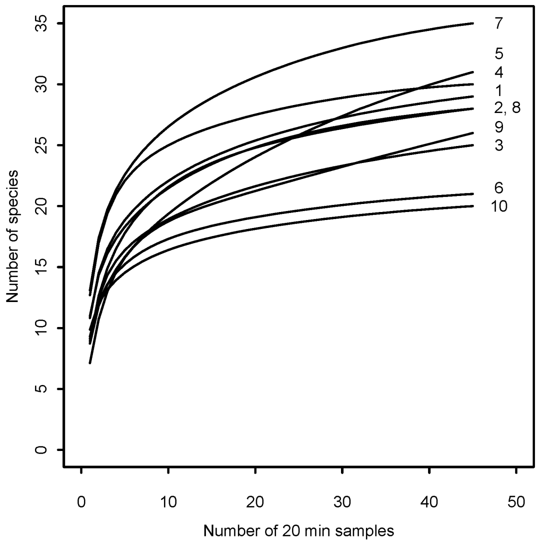

Fig. 3.1. Species accumulation in 10 sites (numbered) for the complete dataset.

The three-sample stopping rule method attained an average completeness of 67%, which was slightly less than the completeness level of the candidate fixed-effort methods at 68–69%, for similar average sampling effort (Table 3.1). The number of samples required until the three-sample stopping rule was triggered and the number of days required for sampling using this method were variable (Table 3.1).

Table 3.1. Average sampling effort and completeness levels of survey methods using acoustic recordings. The three-sample stopping rule was applied to recorded acoustic data to provide a guide for the development of an optimal fixed-effort method. The fixed-effort methods were configured to match the sampling effort used by the three-sample stopping rule method. The random method involved random selection of 10 20-min samples from the first five post-dawn samples over five days (e.g., Wimmer et al. 2013). The 5d2p and 2d5p methods were selected from Franklin et al. (2020). Survey completeness for each method was calculated by dividing the number of species detected by an estimate of total species in each site, and then averaging over the 10 sites. Error terms are standard deviations.

Acoustic method	Survey effort determination	Days	20-min samples	Days x samples	Survey completeness %
3-sample stopping rule	Results-based	1-3	5-14	$\bar{x}$ = 9.1 ± 2.9	67 ± 13
Random	Fixed	5	10 overall	10	68 ± 13
5d2p	Fixed	5	2	10	69 ± 13
2d5p	Fixed	2	5	10	69 ± 12

Of the fixed-effort methods (Table 3.1), we concluded that the 2d5p method was the optimal method (henceforth, the optimal method), because the shorter field-sampling interval minimises the potential for temporal confounding in a study where many sites are surveyed sequentially with a limited number of recorders (Balestrieri et al. 2017). The slightly higher average completeness level of the optimal method compared with the three-sample stopping rule method occurred because the optimal method continued to detect new species in four sites (Sites 1, 3, 8 and 9) after the three-sample stopping rule had been triggered, whereas the opposite occurred in only one site (Site 7, Fig. 3.2).

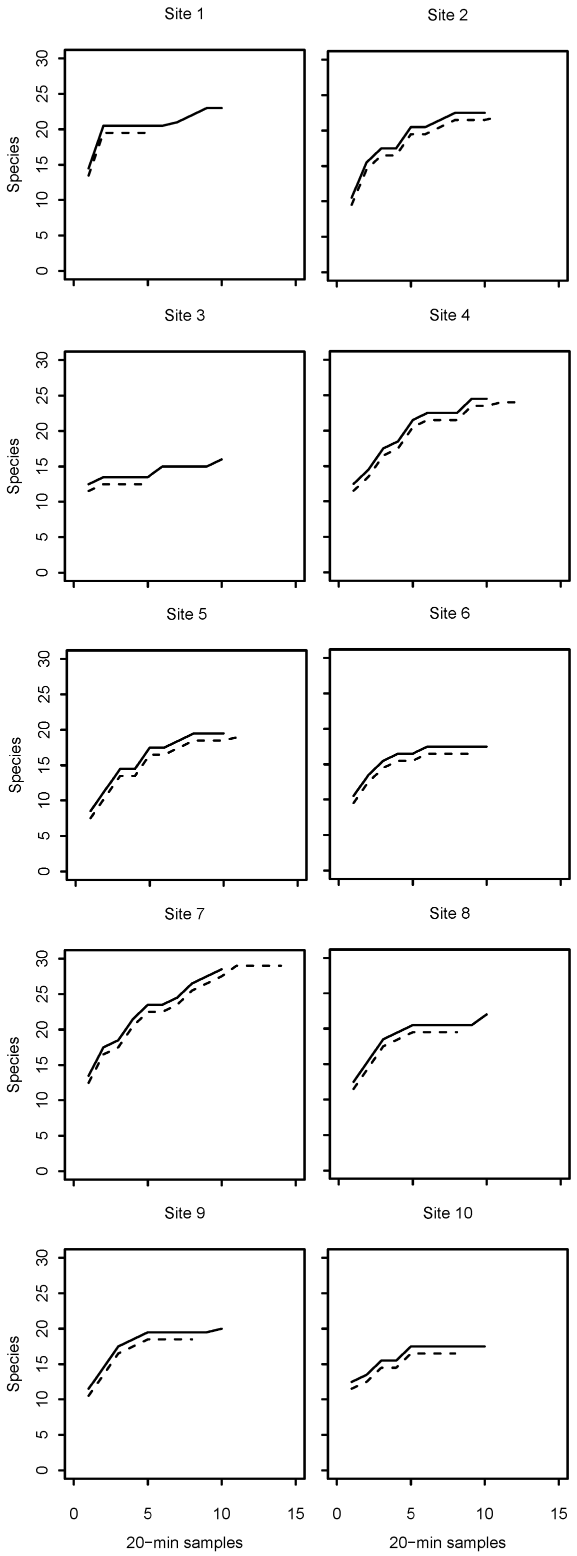

Fig. 3.2. Species accumulation in the 10 sites for the optimal method (solid line) and the three-sample stopping rule (dashed line). Sub-sampling of the complete data set for each site was restricted to the first five 20-min samples following dawn for both methods, so 15 x 20-min samples represents sampling over three mornings. Lines are offset for clarity.

3.5 Discussion

The present study found that manual processing of five 20-min post-dawn acoustic samples on each of 2 days was an effective method of surveying montane dry sclerophyll forest avifauna. This conclusion required (1) the use of a results-based approach (Watson 2003) to establish the amount of survey effort required to achieve a satisfactory level of sampling completeness, and (2) evaluation of alternative acoustic sampling configurations requiring similar effort, to produce the optimal method. This method is also likely to perform well for studies conducted in other forest and woodland types. However, in those situations, some preliminary testing should be undertaken to ensure study aims can be met (Watson 2017). In practice, this could mean assessing the survey completeness levels for a representative proportion of sites by following the approach we have taken in the present study.

The application of the three-sample stopping rule to establish when to conclude each site survey (Watson 2003, 2004) provided a reliable means of establishing the level of sampling effort for subsequent fixed-effort methods. Determining survey effort requirements in this way extends upon the work done by Franklin et al. (2020), who did not focus the configuration of their candidate acoustic protocols for subsequent evaluation of completeness levels. In the present study, when the stopping rule was applied to the complete dataset, the number of 20-min samples included before the rule was triggered in the sites ranged from 5 to 14, which meant that recordings from between 1 and 3 days were required. On average, it required 9.1 20-min samples per site to attain 67% average survey completeness. The three-sample stopping rule has been shown to be an effective method for establishing when to cease a bird survey in other habitats. In four woodland remnants, an average of 9.25 20-min, 5–7-ha area searches conducted by an observer achieved 78% average completeness using this rule (Watson 2004).

We elected not to consider the three-sample stopping rule itself as a candidate optimal method, partly because it would require recorders to be deployed for longer in field sites compared with a similarly structured fixed-effort method, because the total number of days required is not known in advance. Adding a buffer period to account for the uncertainty would extend the overall duration of a study, which may not be problematic for studies with a small number of sites, but could lead to temporal confounding when many sites need to be sampled. Much recorded data would also be collected unnecessarily, representing an inefficient use of resources such as batteries or recorder microphones, which can degrade with increased field deployment time (Turgeon et al. 2017). If the length of recorder deployment is of little consequence, then one could apply a stopping rule to extensive recorded acoustic data as we have done, but go no further and just use those results. However, if an understanding of survey completeness is required, sampling effort beyond the survey stopping points will probably be required to establish robust estimates of the total number of species present (Watson 2010, Franklin et al. 2020). The application of results-based approaches to acoustic data is an area with potential for further research.

Based on the results from the application of the three-sample stopping rule, we sought to develop a candidate set of fixed effort methods using 10 20-min samples, with the aim of achieving at least 67% survey completeness. Varying the temporal arrangement of the 10 20-min samples for the three candidate methods had little effect on the resulting completeness levels (Table 3.1), so the overall time required for each survey method was also considered when selecting the optimal method. When surveys take less time overall, a study or seasonal sampling block can be completed in a shorter time period. Additionally, equipment malfunction would cost less time if affected sites need to be resampled. Longer survey periods mean that there is potentially greater exposure to weather conditions that are unsuitable for recording, which could extend deployments further and so have planning and budgetary implications for large projects that are underway. For these reasons, the method using the first five 20-min samples following dawn on each of 2 days was chosen as the optimal method.

While both methods performed well in individual sites, the optimal method achieved slightly better results than the three survey stopping rule (Fig. 3.2). The three-sample stopping rule method has a potential advantage in that it samples a site with open-ended capacity to commit effort if species are still being detected. However, this attribute did not result in greater average survey completeness than the optimal method, which used fixed effort, established a priori. This was because the optimal method continued to detect species after the stopping rule had been triggered in four sites, whereas the opposite occurred only once.

The optimal method achieved 69% survey completeness and reliably detected all the common and moderately common species in the study area at incidence rates that were very similar to the complete dataset (Appendix B.1). The optimal method detected all species that were present in 3% or more of the 450 20-min samples comprising the complete dataset, including the vulnerable Gang-gang Cockatoo, as well as 50% of species that were detected less frequently.

Species that are common among bird assemblages exert a stronger influence on patterns of spatial variation in species richness than do rare species, so effective studies of the responses of birds to disturbance and environmental gradients can be completed without records of all rare species (Lennon et al. 2004, Pearman & Weber 2007). Additionally, there may be potential to increase statistical power if maximally efficient sampling per site frees up resources to allow more replication at the treatment level (Watson 2010).

The amount of overall survey time allocated to the candidate methods was an important consideration because of the continued accumulation of species in sites as samples were added up to 900 min (Fig. 3.1). The optimal method required a total of 200 min for 69% completeness, which in relative terms provided for very good overall temporal coverage, given that 73% of 194 recently reviewed bird studies surveyed sites for 180 min or less (Watson 2017). The sampling effort apportioned to the optimal method was similar to that of Gosper et al. (2019), who used 12 20-min area searches per site to investigate the responses of birds to woodland fire regimes. In Mediterranean montane forests, site surveys using point counts for 150 min resulted in satisfactorily complete assessment of breeding birds (Balestrieri et al. 2017). The optimal method surveyed assemblages to a completeness level that was very similar to that of a bird study conducted using acoustic recorders in woodland and open forest, where 200 1-min random samples from the post-dawn period over 5 days resulted in ~ 68% average completeness (Wimmer et al. 2013).

Depending on the aims of a study, there may be some time savings to be made by manually processing longer acoustic samples compared with shorter ones, when some of the species in an assemblage are calling frequently. The review of a sound file by an analyst necessarily has to pause so a species can be recorded when it is detected. This recording process is brief, but the time does accumulate and adds to the total time required for a survey. A frequently calling individual or species need only be marked as present once in a 20-min sample, whereas it would need to be recorded 20 times if, say, 20 × 1-min samples were used. Additionally, we found that once familiar with the spectrogram signature of typical calls of frequently calling species, it was possible to visually scan some of the less-complex recordings in faster-than real time without any accompanying audio (Truskinger et al. 2013), which also increased the efficiency of manual processing.

Dry sclerophyll forests on the slopes and ranges of south-eastern Australia are fire prone (Penman et al. 2007), and our acoustic survey method has been tailored to survey bird assemblages in these communities. Individual wildfires in eucalypt forests often burn large areas (Boer et al. 2020). Studies of the responses of birds to fire in these habitats are typically conducted at landscape scales, whether the aim is to investigate responses to single fires (Lindenmayer et al. 2014), or to recent and earlier fires in combination (Robinson et al. 2014). To collect bird data from the field, these studies demand a considerable amount of travel to access remote sites. The use of a set of recorders to survey birds using our method can greatly increase the efficiency and reduce the costs associated with field data collection. The deployment of individual recorders is rapid once the survey location has been accessed, so several recorders can be deployed on a single day with careful route planning. Multiple sites are then sampled simultaneously on subsequent days, until those surveys are complete. Then recorders can be collected and redeployed in the next set of sites on the same day, having swapped the memory cards storing recordings for new ones. Because a site can be surveyed in two clear-weather days with our method, a large set of sites can be sampled in a short time period using this approach. Sampling within a short window is important for fire research because, given the broad scale at which sampling is required, there is a non-trivial probability of some sampling sites being burnt in a particular season before completion of an extended survey period, disrupting good experimental design.

3.6 Conclusion

We have capitalised on the accuracy of manual processing of recorded acoustic data to devise an efficient method of surveying bird assemblages in montane dry sclerophyll forest to a clearly specified level of completeness. The optimal acoustic survey method involves in situ recording for five 20-min samples immediately following dawn, for 2 days without rain or wind. This design can detect 69% of the estimated total number of bird species present in ridge-top forest sites. Survey completeness at this level is maximally efficient and is suitable for the purposes of comparing the effects of environmental variation among a set of sites (Callaghan et al. 2017). Manual processing of recorded acoustic data resulted in records of the presence of species in 20-min samples, which are well suited to a range of powerful statistical analyses, such as occupancy modelling (McGrann & Furnas 2016). Additionally, incidence, or the proportion of samples in which a species was detected, can be easily determined and may be used as an indication of a species fidelity or partiality for a site (Watson 2003). In particular, this method lends itself to use in monitoring bird response to long-term effects of changing fire regimes because of the necessity of sampling multiple sites with low accessibility during short time windows.

3.7 Acknowledgements

We thank Kim Maute, Paul Lester and Darryl McKay for assistance with identification of species from acoustic recordings. MF received funding from the Stuart Leslie Conference Award/Foundation from Birdlife Australia. Animal ethics approval (UOW AE17-13) and a NSW NPWS Scientific Licence (SL101895) were obtained for the project.

Chapter 4. Relative avian mobility linked to use of fire-affected resources in forested landscapes

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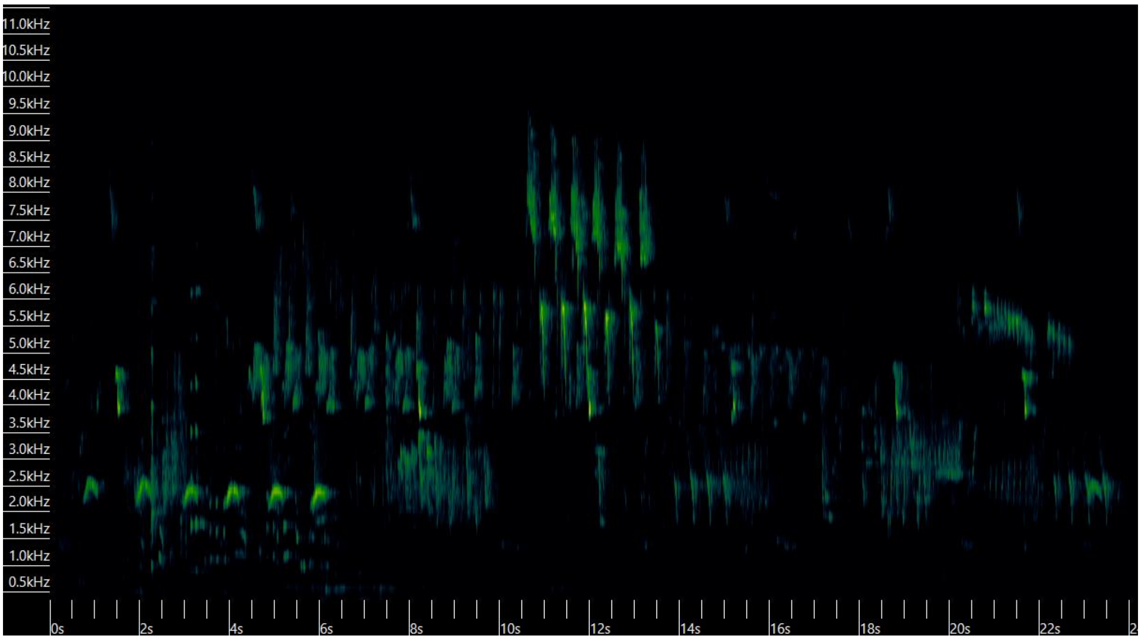

Spectrogram view of an avian dawn chorus, Newnes Plateau 2018

4.1 Abstract

Increased fire frequency is predicted in global forests over the 21st century owing to climate change. Fire–averse animals are expected to be negatively impacted by frequent wildfire events, or corresponding habitat alteration and reduction in the extent of long unburnt forest in landscapes. Mobility is an attribute that may enable bird species persistence in this context, but the capacity to move varies among species. Our aim was to determine whether birds with similar movement strategies, i.e., groups of sedentary, migratory and nomadic species, have similar patterns of occurrence in relation to forest fire frequency and long unburnt forest in the landscape. We modelled occupancy of avian movement groups and species in austral temperate forests in relation to fire frequency in forest patches and the presence/absence of long unburnt forest in the landscape surrounding each patch. We also evaluated relationships between species body size and responses to fire, because larger species tend to disperse further and have larger territories. Migrants responded positively at the group level to the presence of long unburnt forest in the landscape. No other consistent responses of movement groups to fire were detected, although foraging or nesting niche overlaps were evident among species that responded similarly to fire within groups. Of the 20% of 74 total species that responded to one or both fire history predictors, there were twice as many mobile species (migrants, nomads) than sedentary species. Positive responses to the presence of long unburnt forest were dominated by migrants and were much stronger than positive or negative responses to fire frequency. No species was more likely to occur when long unburnt forest was absent from the landscape. Species that responded to fire were large (median body mass 243g) compared with those that did not respond (median 23g). Our structured approach to investigating how avian movement capacity and propensity influences occurrence in relation to fire frequency has increased understanding of the mechanisms that enable avian persistence in fire-prone forests. Many large, mobile bird species can and do move at landscape scales to use resources that may be affected by fire frequency, particularly those that are embodied in long unburnt forest.

4.2 Introduction

Wildfires are predicted to become more frequent in forests around the globe under climate change (Bradstock, 2010, Wotton et al. 2010, Shuman et al. 2017). Consequently, species that are sensitive to frequent fire and/or the resulting changes to habitat are likely to be negatively affected (Woinarski & Legge, 2013). Frequent fire represents a disturbance regime under which birds must seek unburnt refuge to survive each fire event, and then endure or move elsewhere until the forest regenerates sufficiently. Birds are mobile organisms and species have varying capacities to persist and recover from refugia within, or external to, the boundary of large wildfires (Robinson et al. 2013, Robinson et al. 2014, Berry et al. 2015). In this study, we explored avian mobility as a mechanism that may influence species persistence under increased fire frequency in forested landscapes. This was conducted through the lens of species assigned to movement groups, based on whether they were sedentary, migratory or nomadic.

Increased fire frequency will decrease the total amount of long unburnt forest in affected landscapes over time, assuming wildfires vary spatially (McCarthy et al. 2001). Fires are also becoming larger in particular regions under climate change (Abatzoglou & Williams, 2016), thus further reducing long-unburnt habitat across increased proportions of species distributions (Fairman et al. 2016). Forest that is not burnt during a large fire can represent both a refuge during the fire and post-fire habitat for animals (Berry et al. 2015), which in turn can act as a source from which species can recolonise sufficiently regenerated burnt areas (Watson et al. 2012b). The presence of long-unburnt forest also supports landscape habitat heterogeneity, which is important for species that require forest at different successional stages in their range (Nimmo et al. 2019). Therefore, areas of long unburnt forest may be expected to support avian diversity in frequently burnt landscapes, provided they are detectable and accessible to species with different movement strategies.

Given enough time, fire-adapted forests have the potential to recover after a wildfire, and the resources used by animals can eventually return to pre-fire levels. The return interval of fires in an area may have more important longer-term effects on the forest biota than the impact of a single fire (Bradstock, 2008, Lindenmayer et al. 2008). If the periods between successive fires are short, recovery of a community through regeneration, reproduction or immigration may be incomplete, potentially leading to population declines (Whelan et al. 2002, Keith, 2012, Woinarski & Legge, 2013, Nimmo et al. 2019). Furthermore, if subsequent fires burn areas before plants reach maturity, then changes in the structure and composition of the vegetation may occur, including increased representation of fire-tolerant species (Bradstock, 2008, Fairman et al. 2016). Distributions of animals that are sensitive to such changes may be altered in affected landscapes (Kelly et al. 2017).

We investigated the responses of avian movement groups to fire history in montane dry sclerophyll forest, because it occurs extensively on the slopes and ranges of south-eastern

Australia (Keith, 2004), and is important habitat for birds, such as the threatened Glossy Black-Cockatoo (*Calyptorhynchus lathami*) (DECC 2007). Along with other temperate forests worldwide, fire activity is predicted to increase in these eucalypt forests as the climate continues to warm (Bradstock et al. 2009, Dowdy et al. 2019). Regeneration of dry sclerophyll forest via resprouting or seed germination typically commences rapidly after fire. The rate of post-fire recovery will vary across a region due to factors such as the timing and amount of rain (Heath et al. 2016). In these communities most plant species have generally reached maturity within 10 years (Kenny et al. 2004), although seed resources may not be fully replenished at this time (Keith, 2012). Our study was focused on fire frequency in forest patches at a mid-successional stage, having substantially recovered from the most recent fire.

The responses of bird species to fire frequency can vary widely within assemblages and across a range of habitats (e.g., Barlow & Peres, 2004, Reside et al. 2012, Kelly et al. 2017). Several studies have investigated and revealed some of the effects of fire frequency at the functional group level, e.g., foraging, nesting and habitat-use guilds. In savanna woodlands, frequent fire can detrimentally affect frugivores, granivores, insectivores and ground and hollow nesting species by reducing food resources and/or habitat (Valentine et al. 2012, Woinarski & Legge, 2013, Yates et al. 2008). In particular, species that are negatively impacted by frequent fire may have requirements for suitably distributed unburnt vegetation and/or fire-sensitive vegetation (Woinarski & Legge, 2013). Frequent fire can reduce levels of foraging and nesting resources used by forest birds, such as flowering of trees, coarse woody debris, fallen logs and tree hollows (Law et al. 2000, Recher, 2004, Kelly et al. 2017). In Argentinian semi-arid forest, birds that use discrete sections of the vertical forest strata, i.e., understorey species, or subcanopy/canopy species, declined in abundance with high fire frequency, while the opposite was the case for species that use open areas, and generalists were unaffected (Albanesi et al. 2014).

The ability of a bird species to move around in fire-prone landscapes may ultimately influence its occurrence in relation to spatial patterns of fire history (Hidasi-Neto et al. 2012). The abundances of residents and migrants were compared in unburnt, burnt, and burnt and logged boreal forest, with migrants responding negatively to the latter treatment (Stuart-Smith et al. 2002). However, knowledge is lacking about how avian movement groups in assemblages, i.e., sedentary, migratory or nomadic species, respond to forest fire frequency. Species can be expected to occur in frequently burnt forest if resource levels are sufficient, but they must have the mobility to return from refugia after each fire. Species with poor dispersal ability and small home ranges are potentially vulnerable to frequent fire (Yates et al. 2008, Woinarski & Legge, 2013). Sedentary species with these attributes have limited options for suitable refugia and post-fire habitat in relation to any one fire, but these may well be reduced each time a fire in a series of fires burns a forest patch and its surroundings. Migratory species may fare better in this context, because they have been shown to have greater dispersal ability than sedentary species (Paradis et al. 1998, Sutherland et al. 2000, Stevens et al. 2014). For example, partial migrants exhibit the capacity to selectively occupy locations with longer time since fire in landscapes (Kelly et al. 2017, Nimmo et al. 2019). Suitable habitat in forests characterised by frequent fires may also be more accessible to nomadic species, owing to their capacity to track resources over wider areas (Teitelbaum & Mueller, 2019). Because avian body size tends to be positively correlated with dispersal distance and/or territory size (Schoener, 1968, Paradis et al. 1998, Tittler et al. 2009, Thornton & Fletcher, 2014), we considered species body size (as body mass, Callaghan et al. 2019) as a potential influence on responses to fire history, both across species and within movement groups.

Proportional increases in representation of relatively mobile species of arthropods and plants have been observed in the period shortly after disturbance (Pedley & Dolman, 2014). However, little is known about how the occurrence of groups of vertebrate taxa with broadly different movement strategies is influenced by cyclical disturbance from fire. We aimed to determine whether avian movement strategies, represented as groups of sedentary, migratory and nomadic species, were important correlates of bird occurrence in relation to forest fire frequency. Three predictions about avian movement groups and patterns of fire history were explored under this aim. Firstly, it was anticipated that the occurrence of sedentary species would be reduced in forest patches with high fire frequency because of their limited capacity to disperse. Secondly, we predicted that greater proportions of migratory and nomadic species would respond to fire frequency in forest patches than sedentary species, owing to their greater capacity to locate and access preferred habitat across a landscape. Because frequent fire can diminish the levels of several important resources used by birds, we anticipated lower probabilities of occurrence of most migrants and nomads where fire was frequent. Thirdly, because long unburnt forest represents refugia during wildfires, post-fire habitat and increased landscape habitat heterogeneity, we predicted that all movement groups would be more likely to occur in patches where long unburnt forest was present in the surrounding landscape.

4.3 Methods

4.3.1 Study sites

The study was conducted in dry sclerophyll forests of the Greater Blue Mountains World Heritage Area, south-eastern Australia (Fig. 4.1). Two regionally representative areas on the Great Dividing Range were used to study the effects of fire frequency on species and movement groups in avian assemblages. The southern area was the Blue Mountains, in which 16 sites were established as forest patches on ridges that extend north and south from the narrow urban corridor that cuts east-west across the range (Fig. 4.1). To the north, 18 sites were located on the relatively flat and remote Newnes Plateau. Sites were circular with a radius of 325 m (~ 33.2 ha). This radius was adopted for several reasons. Firstly, large sites allowed for better matching of the habitat space use of mobile species with the ecological effects of fire on the habitat (Luck et al. 2012). Secondly, sites of this size reflected the scale of the spatial pattern of discrete fire histories in the study landscapes, given that we standardised sites in terms of vegetation and topographic position. Finally, it was assumed that most birds detected by their calls would have been within the site (Yip et al. 2017). Site centres were at least 1125 m apart (median 1984 m).

In addition to ensuring that all sites were located in dry sclerophyll forest communities with a shrubby understorey (Keith & Simpson, 2012), and at a similar elevation, two rules related to fire history were applied to standardise sites. Firstly, sites were at mid-range time since fire when bird survey were conducted, having all been last burnt in the 2001-2002 or 2002-2003 austral fire seasons (Office of Environment & Heritage NSW 2017). Secondly, most of the area of each site had been burnt to at least a high level of severity by the last fire (Hammill & Bradstock, 2006). The proportion of the site over which the forest canopy was scorched or consumed by the last fire ranged from 69% to 100% (median 91%) among the sites.

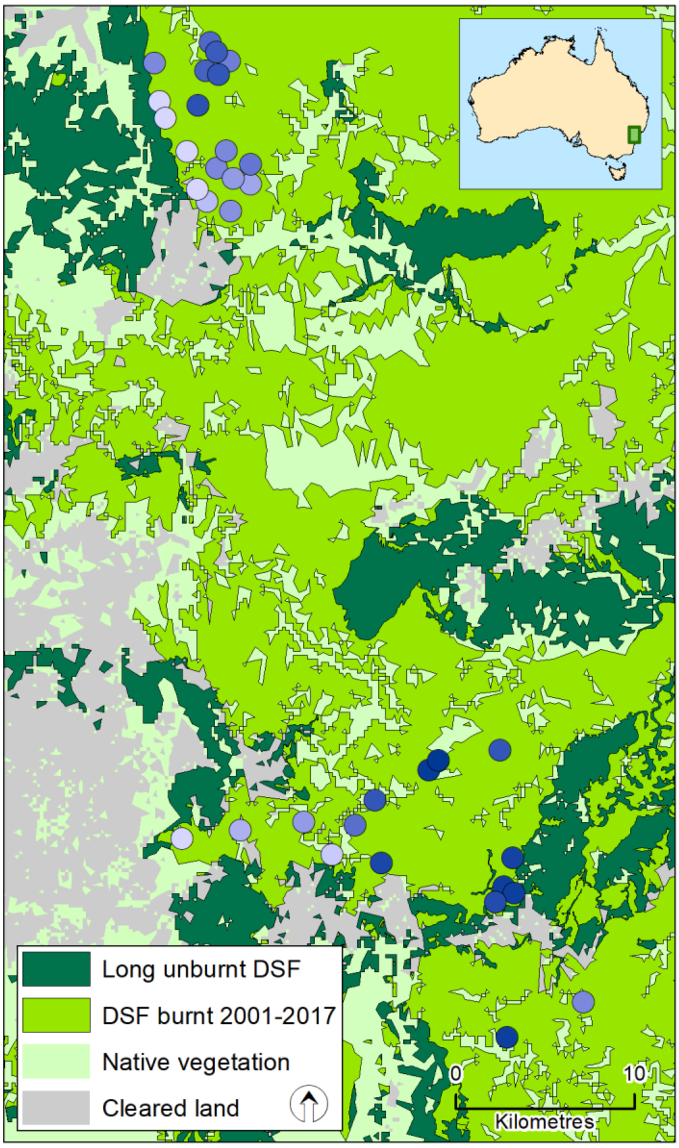

Fig. 4.1. The study was conducted in dry sclerophyll forests (DSF) of the Greater Blue Mountains World Heritage Area, south-eastern Australia. All sites (circles) were located in DSF that was last burnt in 2001-2003, with the blue colour gradient indicating the area-weighted mean number of fires since 1971, ranging from one (light) to five fires (dark). Long unburnt DSF was last burnt prior to 2001-2003.

4.3.2 Bird survey

To allow for inter-annual variation in species occurrence, bird surveys were conducted over two years. In each area (Blue Mountains, Newnes Plateau), half the sites were surveyed between mid-October and mid-December (late spring) in 2018 and the other half in late spring 2019 (Lindenmayer et al. 2014). Acoustic recorders were used to survey bird assemblages in each site. A recorder (Song Meter SM4, Wildlife Acoustics, Massachusetts, United States) was programmed to start recording at dawn and continue for 100-min each day, then attached to a small tree at 2 m above the ground, at the centre of each site. Recorders were left unattended in the field until at least two days without rain and no more than light wind had passed, then collected and redeployed until all sites had been surveyed (Franklin et al. 2020). To determine the species present in recordings (.wav files), bird calls were played and viewed in a spectrogram of frequency/time by MF using acoustic software (Kaleidoscope Pro, Wildlife Acoustics). Species were recorded as present in 20-min subsamples, with five such periods commencing at dawn on each of two days constituting a site survey (Franklin et al. 2020, Franklin et al. 2021a), resulting in a total of 6800-min survey time. All recorder settings, microphone checks, acoustic file processing protocols and quality control measures follow Franklin et al. (2020). Nocturnal species were excluded from data analysis.

4.3.3 Bird movement groups

Species detected in the study were allocated to one of three movement groups according to whether they were migratory, nomadic or exclusively sedentary (Appendix C.1). The three groups represent fundamentally different movement strategies and were based on movement categories assigned by Garnett et al. (2015). The sedentary group consisted of species that move at relatively small spatial scales, with only local juvenile dispersal (Garnett et al. 2015). The migratory group was made up by pooling partial and total national migrants (Sutherland et al. 2000, Callaghan et al. 2019), and international migrants. Partial migrants were species where some individuals undertake wider seasonal movements post-breeding, while others may remain in the breeding location all year round (Garnett et al. 2015). The nomadic group consisted of species that do not necessarily follow regular seasonal movement patterns, but rather track resources that fluctuate in availability over time and space within their distributions (Garnett et al. 2015). Individuals of most species in the nomadic group may have also dispersed locally, or been partial migrants.

Table 4.1. Avian movement groups investigated in relation to forest fire frequency. Species were assigned to movement groups according to whether they possessed the corresponding distinguishing attribute. Movement groups were based on pooled categories (Garnett et al. 2015) shown in the final column, with brackets indicating additional categories to which species could also belong, under our grouping scheme.

Movement group	Distinguishing attribute	National movement category (Garnett et al. 2015)
Sedentary	Short-range movement/ dispersal only	Local dispersal
Migratory	Some/all individuals depart post-breeding	Total migrant, Partial migrant (Local dispersal), International migrant
Nomadic	Track resources in/across landscapes	Nomadic or opportunistic (Local dispersal, Partial migrant)

4.3.4 Fire history predictor variables

We quantified fire frequency as the number of fires that burnt a site from 1971 up to and including the most recent fire (2001-2003) based on the NSW Fire History data set (Office of Environment & Heritage 2017) depicted as a 20-m gridded spatial layer. For each site, the area-weighted mean number of fires over the 830 grid cells was calculated to provide the variable MFC (mean fire count) for modelling.

The presence/absence of long unburnt forest in the landscape around each site was a binary variable (L1785) indicating the presence (1) or absence (0) of at least one patch, with area 5-ha or more, of long unburnt dry sclerophyll forest with a shrubby understorey (Keith & Simpson, 2012) in the landscape. As such, sites and the long unburnt forest in the site surrounds were the same vegetation community. We define a landscape in relation to each site as a circular area of 10 km^2 (1785-m radius from the site centre; Watson et al. 2012b). Sites were circular with a radius of 325 m and were all last burnt in 2001-2003. The search area for long unburnt forest was external to the site but within the landscape boundary. Forest was classified as long unburnt if it was last burnt prior to the sites (before 2001-2003). We set the minimum long unburnt forest patch size to 5-ha because a patch of this size is likely to provide potential refuge for birds during a wildfire, and adequate resources for survival in the post-fire period (Berry et al. 2015).

4.3.5 Data analysis

To estimate bird species and movement group occurrence in relation to fire frequency and the presence/absence of long unburnt forest in the landscape, we used a Bayesian multispecies occupancy model (Zipkin et al. 2009, Zipkin et al. 2010, Tingley & Beissinger, 2013). This approach enables inferences to be made for individual species or groups in assemblages, while accounting for imperfect detection of species, in a single hierarchical model (Iknayan et al. 2014). Response data in the form of records of species detected in replicate acoustic sampling periods for each site is well-suited to this approach (McGrann & Furnas, 2016). We modelled the number of times ($y_{i,j}$) species i was recorded in site j over k replicate periods as per Equation 4.1, where $z_{i,j}$ was the true (unknown) species presence (0 or 1), and $p_{i,j}$ was the probability of detecting the species when present.

$$\mathrm{y}_{i,j} \sim \mathrm{Binomial}(z_{i,j}p_{i,j}, k_j) \qquad \text{Equation 4.1}$$

True species presence was related to a species-specific intercept (β_{0i}), a binary location variable that indicated whether the site was on the Blue Mountains or Newnes Plateau (NPL), fire history predictors (MFC and L1785) and a site random effect (θ_j) via logistic regression (Equation 4.2). Each species was allocated to a prior incidence group (rare, uncommon, moderately common, or common) based on the classification of Smith et al. (2019), tailored to suit dry sclerophyll forest in the study area (Appendix C.1). The intercept for each species was then drawn from a Normal prior distribution for the relevant group, with the prior means being estimated by the model such that their order corresponded to that of the incidence classes (i.e., rare <= uncommon, etc.). Avian movement groups were incorporated in the priors for MFC and L1785. For these predictors, the parameter value for each species was drawn from a Normal distribution for the corresponding movement group (Equation 4.2).

$$z_{i,j} \sim \mathrm{Bernoulli}(\psi_{i,j}) \qquad \text{Equation 4.2}$$

$$\mathrm{logit}(\psi_{i,j}) = \beta_{0_i} + \beta_1\mathrm{NPL}_j + \beta_{2_i}\mathrm{MFC}_j + \beta_{3_i}\mathrm{L1785}_j + \theta_j$$

$$\beta_{0_i} \sim N(\mu_{0[incidence[i]]}, \sigma_0)$$

$$\beta_1 \sim N(0,1)$$

$$\beta_{2_i} \sim N(\mu_{2[movement[i]]}, \sigma_2)$$

$$\beta_{3_i} \sim N(\mu_{3[movement[i]]}, \sigma_3)$$

$$\mu_{0[incidence[\ldots]]} \sim SORT\{\ N(M_0, \sqrt{10})\ \}$$

$$\mu_{2[movement[\ldots]]} \sim N(0{,}1)$$

$$\mu_{3[movement[\ldots]]} \sim N(0{,}1)$$

$$M_0 \sim N(0{,}1)$$

$$\theta_j \sim N(0, \sigma_\theta)$$

$$\sigma_0 \sim \mathrm{Exp}(1)$$

$$\sigma_2 \sim \mathrm{Exp}(1)$$

$$\sigma_3 \sim \mathrm{Exp}(1)$$

$$\sigma_\theta \sim \mathrm{Exp}(1)$$

We related the logit probability of detecting species *i* in site *j* when present ($p_{i,j}$) to a species intercept (γ_{0i}), plus the species-specific influence (γ_{1i}) of terrain variability on the transmission of bird calls (Equation 4.3). The latter term was included because, in addition to the potential for variable terrain to present barriers to call transmission, the degradation of bird calls over distance owing to physical factors varies among species (Catchpole & Slater, 2008). Terrain variability was quantified as the standard deviation of elevation over each site (ESD), based on a 25 m digital elevation model.

$$\mathrm{logit}(p_{i,j}) = \gamma 0_i + \gamma 1_i \mathrm{ESD}_j \qquad \text{Equation 4.3}$$

$$\gamma_0 \sim N(\mathit{\Gamma}_0, 1)$$

$$\gamma_1 \sim N(\mathit{\Gamma}_1, 1)$$

$$\mathit{\Gamma}_0 \sim N(0{,}1)$$

$$\mathit{\Gamma}_1 \sim N(0{,}1)$$

The model was fitted by Markov Chain Monte Carlo (MCMC) sampling using the JAGS library version 4.3.0 (Plummer, 2003), via the runjags package for R (Denwood, 2016, R Core Team, 2020). We ran four MCMC chains, each consisting of 1,000 burn-in iterations, followed by 25,000 sampling iterations, with every 25th sample retained. We assessed convergence using the Gelman-Rubin statistic (Gelman & Rubin, 1992), and by inspecting the number of effective samples for a selection of parameters. Not all combinations of the two fire predictors could be accommodated on both the Newnes Plateau and Blue Mountains (Fig. 4.1), which precluded modelling the interaction between the fire variables. Predictions from the model were generated for individual fire variables while marginalising over the two areas (NPL).

To characterise movement group and species responses to contrasting fire frequency, the posterior distribution of difference in probability of occurrence between low and high fire frequency was calculated for each group and species. We defined low frequency as a single fire, and high frequency as four fires over the ~ 31-year fire history period. Similarly, we characterised movement group and species responses to the presence or absence of long unburnt forest by calculating posterior differences in probability of occurrence based on this predictor. Movement groups and species were considered to have shown a clear positive or negative response to either of these variables if the central 90% of the distribution of differences did not cross zero. In accordance with our overarching aim, responses from movement groups to one or both fire predictors were considered as a function of relative mobility, regardless of the direction (positive or negative) of the response. Of interest was whether relative mobility may influence response to fire history. We were also interested in which species were adversely or positively affected by the two fire predictors and so predictions about the direction of responses of movement groups and species were also evaluated.

4.4 Results

There were 74 diurnal species detected in the study, including 29 sedentary, 36 migratory and nine nomadic species (see Appendix C.1 for species movement group membership). Avian movement groups did not respond clearly to fire frequency, because species responses varied widely in the sedentary (Fig. 4.2a), migratory (Fig. 4.3a) and nomadic (Fig. 4.4a) groups. Species responses to the presence/absence of long unburnt forest in the landscape were also mixed, so there was no response at the group level from sedentary or nomadic birds (Fig. 4.2b, Fig. 4.4b). However, the migratory movement group was more likely to occur where long unburnt forest was present in the surrounding landscape (Fig. 4.3b).

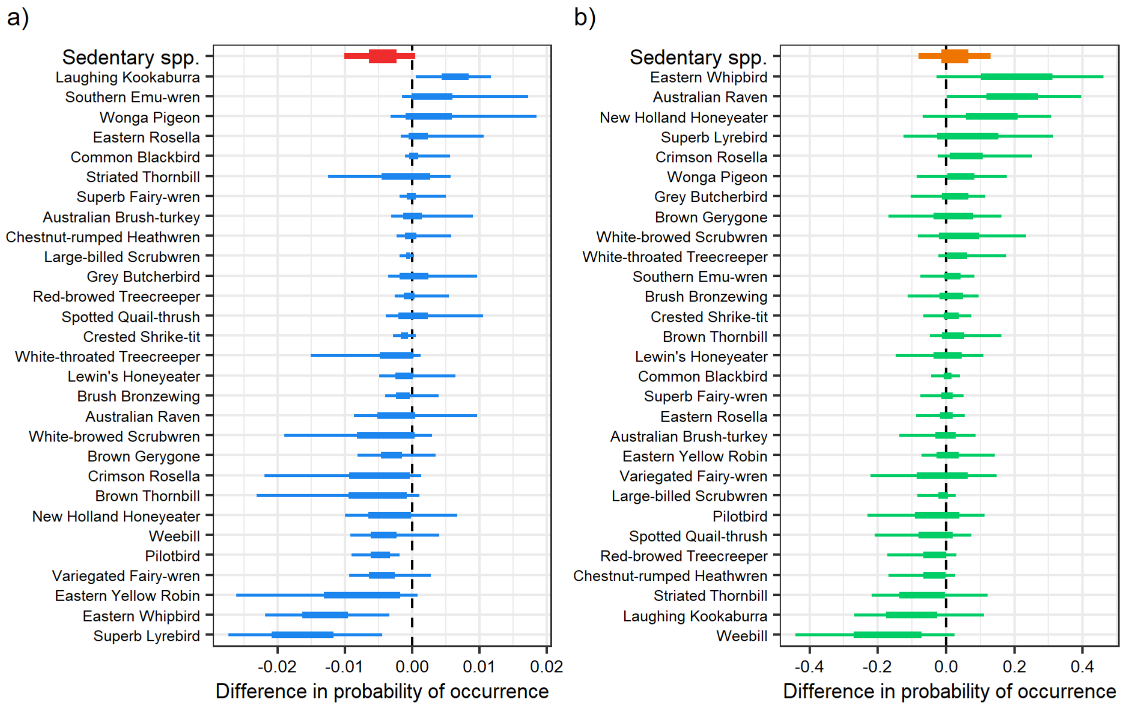

Fig. 4.2. Distributions of the difference in probability of occurrence of sedentary birds at the group and species levels between a) low and high fire frequency, and b) presence and absence of long unburnt forest. Distributions for fire frequency were obtained by subtracting the probability of occurrence at high frequency from the probability at low frequency for 4,000 pairs of model predictions derived from posterior MCMC samples. Distributions for long unburnt forest were similarly acquired (probability of occurrence when present – absent). Bars represent the interquartile range and central 90% of distributions. Responses were considered clear if distributions did not include zero. See Appendix C.1 for species scientific names.

Across the movement groups, 15 species (20% of total) responded either positively or negatively to fire frequency, and/or positively to the presence of long unburnt forest in the landscape (Figs. 4.2-4.4, Appendix C.2). Of the sedentary species detected, five (17%) showed clear responses to either fire frequency or long unburnt forest (Fig. 4.2). A slightly higher proportion (22%) of both migratory species (n = 8, Fig. 4.3) and nomadic species (n = 2, Fig. 4.4) responded to one or both fire predictors. For species that showed clear responses, the differences in probability of occurrence between sites where long unburnt forest was present and where it was absent were much greater than the differences between low and high fire frequency (Figs. 4.2-4.4). On average, the species that did respond to fire frequency, and in particular to the presence of long unburnt forest, had a much larger average body size than the 59 species that did not respond clearly to fire (Table 4.2).

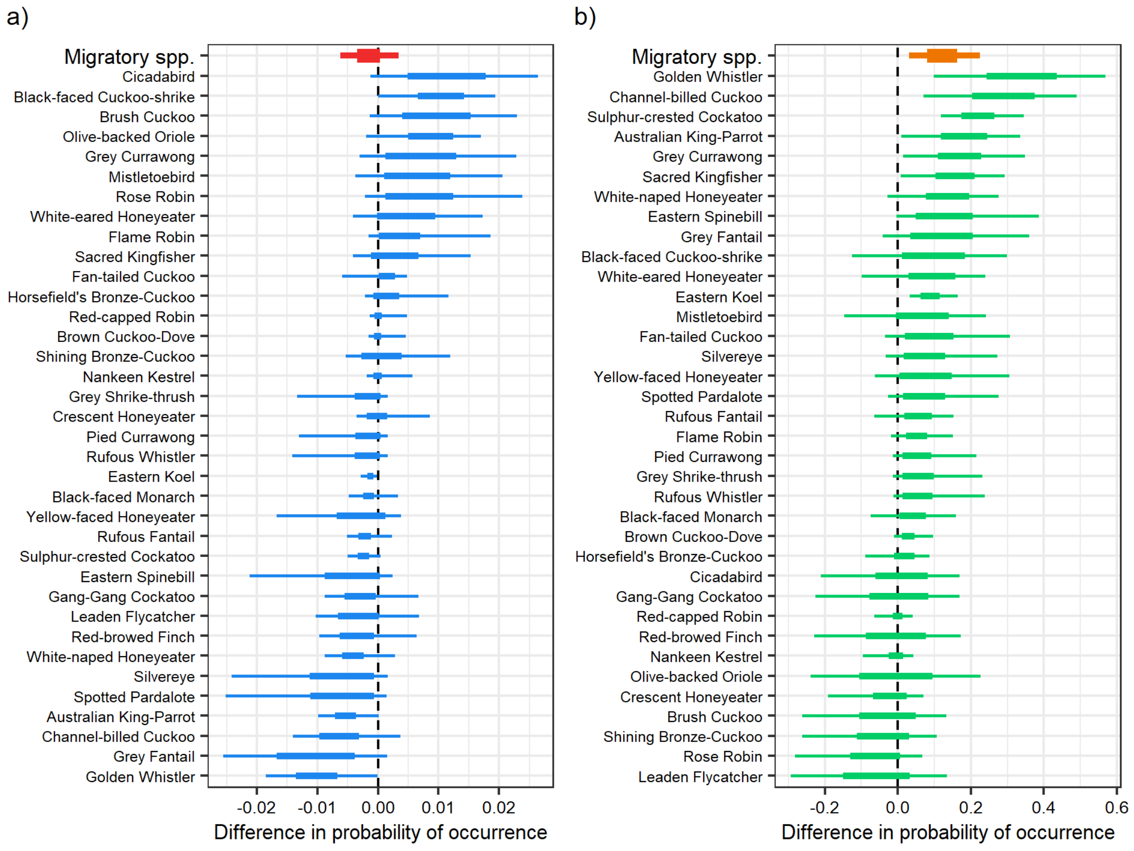

Fig. 4.3. Distributions of the difference in probability of occurrence of migratory birds at the group and species levels between a) low and high fire frequency, and b) presence and absence of long unburnt forest. Distributions for fire frequency were obtained by subtracting the probability of occurrence at high frequency from the probability at low frequency for 4,000 pairs of model predictions derived from posterior MCMC samples. Distributions for long unburnt forest were similarly acquired (probability of occurrence when present – absent). Bars represent the interquartile range and central 90% of distributions. See Appendix C.1 for species scientific names.

There was a clear difference in probability of occurrence between low (burnt once) and high (burnt four times) fire frequency (the distribution of differences in probability of occurrence did not include zero) for several species, but differences were slight. One species from each of the three movement groups; the Laughing Kookaburra *Dacelo novaeguineae* (Fig. 4.2a), Black-faced Cuckoo-shrike *Coracina novaehollandiae* (Fig 3a) and Noisy Friarbird *Philemon corniculatus* (Fig. 4.4a), was more likely to occur where fire frequency was low. In contrast, three sedentary (Eastern Whipbird *Psophodes olivaceus*, Pilotbird *Pycnoptilus floccosus*, Superb

Lyrebird *Menura novaehollandiae*, Fig. 4.2a) and two migratory species (Golden Whistler *Pachycephala pectoralis*, Eastern Koel *Eudynamys orientalis*, Fig. 4.3a) had a higher probability of occurrence in forest patches with high fire frequency. No nomadic species were more likely to occur in frequently burnt forest (Fig. 4.4a).

Of the nine species that had a higher probability of occurrence when long unburnt forest was present in the landscape, seven were migratory (Fig. 4.3b), one was sedentary (Fig. 4.2b) and one nomadic (Fig. 4.4b). No species clearly preferred forest patches lacking long unburnt forest in the landscape. Two migratory species (Golden Whistler, Eastern Koel) responded to both fire predictors; they were more likely to occur where fire frequency was high and long unburnt forest was present in the surrounding landscape (Fig. 4.3).

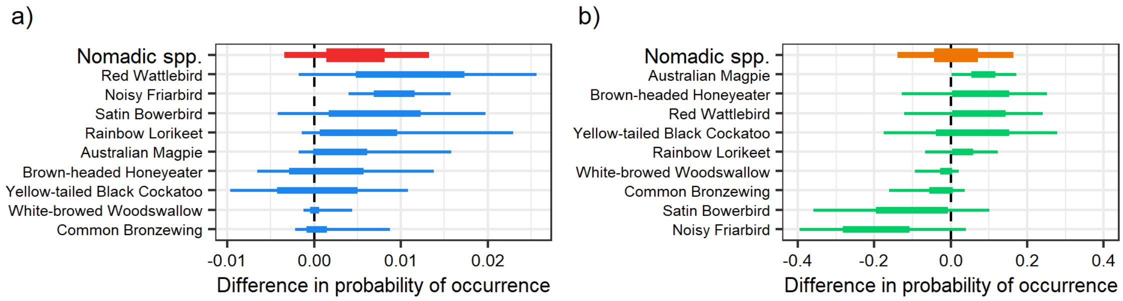

Fig. 4.4. Distributions of the difference in probability of occurrence of nomadic birds at the group and species levels between a) low and high fire frequency, and b) presence and absence of long unburnt forest. Distributions for fire frequency were obtained by subtracting the probability of occurrence at high frequency from the probability at low frequency for 4,000 pairs of model predictions derived from posterior MCMC samples. Distributions for long unburnt forest were similarly acquired (probability of occurrence when present – absent). Bars represent the interquartile range and central 90% of distributions. See Appendix C.1 for species scientific names.

Table 4.2. Summary statistics for average body mass for All species, Fire responders (species that showed clear positive or negative responses to fire frequency and/or long unburnt forest) and Non responders (species that did not clearly respond to either of these predictors). See Appendix C.1 for the average body mass of each species (Garnett et al. 2015).

		Body mass (g)	
	n	Median	Mean (s.e.)
All species	74	34	156 (37)
Fire responders	15	243	328 (81)
Fire frequency	8	108	247 (124)
Long unburnt	9	280	358 (87)
Non responders	59	23	112 (40)

4.5 Discussion

The migratory movement group responded positively to the presence of long unburnt forest in the surrounding landscape. Other group-level responses to fire were unclear, because the responses of individual species were varied within groups. Clear responses to fire frequency and/or long unburnt forest in the landscape were shown by 20% of species recorded in the study. Twice as many migrants and nomads collectively responded to fire compared with sedentary species, consistent with our prediction. Species responded much more strongly to the presence of long unburnt forest than to differences in fire frequency. The 12% of total species that responded positively to the presence of long unburnt forest in the landscape were mostly migrants, consistent with the corresponding group-level result. No species had a higher probability of occurrence when long unburnt forest was absent in the surrounding landscape.

4.5.1 Sedentary species

The probability of occurrence of the sedentary movement group was predicted to be reduced at high fire frequency, but this was not the case. Sedentary species with low mobility may only be capable of dispersing to nearby habitat (Nimmo et al. 2019), which may represent a range of suboptimal, yet tolerable, levels of fire frequency. For example, the mean dispersal distance of the White-throated Treecreeper (*Cormobates leucophaea*) from the natal territory has been measured at 0.55 km (Doerr & Doerr, 2005), and the median natal dispersal distance of the White-browed Scrubwren (*Sericornis frontalis*) was estimated at 1.4 km (Garrard et al. 2012).

Sedentary species are presumably adapted to cope with fluctuations in resources and conditions over time in the one location. This flexibility may have contributed to the lack of clear response at the group level.

Three sedentary ground/understorey species were more likely to occur at high fire frequency. Two of these, the Superb Lyrebird and the smaller Pilotbird, have a commensal foraging association (Smith et al. 2019). Long unburnt habitat is important for the Superb Lyrebird in pyric landscapes (Robinson et al. 2014), but it has also been shown to use areas recently burnt at low intensity, because movement and foraging is presumably easier in the more open understorey/ground habitat (Doty et al. 2015). In the present study, perhaps Lyrebirds were responding to the simplification of habitat structure near the forest floor caused by frequent fire (Woinarski, 1999, Recher, 2004). Only one sedentary species, the hollow-nesting Laughing Kookaburra, that also forages on ground-dwelling prey, showed a clear preference for infrequently burnt forest. This response was perhaps owing to the fact that surveys were conducted in the breeding season, and frequent fire can reduce the density of tree hollows (Haslem et al. 2012, Salmona et al. 2018). Apart from the Pilotbird, the five sedentary species that showed any type of clear response to fire history were all large birds, which may have greater mobility than the smaller species in this group (Schoener, 1968, Paradis et al. 1998).

4.5.2 Migratory species

A reduction in the probability of occurrence of the migratory movement group at high fire frequency was not evident. The migratory species that responded positively or negatively to fire frequency had presumably exercised their ability to locate and move to habitat in the landscape with a preferred fire history. This particularly applies to two of these species, the Golden Whistler and Eastern Koel, because they also had a higher probability of occurrence when long unburnt forest was present in the surrounding landscape. For other migratory species, site-fidelity drives adult birds to reoccupy a forest patch (Schlossberg, 2009), which may be in a suboptimal post-fire state, thereby muting the response of those species to fire.

The migratory movement group showed a clear positive response to the presence of long unburnt forest. This result is consistent with our hypothesis that because of their high mobility, migrants have capacity to locate and use required habitat in fire-prone landscapes. In contrast, only one sedentary species, the large Australian Raven *Corvus coronoides*, was associated with long unburnt forest in the wider landscape. The species from all movement groups that responded positively to long unburnt forest were potentially engaging in landscape complementation (Nimmo et al. 2019), where animals move to access necessary resources that are distributed across different fire histories. For example, both live and dead eucalypts are more likely to contain hollows at longer time since fire (Haslem et al. 2012). This may explain the higher probability of occurrence of the migratory, hollow-nesting Australian King Parrot *Alisterus scapularis*, Sacred Kingfisher *Todiramphus sanctus* and Sulphur-crested Cockatoo *Cacatua galerita* when long unburnt forest was present in the landscape.

Interactions with other species are likely to influence species responses to spatial patterns of fire history. For example, The Golden Whistler and the Rufous Whistler *P. rufiventris* are congeneric partial migrants that responded positively to the presence of long unburnt forest in the landscape, although the response was not clear for the Rufous Whistler. Interspecific competition between these two species may have been responsible for the difference in the magnitude of the response (Watson et al. 2012a; Berry et al. 2015). Furthermore, both the Golden Whistler (Berry et al. 2015, Kelly et al. 2017) and Rufous Whistler (Watson et al. 2012a) have previously been positively associated with habitat at longer time since fire. Nest parasitism is another form of species interaction that could be potentially influenced by the effects of fire regimes, in situations where a brood parasite may follow the habitat preferences of host species. The Eastern Koel and the Channel-billed Cuckoo *Scythrops novaehollandiae* are large frugivorous, brood parasites that responded positively to the presence of long unburnt forest. Both these species parasitise the nests of several species that were also more likely to occur when long unburnt forest was present, such as the nomadic Australian Magpie *Gymnorhina tibicen*.

The mobility engendered by large body size combined with a migratory movement strategy appears to have enabled species with these attributes to use resources in fire-prone forests at wider spatial scales, more so than smaller birds and those with different movement strategies. Avian body size has been shown to be positively correlated with the area of foraging territories during breeding (Schoener, 1968), and greater natal and breeding dispersal distances (Paradis et al. 1998). The species that responded positively to long unburnt forest were on average much larger birds, and were dominated by migratory species. For example, at 388-g, the Grey Currawong *Strepera versicolour* responded positively to the presence of long unburnt forest in the landscape, having previously shown increased probability of occurrence in habitat with longer time since fire (Gosper et al. 2019a).

4.5.3 Nomadic species

Relatively strong responses to fire frequency were expected from nomadic species owing to their capacity to track optimal habitat over wider areas, however there were no clear trends in relation to fire frequency or the presence of long unburnt forest at the group level. The proportion of nomadic species (2/9) that responded clearly to fire was the same as the migratory group. As was the case with the migratory movement group, some species with appreciable niche overlap responded similarly to fire. The Noisy Friarbird and Red Wattlebird *Anthochaera carunculata* are two large nectivores that were more likely to occur at low fire frequency, although the response of the latter, slightly smaller species was not clear. Both these species have the capacity to locate and use rich nectar resources from flowering trees (Ford et al. 1986), which vary spatially and temporally in forested landscapes (Law et al. 2000). The flowering levels of some of the dominant tree species in south-eastern Australian forests have been shown to be reduced under a regime of frequent, low-intensity fire (Law et al. 2000). It is possible that these two honeyeaters were responding to a greater density of nectar resources at low fire frequency in the present study. As with most exclusively sedentary species that responded to fire, the sedentary/nomadic Australian Magpie (Garnett et al. 2015) forages on the ground and was more likely to occur when long unburnt forest was present in the surrounding landscape. Those nomads that did not respond to fire may to some extent be mobilising to use resources at greater spatial scales than that investigated in this study, i.e., responding to resource availability across landscapes rather than within landscapes (as defined in our sampling design).

4.5.4 Future directions

There are several potential explanations for why most movement groups and species did not show clear responses to fire frequency or to the presence of long unburnt forest in the landscape, which in turn imply questions for further research. Some species may not have responded to fire frequency because the resources they require had been replenished when birds were surveyed in forest 16 years after fire. Rare or uncommon species may be influenced by fire frequency or long unburnt forest, but obtaining robust estimates of occurrence for these species is challenging because of limited detections (McGrann & Furnas, 2016). Furthermore, it is uncertain whether the absence of fire responses from many of the smaller species was because fire history was not important, or because they lacked the capacity to locate and move to habitat with optimal fire history. Therefore, further research focused on the individual fire responses of rare and/or small species would be valuable. Other non-responders were perhaps able to preferentially occupy forest habitat with special attributes, that we did not investigate (e.g., gullies, short time since fire). Further work involving site-selection to test such attributes may reduce the uncertainty around movement group and species responses to fire frequency.

4.6 Conclusions

This study has advanced understanding of avian movements in fire-prone landscapes, because we have shown that it is the larger and/or more mobile migratory and nomadic species that have demonstrated capacity to respond to fire regimes. The migratory group preferred long unburnt forest in the landscape. Within groups there were similarities in fire responses among particular species that interact or have overlapping niches. Our results confirm that long unburnt forest in the landscape is important for birds, however the proportion of forest at this successional stage is likely to decline in natural landscapes, as fire frequency increases under climate change.

4.7 Data accessibility

The complete model R code and input data is available online at https://github.com/mfrnkln/birdsfirefrequency1.

4.8 Acknowledgements

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Chapter 5. Forest avifauna exhibit enduring responses to historical high-severity wildfires

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Gospers Mountain area, Wollemi National Park

5.1 Abstract

Forest fire size, frequency and severity are increasing worldwide, with corresponding reductions in long-unburnt habitat and greater modification of forest structure over wider areas. Understanding the implications for animals is imperative in optimizing management for species persistence and overall biodiversity. We investigated how avian responses to historical high-severity fire differ in forests at short (five years) and mid-range (16 years) time since fire, including whether increased time since fire mitigates any negative responses to high-severity fire. Sites were established in fire-prone dry forests of the Greater Blue Mountains World Heritage Area, Australia. A Bayesian latent variable analysis of bird data obtained from acoustic recordings was used to estimate the occurrence of 74 species in relation to time since fire (short, mid-range), the spatial extent of historical high-severity fire (limited, extensive), and their interaction. Time since fire influenced the number of species present, but only where high-severity fire had been extensive. Here, the lowest and highest number of species in the study occurred where time since fire was short and mid-range, respectively. At least 10 species responded either positively or negatively to high-severity fire, but for nine of these species the response did not change with time since fire, potentially implicating persistent effects of such fires on habitat. Six other species were unlikely to occur at short time since fire, requiring habitat at mid-range time since fire. This finding suggests that these species would benefit from strategic retention of forest with longer fire-ages under increased fire activity associated with climate change.

5.2 Introduction

Periodic disturbance from fire is natural in many types of forest, however fire regimes are trending towards increased fire activity at a rate that can challenge the capacity of species to adapt (Whitman et al. 2019). Fires are becoming larger, and the area burnt at high-severity is increasing, owing to climate change in many forested regions of the globe, including diverse systems in Australia (Tran et al. 2020, Collins et al. 2021), Eurasia (Shuman et al. 2017) and North America (Hurteau et al. 2014, Singleton et al. 2019). Larger, more frequent fires will also increase the proportion of habitat with short fire-ages in forested landscapes over time (McCarthy et al. 2001). These changes represent threats to forest birds that require greater species-level understanding, which may be incorporated into fire management that promotes ecosystem diversity and resilience (IUCN 2020). Forest structure is an important component of avian habitat (Robinson & Holmes 1982) that can be substantially and persistently altered by high-severity fire (Kane et al. 2014). Forests regenerate with time since fire, but the extent to which time since fire moderates avian responses to high-severity fire is uncertain, particularly in the context of the temperate forests of the southern hemisphere.

Fire severity refers to the extent to which vegetation is consumed by fire (Keeley 2009). Large wildfires burn through landscapes at different levels of severity because of factors such as variation in topography, vegetation, or changing weather conditions, so fire severity is typically spatially heterogeneous within fire footprints (Bradstock 2008, Clarke et al. 2014). However, homogeneous patches of severely-burnt forest are increasing in area within fire-prone landscapes (Steel et al. 2021). Fire severity is commonly categorised according to the effects of fire on the vertical vegetation strata, for e.g., low-severity fire may only burn vegetation close to the ground, while moderate-severity fire may burn all ground and understorey vegetation (Chafer et al. 2004). Here, we focus on the effects of the highest level of fire severity (henceforth, high-severity fire) on forest biota, where all standing vegetation is fire-damaged, and leaves, branches and stems < 10 mm are incinerated (Chafer et al. 2004, Hammill & Bradstock 2006).

High-severity fire can substantially modify forest structure (Karna et al. 2020), and the effects may persist for decades (Kane et al. 2014, Wardell-Johnson et al. 2017). However, most work on dry sclerophyll forest (Keith & Simpson 2012) has focused on the decade after fire, so the rates of regeneration over the medium/long term are largely unknown. At different times in the decade after high-severity fire in the dry sclerophyll forests of south-eastern Australia, canopy cover (Bassett et al. 2017, Karna et al. 2020), and canopy connectivity and height were reduced (Karna et al. 2020). Similarly, mortality of medium/large trees was greater at higher levels of fire severity (Bennett et al. 2016). Increased fire severity in dry eucalypt forest is associated with inhibited resprouting, but also vigorous regeneration from seed, evidenced as higher densities of seedlings and saplings (Bennett et al. 2016, Bassett et al. 2017).

The changes in forest structure wrought by high-severity fire may increase habitat suitability for some bird species, while diminishing habitat quality for others. For example, insectivorous bird species forage through foliage at different rates and distances, using different manoeuvres; all of which are suited to habitat with particular structural attributes (Robinson & Holmes 1982). Structurally complex forest canopies promote diversity of canopy-dwelling animals because they represent heterogeneous, resource-rich habitats (Ishii et al. 2004). Accordingly, in fire-prone dry sclerophyll forest, avian species richness increased with greater vertical vegetation diversity, based on % cover of discrete levels of forest strata (Sitters et al. 2016). In montane eucalypt forests dominated by obligate-seeding trees, bird species known to prefer open habitat structures were lacking during the early stages of post-fire succession, perhaps because vigorous regrowth of vegetation rapidly reduces open areas after severe fire (Lindenmayer et al. 2014). In these forests, most bird species responded negatively to the extent of severely-burnt forest in the landscape, corresponding with reduced species richness (Lindenmayer et al. 2014). Similarly, fewer species were observed where fire severity had been higher in forests dominated by other species of *Eucalyptus* (Robinson et al. 2014). However, species such as the Flame Robin (*Petroica phoenicea*) may benefit from severely-burnt forest (Robinson et al. 2014, Lindenmayer et al. 2018). A more open habitat caused by severe fire suits a number of bird species occurring in boreal forests (Knaggs et al. 2020), and various North American mixed pine and/or hardwood forests (Greenberg et al. 2013, Brown et al. 2015), contributing to total species richness.

Avian responses to time since fire are associated with the temporal changes in habitat as it regenerates. Bird assemblage composition differed with time since fire in severely-burnt North American mixed-evergreen forests, which was linked to variation in forest structure (Fontaine et al. 2009). Boreal species associated with long unburnt habitat may not use forest recently burnt at high severity, because of the loss of structural complexity (Knaggs et al. 2020). In a range of austral woodland and shrubland communities, it has been established that a substantial amount of habitat with mid-range/long time since fire is essential for the maintenance of particular bird species and overall avian diversity (Taylor et al. 2012, Watson et al. 2012a, Kelly et al. 2015, Davis et al. 2016, Connell et al. 2017, Gosper et al. 2019a). For example, of the 70 bird species detected in semiarid shrubland, 16 widely distributed species responded to time since fire, however, all but one of these were more likely to occur after 20 years since fire in mid-late successional habitat (Watson et al. 2012a). There is evidence that habitat at longer time since fire is important for birds in the temperate eucalypt forests of the southern hemisphere (Robinson et al. 2014, Kelly et al. 2017, Franklin et al. 2021b), but current knowledge needs to be consolidated to further support fire management of these large tracts of forest for biodiversity conservation.

Much of our understanding of the interactive effects of fire severity and subsequent time since fire on birds has been generated from studies conducted in North America. In dry mixed-conifer forest, 60% of species responded positively to fire, but responses were unique and associated with narrow combinations of time since fire and fire severity (Hutto & Patterson 2016). Species richness increased with time since fire in semi-arid conifer forests burnt at high-severity, although the effect was dependent on the proximity to forest burnt at low-severity (Steel et al. 2021). Increasing dissimilarity in avian assemblage composition in montane conifer forests was attributed to differences in the responses of vegetation to a gradient of fire severity up to 10-years following fire (Tingley et al. 2016).

High-severity fire alters structural attributes of forests that are important for birds, such that the habitat differs substantially from forest burnt only at low severity, with effects potentially evident for decades (Fig. 5.1). In the years shortly after fire, regeneration of vegetation and corresponding avian resources may proceed at different rates depending on whether a high-severity fire had occurred at some point in recent fire history, or not (Karna et al. 2020). Habitat differences in the post-fire decade can be expected to result in different patterns of occurrence among bird species, in accordance with their habitat preferences, life history traits and mobility. However, there is considerable uncertainty around the extent to which bird responses persist or change beyond 10 years since fire.

We address this lack of knowledge by asking: does time since fire moderate avian responses to historical high-severity fire in montane forest ecosystems in south-eastern Australia? In this study, we investigated whether the effects of the spatial extent of high-severity fire on birds differ in forests at mid-range (16 years) time since fire, compared with short (five years) time since fire. Where forest has been regenerating for well over a decade, the total resources available to particular species may be sufficient to render the habitat suitable, despite potentially negative responses to the effects of high-severity fire at short time since fire (Fig. 5.1). The occurrence of other species may not change because the effects of high-severity fire on required resources persist.

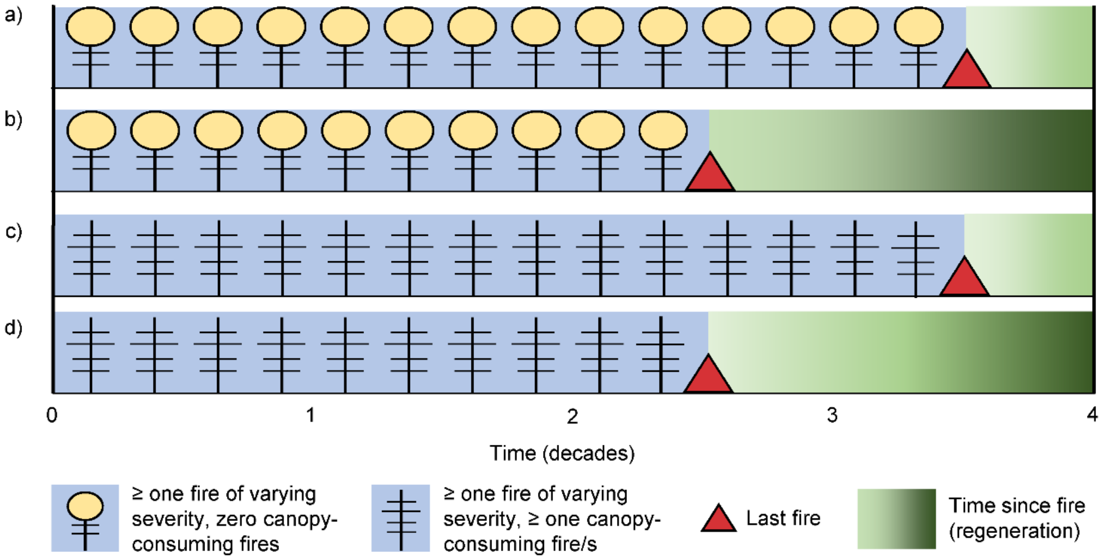

Fig. 5.1. Forest that has not been burnt by a high-severity (canopy-consuming) fire in recent decades (a, b), represents different habitat for birds than if such a fire had occurred (c, d). Resources used by birds may regenerate at different rates depending on the occurrence of high-severity fire, so fire history may be important for particular birds at short time since fire (a, c). However, the importance of historical high-severity fire for birds at mid-range time since fire (b, d) is uncertain.

5.3 Material and methods

5.3.1 Study sites

The study was conducted in montane dry sclerophyll forests of the one million-ha Greater Blue Mountains World Heritage Area, south-eastern Australia. The World Heritage Area is of global conservation significance with a rich diversity of eucalypts, ecological communities and species of plants and animals, including 254 native bird species, of which 34 are listed as threatened (Smith et al. 2019). However, the conservation outlook of the World Heritage Area was recently assessed by the IUCN as being of *significant concern* (Osipova et al. 2020), primarily because of threats represented by increased wildfire activity and other effects of climate change (IUCN 2020). Circular sites (n = 48) with a radius of 325 m were established in dry sclerophyll eucalypt forests, with understories consisting of shrubs from the families *Ericaceae*, *Fabaceae*, *Myrtaceae* and *Proteaceae* (Keith & Simpson 2012). The sites were located on ridges or plateaux at a similar elevation (median 935 m) on the high parts of a remote ~ 80 km section of the Great Dividing Range (Fig. 5.2). Annual mean rainfall varied across the study area, with values up to 1340 mm in southern sites, declining to 825 mm in the north (Xu & Hutchinson

2011). Annual mean temperatures ranged from 11 to 14 °C among the sites (Xu & Hutchinson 2011). This study was part of a wider investigation into the fire ecology of birds in the fire-prone temperate forests of south-eastern Australia, and included 17 sites that had been previously used by Franklin et al. (2021a).

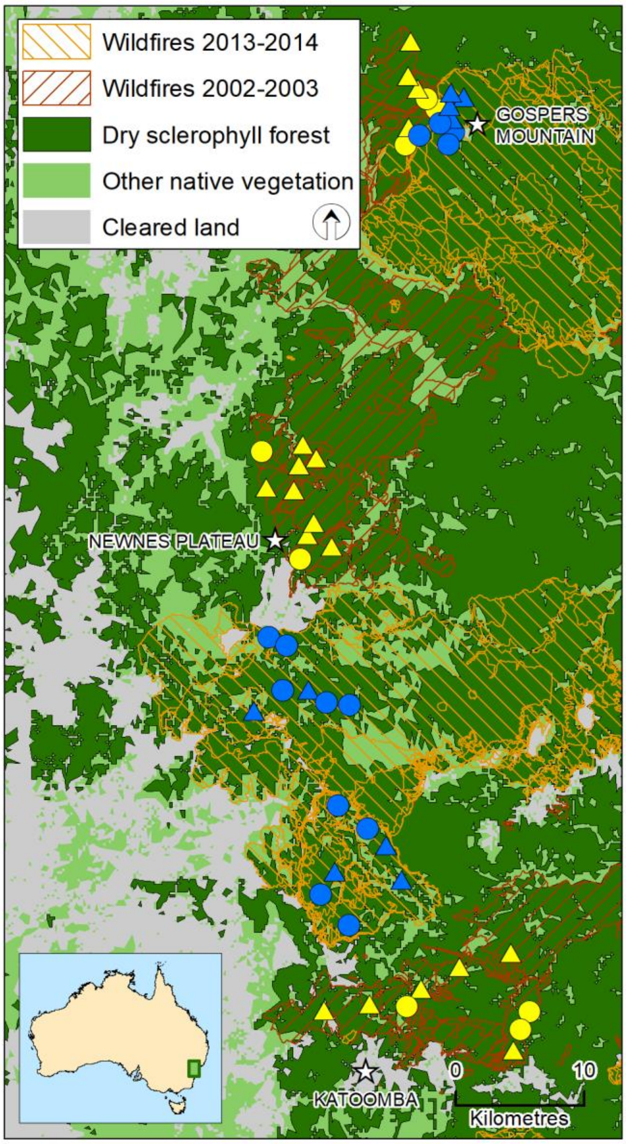

Fig. 5.2. The study was conducted in montane dry eucalypt forests of the Greater Blue Mountains World Heritage Area. The 48 sites were last burnt in either the 2002-2003 (yellow) or 2013-2014 (blue) fire seasons. Shapes indicate whether less than (circles) or more than (triangles) half the 33-ha site had been burnt by at least one high-severity fire since 1982.

5.3.2 Bird surveys

Birds were surveyed using acoustic recorders (Song Meter SM4, Wildlife Acoustics, Massachusetts, United States) that were deployed in sites during the late austral spring/early summer of 2018. The year leading up to bird surveys had been drier and warmer than average across New South Wales (Bureau of Meteorology 2021). Recorders were configured to record for 100-min immediately following dawn, then affixed to a small tree at 2-m above the ground at the centre of the site. Site centres were at least 1-km apart. Devices were left to passively record until at least two days without rain or appreciable wind had passed, and then collected for redeployment (Franklin et al. 2020). Recordings were checked for weather effects on retrieval of devices and sites re-sampled if there was insufficient effect-free data. A set of eight recorders was circulated around the 48 sites until sampling was complete. Recorder microphones were checked at the start and conclusion of the survey period to ensure that their sensitivity was within the range specified by the manufacturer for new devices (Turgeon et al. 2017). Desktop processing of the recorded acoustic data (.wav files) was conducted by the first author and involved identifying species by listening to their calls and/or viewing calls represented in a spectrogram (Kaleidoscope Pro, Wildlife Acoustics). To ensure accurate identification of species, the quality control process of Franklin et al. (2020) was implemented. This included the use of reference calls and consultation with other experts for verification of species responsible for uncertain calls (see acknowledgments). A total of 9600-min of recordings were used in the study. Surveys of each of the 48 sites used 200-min of recordings, consisting of 100-min commencing at dawn on each of two clear-weather days (Franklin et al. 2020, Franklin et al. 2021a). In accordance with this method, species were recorded as detected in 20-min subsamples during manual processing. The data were then aggregated across subsamples and days to species detection/non-detection (1/0) in each site (Sitters et al. 2016), with nocturnal species excluded from the final dataset.

5.3.3 Fire history variables

Fire history predictor variables were measured in circular sites with a radius of 325 m (~ 33 ha). This radius was selected so that the wider use of the habitat by relatively mobile species was still associated with the defined fire history of the site, and most recorded calls were likely to have been made by birds within the site (Franklin et al. 2021b). Sites larger than this would not have met our design criteria for montane dry sclerophyll forest, owing to the existing pattern of fire histories in the study landscapes.

We expanded upon the work of Lindenmayer et al. (2014), who used the proportion of high-severity fire in 500-m and 1-km radius circles as predictors, by accounting for the contributions of a chronological series of fires to historical high-severity fire over each site. Initially, we obtained spatial fire severity layers that had been derived by Hammill et al. (2010) and Hammill Stone (2014) from 30-m Landsat imagery as before/after NDVI (Normalised Difference Vegetation Index) ratios, although some were based on SPOT (20 m) imagery, and some used Normalised Burn Ratio. The processing methodology used for each fire was governed by the availability and quality of satellite data at the required times. While the results generated by these methods are broadly similar across landscapes, they can differ in particular contexts (Hammill & Bradstock 2006, Chafer 2008). However, the severity mapping was underpinned by a study that validated severity classes derived from both Landsat and SPOT imagery against field measurements and interpretation of aerial photography (Hammill & Bradstock 2006).

The number of high-severity fires was counted at the 20-m grid cell level over each site using the Hammill et al. (2010) and Hammill Stone (2014) layers for major wildfire years in recent decades: 1982, 1993, 1997, 2001, 2002, 2006 and 2013. The counts of high-severity fires were then summarised for each site by establishing the proportions of the site associated with each count value. We refined this further for analysis and interpretability, producing a binary variable (SEV) where 0 indicated that less than or equal to 50% of the site had been burnt by one or more historical high-severity fires, and 1 indicated that more than 50% of the site had been burnt by such fires. The break point was set at 50% to optimise the numerical and spatial balance among replicates for the study, and also coincided with natural gaps in the data along the continuous scale under each level of time since fire. The category with value 1 was comprised of 24 sites mostly burnt by one historical high-severity fire and three sites burnt by two such fires over most of their area. Given required site attributes in terms of elevation, topographic position, time since fire and accessibility, the availability of suitably large areas of dry sclerophyll forest that had been burnt by more than one high-severity fire was limited.

Time since fire (TSF) was constant across each site and expressed as a binary (0/1) variable, where 0 indicated mid-range (16 years) and 1 indicated short (five years) time since fire. Thus, there were four combinations of time since fire (mid-range, short) and the spatial extent of historical high-severity fire (limited, extensive) represented across the study area (Fig. 5.2, Table 5.1). In general, greater complexity in forest structure was observed once time since fire had passed into the mid-range (Fig. 5.3). Time since fire was calculated in relation to 2018, the year in which bird surveys were conducted, using the NSW Fire History spatial data set (Office of Environment & Heritage NSW 2017). This spatial data set was also used to count the number of wildfires and prescribed fires that burnt all or part of each site since 1982. This enabled an assessment of whether the number of fires had potential to confound either time since fire or the extent of historical high-severity fire. The number of fires was not related to the cumulative proportion of high-severity fire, but there were higher numbers of fires where time since fire was short. To account for this effect, a covariate for the area-weighted mean number of fires over each site (MFC) was included in statistical models.

Table 5.1. The number of sites in each fire history category.

Historical high-severity fire (% cover)	Time since fire 5 years	16 years	Total
< 50	13	8	21
> 50	9	18	27
Total	22	26	48

Fig. 5.3. Dry sclerophyll forest habitat at five (a, b) and 16 years (c, d) since fire. These locations were within 33 ha sites that had been burnt by extensive (a, c) or limited (b, d) high-severity fire in recent decades.

5.3.4 Data analysis

To investigate the responses of birds to time since fire and the extent of historical high-severity fire, we fitted a Bayesian latent variable model (Equation 5.1) using the boral package (Hui 2016) in R (R Core Team 2021). A boral model with predictor variables fits separate generalised linear models to each species, with correlation among species induced with the addition of latent variables, thus allowing for interactions among species, such as competition and predation (Warton et al. 2015). In this context, latent variables act as random effects and can be considered as representing unmeasured predictor variables. Records of species detections in subsamples were aggregated at the site level to produce a response dataset that had the form of species (n = 74) detection/non-detection (1/0) in each site (Sitters et al. 2016). The occurrence of species i in site j (μ_{ij}) was modelled as:

$$\text{probit}(\mu_{ij}) = \alpha_j + \beta_{0i} + \beta_{1i}\text{LAT}_j + \beta_{2i}\text{MFC}_j + \beta_{3i}\text{TSF}_j + \beta_{4i}\text{SEV}_j + \beta_{5i}\text{INT}_j + z_j^{\text{T}}\theta_i \quad \text{Equation 5.1}$$

where α_j is a random effect for site j and β_{0i} is a species-specific intercept. An unconstrained ordination generated from a preliminary model that included two latent variables, but no predictor variables (Hui 2016), revealed that avian assemblages were structured according to latitude (Appendix D.1), corresponding to the spatial distribution of sites (Fig. 5.2). Consequently, we accounted for the effect of latitude by including it as a standardised covariate (LAT). A standardised covariate for the mean number of fires that burnt each site (MFC) was also included, along with fire predictors TSF, SEV, and their interaction (INT). Finally, z_j is a vector of two latent variables for $j = 1, \ldots, 48$ sites, and θ_i represents a vector of coefficients that relate species ($i = 1, \ldots, p$) responses to the latent variables (Hui 2016).

Normal priors with zero mean and a variance of 1 were used for the predictors and latent variables, with a half-Cauchy (1) prior for standard deviation parameters (McElreath 2016). The boral default MCMC settings were used, that is, a single chain was run with a thinning rate of 30 applied to 30,000 iterations, having discarded the initial 10,000 samples (Westgate et al. 2021). The responses of all species to the four fire history combinations are presented in graphical form in the Results section, or in Appendix D.3. Positive or negative species responses to the main effects of fire predictors or their interaction are presented in the Results section if the 90% highest posterior density interval for the relevant model coefficient did not cross zero (Westgate et al. 2021).

To determine the influence of time since fire, extent of historical high-severity fire, and their interaction on the number of species present, we used a Bayesian generalised linear model (Equation 5.2). A generalised-Poisson distribution with a log link function were implemented to account for the under-dispersed nature of the species count data (Hilbe et al. 2017). The model was fitted using JAGS 4.3.0 (Plummer 2003), through the runjags package (Denwood 2016) in R (R Core Team 2021). The number of species i present in site j was modelled as a function of an intercept, covariates for latitude and mean number of fires, and the fire predictors of interest:

$$\log(y_{ij}) = \beta_0 + \beta_{1i}\text{LAT}_j + \beta_{2i}\text{MFC}_j + \beta_{3i}\text{TSF}_j + \beta_{4i}\text{SEV}_j + \beta_{5i}\text{INT}_j \quad \text{Equation 5.2}$$

Normal priors with zero mean and a variance of 10 were set for regression coefficients, with a uniform (-1, 1) prior for the delta parameter of the generalised Poisson distribution (Hilbe et al. 2017). Four MCMC chains were run to obtain 8,000 samples (2,000 per chain), after having been thinned at a rate of 10, and the initial 4,000 discarded. The model converged satisfactorily, as indicated by the Gelman-Rubin statistic (Gelman & Rubin 1992) and number of effective samples for parameters.

Species detectability among fire history combinations

To evaluate the potential for bird detectability to systematically vary among the four fire history combinations because of differences in the effects of fire on habitat, a multispecies occupancy model was used to estimate the probability of detection of species (Appendix D.2). In the results, no systematic patterns were evident that could be explained by increased attenuation of bird calls where vegetation may have been denser at mid-range time since fire and/or where high-severity fire had been limited in extent (Fig. B.1). There were differences in detectability among fire history combinations for some species, but uncertainty around the estimates was typically high. Several species with loud, conspicuous calls appeared to be less detectable where time since fire was short and/or where historical high-severity fire had been extensive. It is unlikely that the calls of these species would not be recorded if they were present and calling. Variation in species calling rates in habitat with different fire histories has the potential to influence detectability, although our current understanding is very limited (but see Mathers-Winn et al. 2018). Because of the risk of introducing bias to inferences owing to uncertainty around model assumptions, we elected to not account for detectability in latent variable or generalised-Poisson modelling (Welsh et al. 2013). In addition, doing so would have increased model complexity, thereby increasing the risk of overfitting. Moreover, the acoustic survey method we used has been thoroughly tested and was shown to substantially outperform an established observer-based method in its capacity to detect many of the species recorded in the present study, in the same forest type at mid-range time since fire (Franklin et al. 2020, Franklin et al. 2021a).

5.4 Results

A total of 74 species were detected in the study, including four species that were recorded in all 48 sites (Appendix D.4). The number of species recorded in each site ranged between 16 and 39 (Fig. 5.4). Where less than half the 33-ha site had been burnt by historical high-severity fire, no difference between the number of species at short and mid-range time since fire was detected (Fig. 5.4). However, where most of the site had been burnt at least once at high-severity in recent decades, a mean of three additional species were predicted at mid-range time since fire than at short time since fire. This particular combination of the two fire variables resulted in the highest predicted number of species (n = 30).

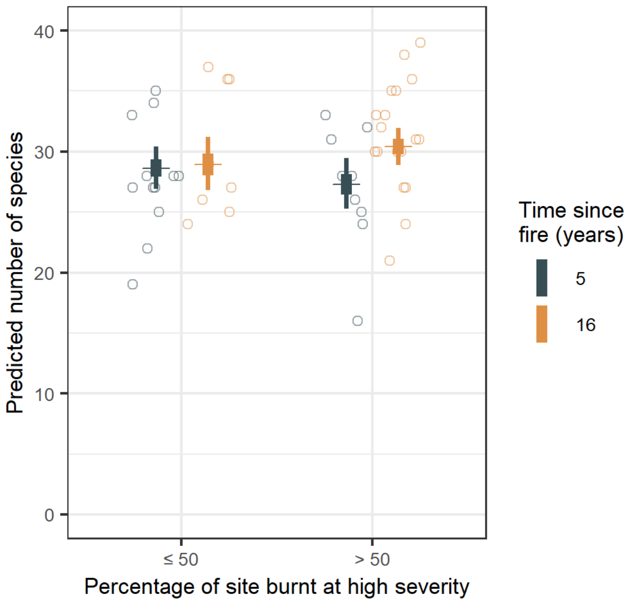

Fig. 5.4. The number of species recorded (horizontally offset open circles) and predicted to occur under combinations of time since fire and the spatial extent of historical high-severity fire. Vertical bars around medians (horizontal bars) represent the interquartile range and central 90% of distributions of Bayesian generalised-Poisson model predictions.

We detected 42 partial/total migrants (Garnett et al. 2015) in our late spring/early summer surveys, that were timed to include migratory species that move into montane parts of the region in early spring to breed (Smith et al. 2019). Substantially positive or negative responses to fire (90% highest posterior density interval for the relevant model coefficient did not cross zero) were detected for 23% (n = 17) of total species. Of these, 10 were migrants, which may have greater capacity than sedentary species to locate and access preferred fire-affected habitat in landscapes because of their relative mobility (Franklin et al. 2021b). Effect sizes varied widely among the responses of species to fire, ranging from small to large, but for 10 species, the probability of occurrence was reduced to ~ zero at short time since fire and/or where high-severity fire had been extensive (Figs. 4-6).

Two species responded to both time since fire and the extent of historical high-severity fire (Fig. 5.5). However, only the Variegated Fairy-wren (*Malurus lamberti*) responded to the interaction between these variables, being unlikely to occur where both time since fire was short and most of the site had been burnt by historical high-severity fire. The Rose Robin (*Petroica rosea*) responded negatively to increased levels of historical high-severity fire, and was more likely to occur where time since fire was short (Fig. 5.5).

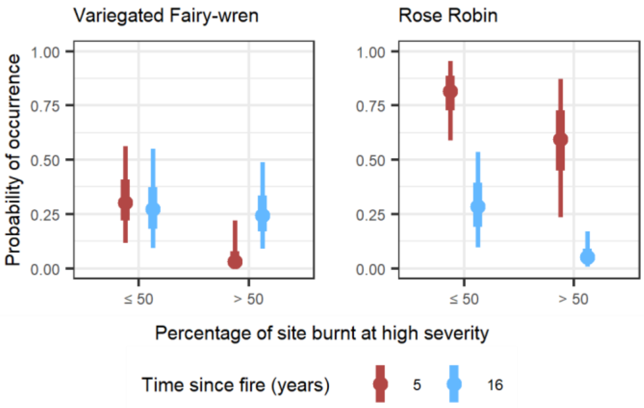

Fig. 5.5. The probability of occurrence of species that responded to both time since fire and the spatial extent of historical high-severity fire. The Variegated Fairy-wren was the only species that responded to the interaction between time since fire and high-severity fire. The Rose Robin responded to the main effects of both fire variables. Vertical bars around medians (circles) represent the interquartile range and central 90% of distributions of Bayesian latent variable model predictions. See Appendix D.4 for species scientific names.

Eight species were influenced exclusively by high-severity fire extent (Fig. 5.6), with both positive and negative responses recorded. Differences between habitat at five and 16 years since fire did not have an important bearing on the occurrence of these eight species. The Sulphur-crested Cockatoo (*Cacatua galerita*), Rufous Fantail (*Rhipidura rufifrons*) and Red-browed Treecreeper (*Climacteris erythrops*) were more likely to occur where historical high-severity fire had been limited in extent. In contrast, five species had a higher probability of occurrence where most of the site had been burnt at high severity in recent decades (Fig. 5.6).

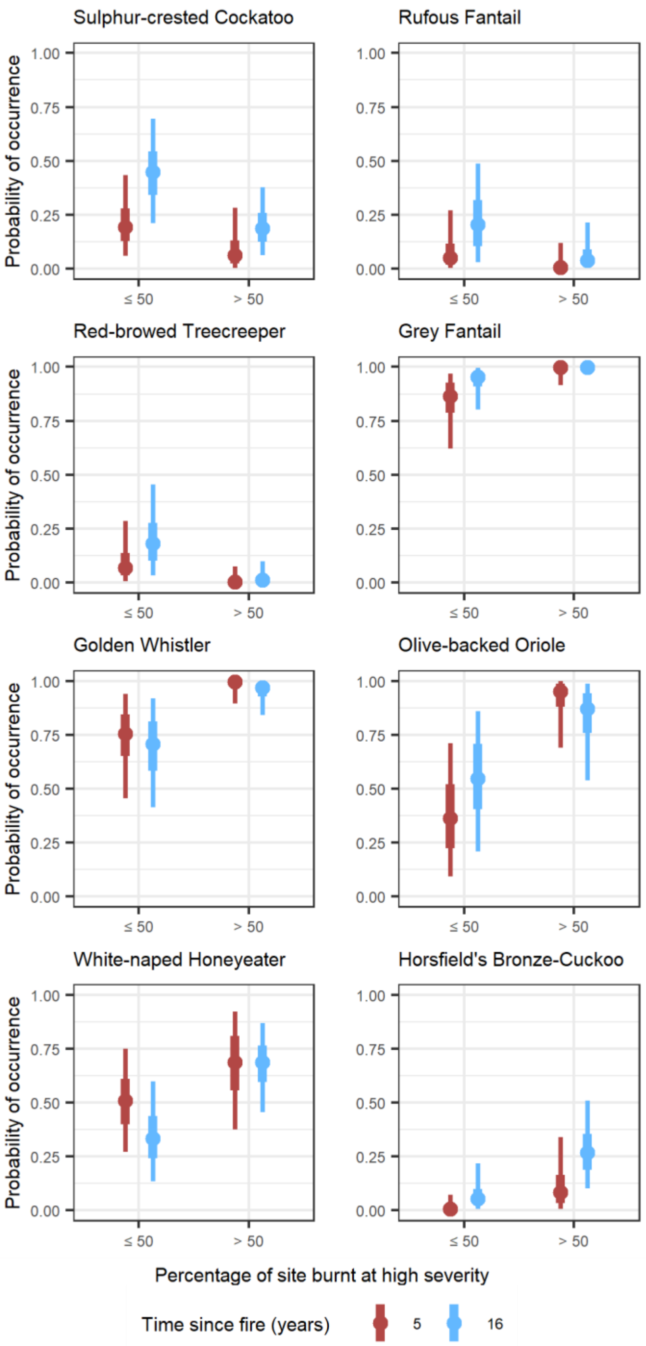

Fig. 5.6. The probability of occurrence of species that responded exclusively to the spatial extent of historical high-severity fire. Vertical bars around medians (circles) represent the interquartile range and central 90% of distributions of Bayesian latent variable model predictions. See Appendix D.4 for species scientific names.

Nine species in total responded to differences between forest at five and 16 years since fire. Of these, two species were already mentioned because they also responded to high-severity fire (Fig. 5.5), and seven responded exclusively to time since fire (Fig. 5.7). The Laughing

Kookaburra (*Dacelo novaeguineae*) was the only species of the latter group that was more likely to occur at short time since fire. The Eastern Whipbird (*Psophodes olivaceus*), Pilotbird (*Pycnoptilus floccosus*), Grey Currawong (*Strepera versicolor*), Lewin's Honeyeater (*Meliphaga lewinii*), Eastern Koel (*Eudynamys orientalis*) and Spotted Quail-thrush (*Cinclosoma punctatum*) were unlikely to occur at short time since fire (Fig. 5.7).

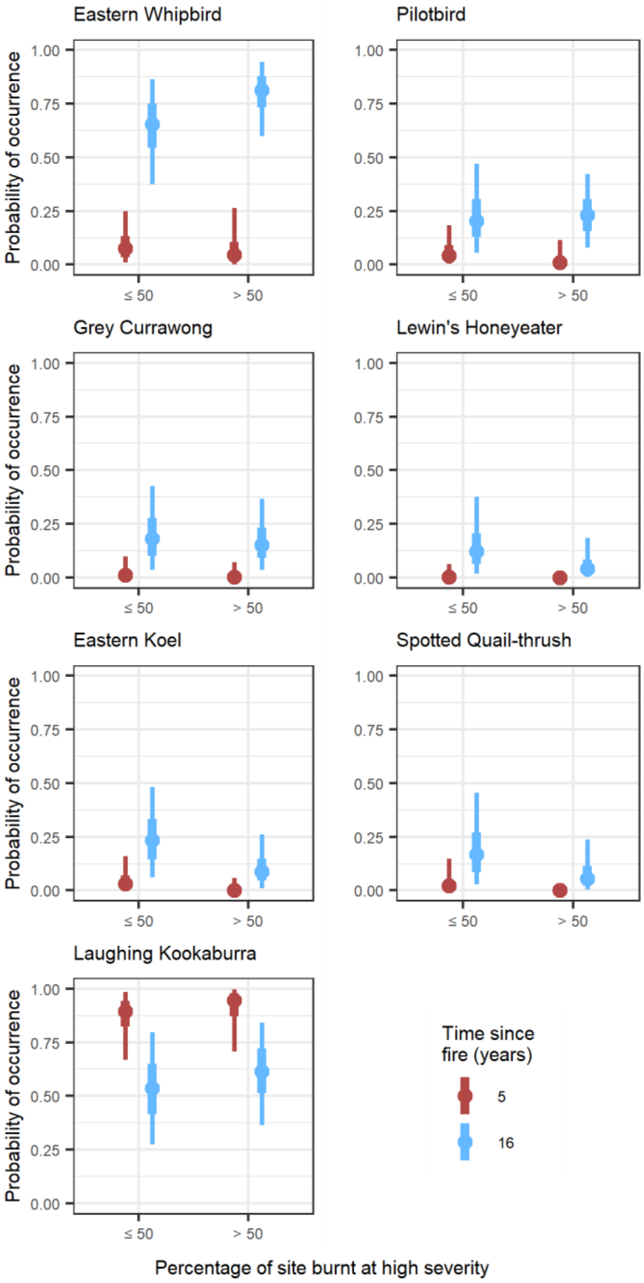

Fig. 5.7. The probability of occurrence of species that responded exclusively to the effect of time since fire. Vertical bars around medians (circles) represent the interquartile range and

central 90% of distributions of Bayesian latent variable model predictions. See Appendix D.4 for species scientific names.

5.5 Discussion

Time since fire moderated the effects of the extent of historical high-severity fire on the number of bird species present in montane, dry sclerophyll forests of south-eastern Australia. The highest number of species were present where high-severity fire had been extensive and time since fire had advanced into the mid-range. Time since fire did not moderate the responses of individual species to historical high-severity fire, with one exception. Structural attributes of forest, such as canopy height, can remain diminished for several years following high-severity fire (Karna et al. 2020). The effects of such fires on forest habitat may persist well into the second decade following fire, because a balanced mix of positive and negative responses to high-severity fire among species were unaffected by time since fire. Historical high-severity fire, however, was not important for another group of species that were more likely to occur where time since fire was in the mid-range, compared to where it was short. Thus, avian responses to historical high-severity fire are complex, potentially reflecting divergent responses of key elements of habitat, their sensitivity to fire severity and their resilience.

5.5.1 High-severity fire and forest structure

The effects of the extent of historical high-severity fire on tree structure may have directly influenced the occurrence of species that either inhabit the mid-strata/canopy, or use all strata. Tree density and canopy cover are reduced by high-severity fire (Bennett et al. 2016, Karna et al. 2020), which diminishes habitat utility for species that require higher levels of these attributes. The Rufous Fantail is one such species (Cameron 1985), which is perhaps why it was less likely to occur where high-severity fire had been extensive. Furthermore, this species was more likely to be detected where high-severity fire had been extensive and time since fire was short, so the negative response to extensive historical high-severity fire shown by this species may be stronger. The migratory Rose Robin forages mostly in the canopy, and was more likely to occur where historical high-severity fire had been limited, in accordance with its preference for forest with greater canopy cover and larger trees (Kelly et al. 2017). In contrast, the relatively open canopy structure following high-severity fire (Karna et al. 2020) may have contributed to the higher probability of occurrence of species such as Horsfield’s Bronze Cuckoo (*Chalcites basalis*) and the widely-distributed Grey Fantail (*Rhipidura albiscapa*). The

Grey Fantail occupies a broader niche in terms of vegetation density and cover than the congeneric Rufous Fantail, but prefers comparatively open structure (Cameron 1985), which presumably suits its aerial foraging behaviours. Grey Fantails were a little more likely to be detected where high-severity fire had been extensive and time since fire was short, so their preference for this habitat may be slightly weaker than shown.

5.5.2 Habitat regeneration over time since fire

Species with requirements for habitat at longer time since fire can comprise substantial proportions of avian assemblages in varied global forests. For example, in a range of different North American forests, 25% of bird species were present in peak densities towards the end of a 15-year post-fire period (Taillie et al. 2018). We found that both the lowest (short time since fire) and highest (mid-range time since fire) number of species in the study were likely to occur where historical high-severity fire had been extensive. Similarly, over eight years in tall eucalypt forests at higher latitudes, the greatest rate of increase in numbers of species among disturbance treatments occurred from initially low numbers where forest canopies had been consumed (Lindenmayer et al. 2018). In the present study, all but one species that responded exclusively to time since fire were more likely to occur where it was relatively long (Fig. 5.7). Furthermore, their probability of occurrence was reduced to ~ zero where time since fire was short, emphasizing the particular importance of habitat at longer time since fire for these species.

The availability of resources used by birds is influenced by fire history, which affects patterns of species occurrence in fire-prone landscapes (Gosper et al. 2019a). The Grey Currawong and Lewin’s Honeyeater responded positively to the main effect of time since fire and consume seed and/or fruit (Garnett et al. 2015), which are often present at higher levels beyond short time since fire (Green 2013, Valentine et al. 2014). Furthermore, species that consume some fruit are positively associated with increased canopy cover (Sitters et al. 2016), which generally increases as time since fire passes (Catling et al. 2001). The Grey Currawong was also less likely to occur at short time since fire in woodland (Gosper et al. 2019a), consistent with the importance of longer time since fire for this species at the forest patch (present study) and landscape (Franklin et al. 2021b) scales. Higher densities of invertebrate prey are associated with abundant young eucalypt foliage at shorter time since fire (Recher 1985), and possibly also where there are greater densities of saplings resulting from extensive high-severity fire (Heatwole et al. 1999, Bassett et al. 2017). The insectivorous Rose Robin, Grey Fantail and

Golden Whistler (*Pachycephala pectoralis*) may have been responding positively to greater food availability in these habitats. The Eastern Whipbird and Pilotbird forage in dense shrubby understories, and were unlikely to occur at short time since fire, potentially because of insufficient regeneration of this forest strata. There were weak if any differences in detection probability among fire histories for the Rose Robin, Horsfield's Bronze Cuckoo, Grey Currawong and Lewin's Honeyeater. Several species with conspicuous calls, such as the Eastern Whipbird, were less likely to be detected at short time since fire. These species may have been foraging both within and beyond the effective detection range of the recorder during the sampling period, to obtain resources that may have been less dense in these habitats. If this was the case, then the assumption of a closed population during the period of sampling that is required for estimation of detection probability in multispecies occupancy modelling (Iknayan et al. 2014) would not have held. Variation in bird foraging patterns in relation to fire history would be a worthwhile area for further research.

5.5.3 Implications of changing fire regimes

Responses to high-severity fire differ among species in assemblages of forest birds around the world (Hutto & Patterson 2016, Knaggs et al. 2020). Heterogeneous burn severities within the extent of fires in North American conifer forest may be required for the maintenance of avian diversity (Tingley et al. 2016). In the present study, the highest number of species present was in forest at longer time since fire, where historical high-severity fire had been extensive. Because we included the contributions of multiple fires with unique spatial patterns of fire severity to the extent of historical high-severity fire, habitats in sites with extensive high-severity fire may have been more heterogeneous, with a greater variety of niches for birds. However, the temporal and spatial aspects of fire regimes are shifting towards greater fire activity under climate change, including increases in the extent of high-severity fire (Steel et al. 2021, Collins et al. 2021). These trends have important implications for forest avifauna that would find such fire-affected habitats unsuitable. Ten of the 74 total species responded negatively to high-severity fire and/or time since fire at levels representative of future fire regimes. The negative responses of three species to extensive historical high-severity fire persisted into mid-range time since fire, so their habitat was presumably in a less-suitable state for well over a decade following fire. A sustained temporal reduction in habitat quality could interact with the trend of increasing amounts of area burnt at high-severity, to further reduce the availability of suitable habitat in landscapes for affected birds. In contrast, the five species that were more likely to occur where historical high-severity fire had been extensive may benefit from future increases in fire activity, at least where wildfire severity is spatially heterogeneous, and habitats with different fire-ages are available in landscapes. Habitat at longer time since fire was important for seven species, which is broadly consistent with the findings of other studies conducted in temperate eucalypt forests (Robinson et al. 2014, Kelly et al. 2017, Franklin et al. 2021b).

5.6 Conclusion

The extent of historical high-severity fire had the same influence at short and mid-range time since fire for nine out of 10 species that responded either positively or negatively to high-severity fire. Understanding of the longer-term pattern of dry eucalypt forest regeneration following high-severity fire is incomplete, but the enduring responses of these birds at 16 years since the last fire suggests that some effects on forest structure persist. Ongoing increases in the extent of high-severity fire have the potential to diminish structural aspects of affected forests at large spatial scales (Karna et al. 2020), thus influencing the wider occurrence of sensitive bird species. This study reinforces the importance of retaining suitably distributed areas of forest with longer fire-ages in fire-prone landscapes, because seven of the nine species that responded to time since fire were unlikely to occur where it was short.

5.7 Data accessibility

The R code for statistical models and input data is available online at https://github.com/mfrnkln/birdsfireseverity1.

5.8 Acknowledgements

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Chapter 6. Canopy structure mediates the effects of time since fire on arboreal birds

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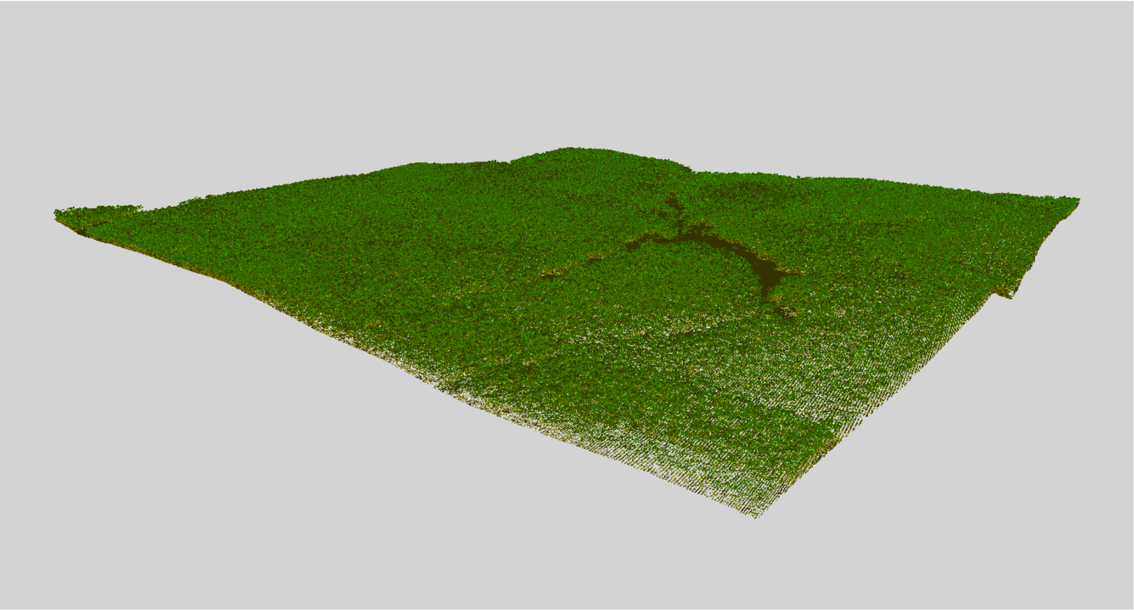

Light Detection and Ranging (LiDAR) point cloud, 2 × 2-km tile, Newnes Plateau

6.1 Abstract

Wildfires alter forest structure which then regenerates over time, with corresponding direct and indirect effects on animals. Because wildfire activity is increasing globally under climate change, proportions of regional forests with short fire-ages and diminished structure will continue to increase. This study investigated the importance of post-fire changes in canopy structure for birds. We aimed to determine the extent to which canopy structure mediates the effects of time since fire on the richness and occurrence of canopy bird species. Sites at either short (5 years) or mid-range (16 years) time since fire were established in montane dry sclerophyll forests of south-eastern Australia. Canopy cover estimates were derived from airborne LiDAR data. Birds were surveyed using acoustic recorders, with the resulting data analysed using Bayesian mediation models to partition direct (mortality, emigration) and indirect (canopy structure) effects of time since fire on canopy birds. The predictive accuracy of models representing partial mediation (direct and indirect effects) and complete mediation (indirect effects only) were then compared. The direct effects of wildfire on birds were minimal between five and 16 years since fire. Instead, indirect effects prevailed, with species richness and the occurrence of most canopy species increasing as canopy structure regenerated over time since fire. As these forests transition from short to mid-range time since fire, ongoing increases in canopy structure are of primary importance for birds. A management approach that incorporates canopy structure in fire planning to optimise the retention of dwindling amounts of older forest for avian diversity is recommended.

6.2 Introduction

Time since fire has long been used effectively in fire ecology research (e.g., Specht et al. 1958), as a simple and convenient predictor for a range of ecological processes that occur and interact at variable rates post-fire (Swan et al. 2015, Hradsky et al. 2017). Animal responses to time since fire can vary between habitats (Watson et al. 2012a, Rainsford et al. 2021), over environmental gradients (Kelly et al. 2017), and depending on the state of fire-affected landscapes (Nimmo et al. 2019). Consequently, there is strong potential to increase understanding of animal responses to fire by isolating and separately examining processes that affect animals and their habitat. For example, changes in animal occupancy and diversity over time since fire can be attributed to variable rates of regeneration of vegetation, and/or population recovery (Whelan et al. 2002). To better support management for avian diversity in fire-prone forests, the different effects of time since fire must be disentangled to enable the specific driver/s of avian responses to be identified. The need for such insights is heightened because of increasing wildfire activity in global forested landscapes under climate change (Singleton et al. 2019, Fairman et al. 2016).

Wildfires affect animals directly through mortality and by triggering emigration, and indirectly through loss of vegetation structure and associated resources (Whelan et al. 2002). Both types of effect continue to exert influence on birds over variable periods of time after fire, depending on context. Very little quantitative information is available about the extent to which vertebrates are killed directly by wildfires, although proportions may be small where fire severity is low, with more killed where fires are severe (Jolly et al. 2022). Post-fire recovery of species populations depends on breeding success and/or immigration (Lindenmayer et al 2016). Diminished post-fire bird populations may be subject to reduced genetic diversity and inbreeding, that potentially contribute to declines in population viability (Brown et al. 2013). The duration of direct effects is also influenced by the extent to which the burnt landscape matrix is conducive to animal movements that enable recolonisation (Nimmo et al. 2019). For example, it can take longer for bird species to reoccupy large areas that were homogeneously burnt at high-severity (Steel et al. 2021), partly because immigration may be delayed if source habitats are distant (Watson et al. 2012b). Structural attributes of forests regenerate over time since fire (Haslem et al. 2016) and particular bird species respond to the indirect effects of time since fire on habitat structure (Sitters et al. 2014b, Kelly et al. 2017). Vegetation structure is associated with a range of resources used by birds, including food (Law & Chidel 2008), nest hollows (Salmona et al. 2018), and cover for protection from predators (Doherty et al. 2022).

The structure of resprouting eucalypt forest canopies regenerate over decadal scales following wildfire (Catling et al. 2001, Haslem et al. 2016, Price & Gordon 2016), although the post-fire rate of increase in canopy structure is spatially variable, because environmental factors, such as topography, influence regeneration (Jucker at al. 2018). Habitat structure variables are thus often better predictors than time since fire in models of avian (Sitters et al. 2014b) and mammal (Swan et al. 2015) occurrence. Complex canopy structures contribute to increased diversity of canopy animals, because of the greater variety and extent of niche spaces (Ishii et al. 2004). Bird species with frugivorous or generalist foraging traits have been shown to respond positively at the functional group level to canopy cover in dry eucalypt forest (Sitters et al. 2016). Species-level responses to canopy structure have also been recorded (Barton et al. 2014), which can vary widely within bird assemblages according to the particular requirements of constituent species (Knaggs et al. 2020). Avian assemblage composition varied over 30 years following fire in boreal forest, reflecting changes in the occurrence of species with requirements for suitable levels of habitat structure that were only available for particular periods in the regenerating forest (Haney et al. 2008). However, the relationships between time since fire, forest canopy cover and canopy-foraging birds (hereafter, canopy birds) in forests around the world remain poorly understood.

A range of analytical approaches incorporating hypothesised causal relationships in the system under investigation have been applied to study the effects of fire on plants and animals. These approaches have demonstrated capacity to disentangle some of complex responses inherent to the problem. Relationships among fire, habitat and fauna have also been investigated in causal frameworks using spatial simulation models (Bradstock et al. 2005), moderated-mediation analyses (Lindenmayer et al. 2016), and Bayesian Networks (Hradsky et al. 2017). Structural equation modelling has been used to investigate causal influences of fire history, local conditions, and position in the landscape on alien plant dominance (Keeley et al. 2005) and plant species richness (Grace and Keeley 2006) in North American shrubland. The form of a structural equation model reflects the causal pathways hypothesised in a corresponding conceptual diagram (Grace et al. 2009). Mediation analysis is a form of structural equation modelling that enables partitioning of the effects of a causal antecedent variable on a consequent variable into direct effects, and indirect effects that influence the response through a third mediating variable (Grace et al. 2009, Hayes 2018). Bayesian mediation analysis (Yuan and MacKinnon 2009) can be conducted using a single model with recently developed statistical tools (Bürkner 2017). In this study, we investigated the direct and indirect (via canopy cover) effects of time since fire on canopy birds using Bayesian mediation models.

We address the importance of changes in canopy cover over time since fire for birds by asking: to what extent does canopy cover mediate the effects of time since fire on the richness and occurrence of canopy bird species, in montane dry sclerophyll forests? We expect some level of positive avian response to increases in canopy cover through time since fire, but know very little about the relative influence or direction of the direct effects of time since fire. Dry sclerophyll forests with shrubby understories (Keith & Simpson 2012) are widespread in south-eastern Australia and have evolved with fire (Gill 1981), however fire activity is increasing in these communities (Fairman et al. 2016, Canadell et al. 2021). A fire return interval of 7-30 years over at least 50% of the distribution of this forest type has been recommended for fire management, to enable community persistence given predominant regenerative/reproductive mechanisms and time to maturity of the flora (Bradstock and Kenny 2003). Over recent decades, the proportion of these forests with a fire-age of 10 years or less has increased in high conservation value landscapes of the region (Fig. 6.1). This represents a potentially extensive reduction in canopy structure and complexity (Haslem et al. 2016), which has implications for birds of the region that occur in this forest strata.

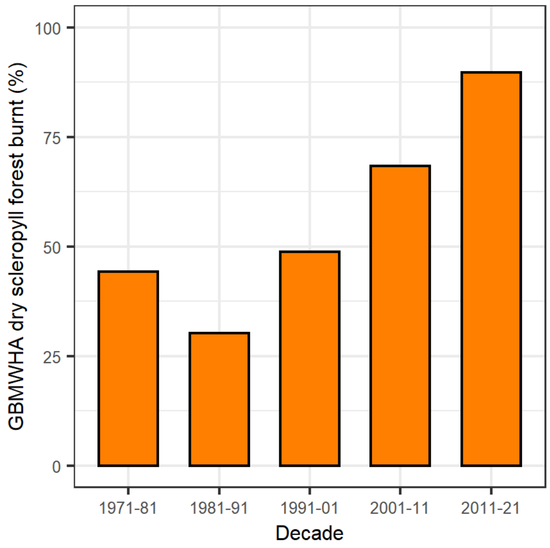

Fig. 6.1. The percentage of the distribution of dry sclerophyll forest (shrubby sub-formation, Keith & Simpson 2012) burnt in each decade from 1971 to 2021 (Office of Environment & Heritage NSW 2017) in the one million-ha Greater Blue Mountains World Heritage Area (GBMWHA), south-eastern Australia. This forest type covers approximately 70% of the World Heritage Area. Overlaps in the decadal year ranges reflect the start and ends of austral fire seasons, which span from spring at the end of one year into and through the summer of the following year.

6.3 Methods

6.3.1 Study area

The study was conducted in montane dry sclerophyll forests of the Greater Blue Mountains World Heritage Area. Study sites were located in or adjacent to the Blue Mountains, Gardens of Stone, and Wollemi National Parks. The 46 sites were circular with a radius of 325 m, covering ~33 ha each. These sites were a subset of sites established for a multi-faceted study of the fire ecology of birds in the region (Franklin et al. 2021, Franklin et al. 2022). Sites were located along an 80-km latitudinal gradient from 33°41'S 150°26'E in the south to 32°59'S 150°22'E in the north, at a similar elevation on the highest parts of this section of eastern Australia's Great Dividing Range. A rainfall gradient corresponded to the latitudinal gradient, with annual mean rainfall of up to 1340 mm over sites in the south of the study area, reducing to 62% of that amount in the north (Xu and Hutchinson 2011). Bird species distributions can be influenced by rainfall gradients over dry eucalypt forests (Kelly et al. 2017), so we accounted for potential avian responses to rainfall and other environmental change across the study area by including latitude as a covariate in modelling. The tree canopies of montane dry sclerophyll forests are dominated by species of *Eucalyptus*, including *E. sclerophylla*, *E. sieberi* and *E. piperita*, which occur with typically diverse understories of shrubs in low-nutrient, sandy soils over sandstone geology. These fire-prone forests are extensive in the region and many of the eucalypts have the capacity to resprout following fire, however the flora have tolerance limits in response to fire frequency, intensity and season, hence fire regimes shape the composition of these plant communities (Keith 2004).

6.3.2 Bird surveys

Birds were surveyed using acoustic recorders (SM4, Wildlife Acoustics, Maynard, MA, USA) in the late spring/early summer of 2018. Recorders were programmed to record daily for 100 minutes commencing at dawn, then fastened to a small tree at 2-m above the ground, at the centre of the sites. All recorder settings and microphone checks were as per Franklin et al. (2020). The set of eight recorders were collected after at least two clear-weather days had passed, then redeployed, with this process repeated until all sites had been surveyed. Recordings were collected as .wav files and manually processed at the desktop by the first author. This involved listening to calls while viewing them in a spectrogram of frequency/time in Kaleidoscope (Wildlife Acoustics), and recording species detections (Franklin et al. 2020, Franklin et al. 2021a). A site survey involved the processing of a total of 200 min of recordings, which was made up of 100 min of post-dawn recordings on each of two days. This represents a level of sampling effort that is well above average (Watson 2017). This method has also been shown to be more likely than an established observer-based method to detect many of the same species, given equal sampling time (Franklin et al. 2020). Furthermore, with this method there is no systematic pattern of bias in species detectability that could be attributed to increased bird call attenuation in older, more structurally complex dry sclerophyll forest (Franklin et al. 2022). Ten avian response variables were produced for analysis, including counts of the total number of species, counts of the number of canopy species, and the detection/non-detection (1/0) of individual canopy species detected in > 20% and < 80% of sites (n = 8).

6.3.3 LiDAR-derived canopy cover estimates

Canopy cover estimates for the sites were derived through a process of converting Light Detection and Ranging (LiDAR) point clouds to raster layers of point counts for 0.5 m vertical strata, aggregating these layers vertically to capture the vertical span of canopies, then calculating canopy cover. Source data were multiple 2x2-km LiDAR point cloud tiles for the study area produced by the Spatial Services division of the NSW Department of Finance, Services and Innovation, using an airborne scanner, and obtained via the Elvis Elevation and Depth data portal https://elevation.fsdf.org.au/. Data processing was conducted in R (R Core Team 2022) using the CERMBlidar (Bedward 2022) and terra (Hijmans 2022) packages. All LiDAR data used in this study were obtained from flights over the study area in 2017 and 2018. These data were partly processed, including removal of flight line overlap and normalisation of point heights, and stored as part of a regional set in a database on a University of Wollongong server as raster layers (10-m cells) of point counts at 0.5-m height intervals. For this study, the 10-m cell point counts were aggregated to 20-m cell counts to match the spatial resolution of fire history data. The 20-m cell counts for 0.5 m strata were then summed over the vertical range in which tree canopies occurred in the sites. To establish the overall vertical range within which tree canopies occurred, maximum canopy heights derived from LiDAR data and a framework for classification of Australian vegetation based on structural form (Specht 1970) were used. Inspection of distributions of maximum canopy heights across sites revealed that some tree canopies were present between five and 10 m (low forest), most occurred between 10-30 m (forest), and some were > 30 m above ground (tall forest, Specht 1970). Consequently, we defined the canopy as all vegetation > 5 m above ground (Haslem et al. 2016, Price & Gordon 2016). Counts of points in the canopy strata were then converted to proportional cover estimates by taking the ratio of the number of canopy points to the total number of points for each 20-m cell. The median value among ~ 830 20-m cells/site represented the proportion of canopy cover over each site in modelling.

6.3.4 Fire history variables

Time since fire for each site was determined using the NSW Fire History spatial data set (Office of Environment & Heritage NSW 2017), and expressed in relation to the year of bird surveys (2018). Sites were located entirely within the boundaries of the footprints of large fires that occurred during either 2002 or 2013, that were spatially interspersed across the study area. Accordingly, time since fire (TSF) was prepared as a binary variable for modelling, with 0 representing 5 years since fire and 1 assigned to 16 years since fire. While not a focus of this study, the severity of the last fire across each site was included as a covariate in modelling because there was potential for it to influence canopy cover (Haslem et al. 2016, Karna et al. 2020) and/or bird occurrence (Robinson et al. 2014). The severity of the last fire (SEV) was expressed as the proportion of each site that had been burnt by high-severity fire, such that the tree canopy had been scorched or incinerated. Gridded fire severity layers for the 2002 and 2013 fires were used to obtain the data required to calculate this proportion (Hammill et al. 2010, Hammill Stone 2014). These data were based on NDVI (Normalised Difference Vegetation Index) ratios from corresponding pairs of pre and post-fire Landsat images.

6.3.5 Data analysis

To establish the extent to which canopy cover mediated the effects of time since fire for each of the 10 avian response variables (Table 6.1), we conducted mediation analyses (Hayes 2018) using Bayesian models (Kurz 2021). Our approach was to run models representing partial and complete mediation (henceforth partial and complete mediation models, respectively) for each response, and then formally compare their estimated out-of-sample predictive accuracy (Vehtari et al. 2017). Predictions were then obtained from the model form with the best predictive performance. If predictive performance did not differ, predictions were taken from the more parsimonious complete mediation model. Paired complete and partial mediation models differed in one way only: the addition of time since fire as a direct predictor of the bird response in the partial mediation model (Fig. 6.2).

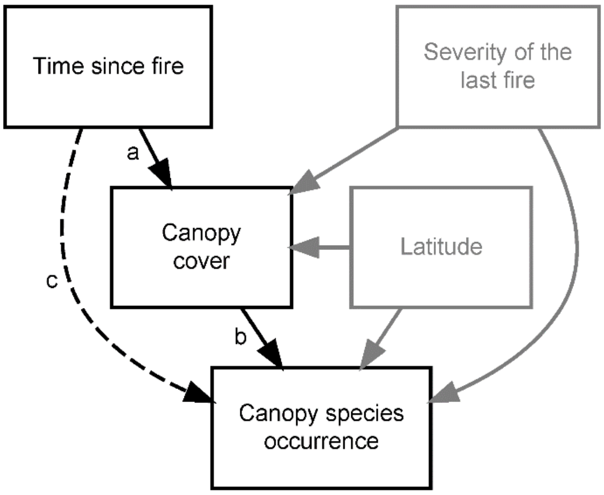

Fig. 6.2. Graphical model of hypothesised causal relationships among fire history, site attributes and canopy birds in montane dry sclerophyll forest. Two statistical models were built and compared to investigate the extent to which canopy cover mediated the effect of time since fire on canopy birds. The partial mediation model partitioned the indirect effect of time since fire that passes through canopy cover (path ab), and the direct effect (path c), within the total effect (path ab + path c). The complete mediation model did not include the c pathway, with all of the effect of time since fire on canopy birds mediated by canopy cover. The severity of the last fire and latitude had the potential to influence canopy cover and/or canopy birds, so they were included in both models as background covariates.

All forms of mediation model (Equations 6.1-6.4) consisted of two submodels that were fitted as bivariate models using the brms package (Bürkner 2017) in R (R Core Team 2022). Canopy cover was the mediator in all mediation models, and the submodel predicting canopy cover did not vary among mediation model forms. However, the distributions of bird response variables differed between counts of species (Equations 6.1-6.2) and individual species occurrence (Equations 6.3-6.4).

Complete mediation models for the total number of species and the number of canopy-foraging species were of the form:

$$\text{logit}(\text{CPY}) = \beta_1 + \beta_2\text{LAT} + \beta_3\text{SEV} + \beta_4\text{TSF}, \qquad \text{Equation 6.1}$$

$$\log(\text{Number of sp.}) = \beta_5 + \beta_6\text{LAT} + \beta_7\text{SEV} + \beta_8\text{CPY}$$

Where CPY, the proportion of canopy cover over the site, was treated as being drawn from a Beta distribution (Douma & Weedon 2019) with a mean value related to an intercept, latitude (LAT), severity of the last fire (SEV) and time since fire (TSF) via a logit link function. The total number of species and the number of canopy species were count variables that were modelled using the Conway-Maxwell Poisson distribution, since exploratory analyses indicated that the count values were under-dispersed (Guikema & Goffelt 2008, Lynch et al. 2014). The number of total/canopy species was related to an intercept, latitude, severity of the last fire and canopy cover via a log link function.

Partial mediation models for the total number of species and the number of canopy foraging species were the same as their corresponding complete mediation model, except for the addition of time since fire (TSF) as a predictor for the number of species (Equation 6.2).

$$\text{logit(CPY)} = \beta_1 + \beta_2\text{LAT} + \beta_3\text{SEV} + \beta_4\text{TSF}, \qquad \text{Equation 6.2}$$

$$\log(\text{Number of sp.}) = \beta_5 + \beta_6\text{LAT} + \beta_7\text{SEV} + \beta_8\text{CPY} + \beta_9\text{TSF}$$

Complete mediation models for the occurrence of eight canopy species were structured similarly to complete mediation models for the number of species (Equation 6.1), except that species occurrence was modelled using a Bernoulli distribution with a logit link:

$$\text{logit(CPY)} = \beta_1 + \beta_2\text{LAT} + \beta_3\text{SEV} + \beta_4\text{TSF}, \qquad \text{Equation 6.3}$$

$$\text{logit(Sp. occurrence)} = \beta_5 + \beta_6\text{LAT} + \beta_7\text{SEV} + \beta_8\text{CPY}$$

Partial mediation models for individual canopy species had the same structure as their complete mediation model counterpart (Equation 6.3), but included time since fire (TSF) as an additional predictor of species occurrence (Equation 6.4).

$$\text{logit(CPY)} = \beta_1 + \beta_2\text{LAT} + \beta_3\text{SEV} + \beta_4\text{TSF}, \qquad \text{Equation 6.4}$$

$$\text{logit(Sp. occurrence)} = \beta_5 + \beta_6\text{LAT} + \beta_7\text{SEV} + \beta_8\text{CPY} + \beta_9\text{TSF}$$

Results for individual canopy species are presented if they were detected in > 20% and < 80% of sites (Sitters et al. 2014b). The lower limit was chosen to ensure that there were adequate detections to support inferences given the species occurrence submodel structures, while the upper limit was applied to allow for sufficient contrast in species habitat preferences.

In all models, Normal (0, 10) priors were used for the intercept, background covariates and predictor variables of interest. The brms default gamma(0.01, 0.01) priors were used for phi, the precision parameter of the beta distribution used to model the proportion of canopy cover over each site. This gamma prior was also used for the shape parameter of the Conway-Maxwell Poisson distribution used to model under-dispersed counts of total and canopy-foraging species. Models were fitted using Markov Chain Monte Carlo (MCMC) in Stan (Stan Development

Team 2022) through the brms package (Bürkner 2017) in R (R Core Team 2022). For all models, four MCMC chains were run to obtain 1,000 samples per chain, having discarded 1,000 warmup samples and thinned at a rate of 10. The samples from each chain were then consolidated into a single matrix of 4,000 samples, from which predictions were generated. Model convergence was evaluated and confirmed using the Gelman-Rubin statistic (Gelman & Rubin 1992), and by checking the number of effective samples for all parameters. Pairs of complete and partial mediation models for each bird response were compared using leave-one-out cross-validation (LOO) with the loo package (Vehtari et al. 2022) implemented via brms (Bürkner 2017) in R (R Core Team 2022). In cases where Pareto *k* values exceeded 0.7 in the initial comparison, we applied moment matching (Paananen et al. 2021) and repeated the comparison.

6.4 Results

A total of 74 diurnal bird species were detected in the study, including 17 that forage primarily in the canopy, 23 that forage in the understorey or on the ground, one species that forages in the air and on the ground, and 33 species that forage throughout the forest strata (Appendix E.1). Paired complete and partial mediation models were fitted and formally compared for the total number of species, the number of canopy species and the eight individual canopy species that were recorded in > 20% and < 80% of sites (Table 6.1).

The complete mediation model was estimated to have better predictive performance capabilities than the partial mediation model for the number of species, number of canopy-foraging species, and the occurrence of six of the eight focal canopy-foraging species (Table 6.1). However, for several of the comparisons, standard errors of the differences were large relative to the estimates, suggesting that differences in the predictive performance between those particular model pairs may have been slight, or potentially non-existent (Sivula et al. 2020).

Partial mediation models for the Brown-headed Honeyeater (*Melithreptus brevirostris*) and Straited Thornbill (*Acanthiza lineata*) were estimated to have slightly better predictive accuracy than their corresponding complete mediation models. However, in both cases, the standard error was much greater than the estimate of the difference in predictive accuracy between model forms (Table 6.1). Because prediction of bird species numbers or occurrence was not clearly improved by fitting time since fire as a direct predictor of bird responses in partial mediation models, we generated predictions from the more parsimonious, complete mediation models (Figs. 3-4).

Table 6.1. Comparison of the predictive accuracy of complete and partial mediation models using leave-one-out cross-validation. The model form with zero for the difference in expected log predictive density (ELPD) has the better predictive accuracy. Negative values (± their standard errors) for the ELPD difference are provided under the alternative model. Results for canopy-foraging species recorded in < 20% and > 80% of sites are not shown. See Appendix E.1 for species scientific names.

	ELPD difference	
Response	Complete mediation model	Partial mediation model
Total no. species	0	-0.8 ± 0.8
No. canopy-foraging species	0	-1.2 ± 0.2
Brown-headed Honeyeater	-1.1 ± 1.8	0
Channel-billed Cuckoo	0	-1.6 ± 0.3
Cicadabird	0	-0.8 ± 0.8
Gang-gang Cockatoo	0	-0.4 ± 1.6
Leaden Flycatcher	0	-1.2 ± 0.5
Mistletoebird	0	-1.2 ± 0.4
Olive-backed Oriole	0	-0.6 ± 1.0
Striated Thornbill	-1.0 ± 1.7	0

Canopy cover increased from a median of 31% at five years since fire to 46% at 16 years since fire (Fig. 6.3a). There were strong positive relationships between canopy cover and the total number of species (Fig. 6.3b), and the number of canopy-foraging species (Fig. 6.3c). Over the range of median canopy cover values among the sites, the total number of species increased from 23.1 to 35.0 species on average, and the number of canopy foraging species doubled: increasing from 4.6 to 9.2 species (Fig. 6.3b-c).

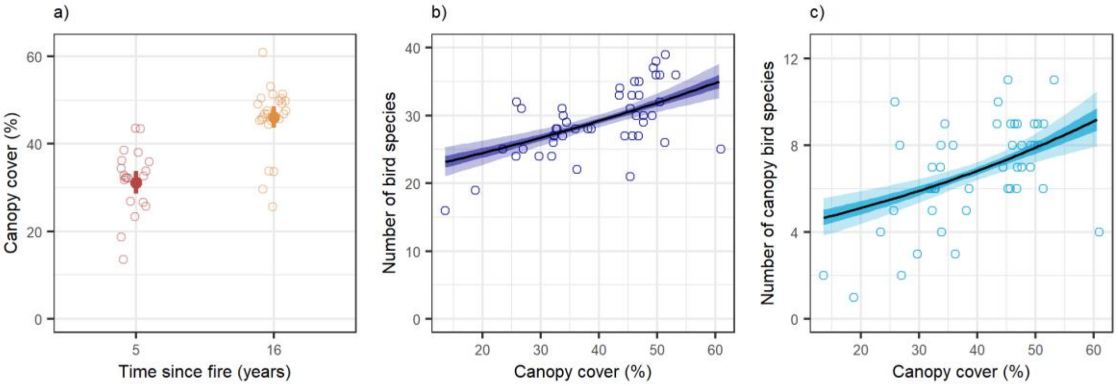

Fig. 6.3. Predicted and observed (open circles) relationships between a) canopy cover and time since fire, b) the total number of bird species and canopy cover, and c) the number of canopy-foraging bird species and canopy cover. In a), bars around medians (circles) represent the central 90% of distributions of Bayesian complete mediation model predictions. In b) and c), lines are medians with bands representing the central 50% and 90% of distributions of Bayesian complete mediation model predictions.

The probability of occurrence of most of the individual canopy-foraging species recorded in > 20% and < 80% of sites increased with greater canopy cover (Fig. 6.4). The strongest positive response among these eight species was shown by the Striated Thornbill, which increased in probability of occurrence by ~ 63% over the range of canopy cover. No canopy species exhibited a clear negative response to canopy cover (Fig. 6.4). Of these species, only the Striated Thornbill was exclusively sedentary, while the remainder were relatively mobile, undertaking nomadic and/or migratory movements at the individual or species levels (Garnett et al. 2015).

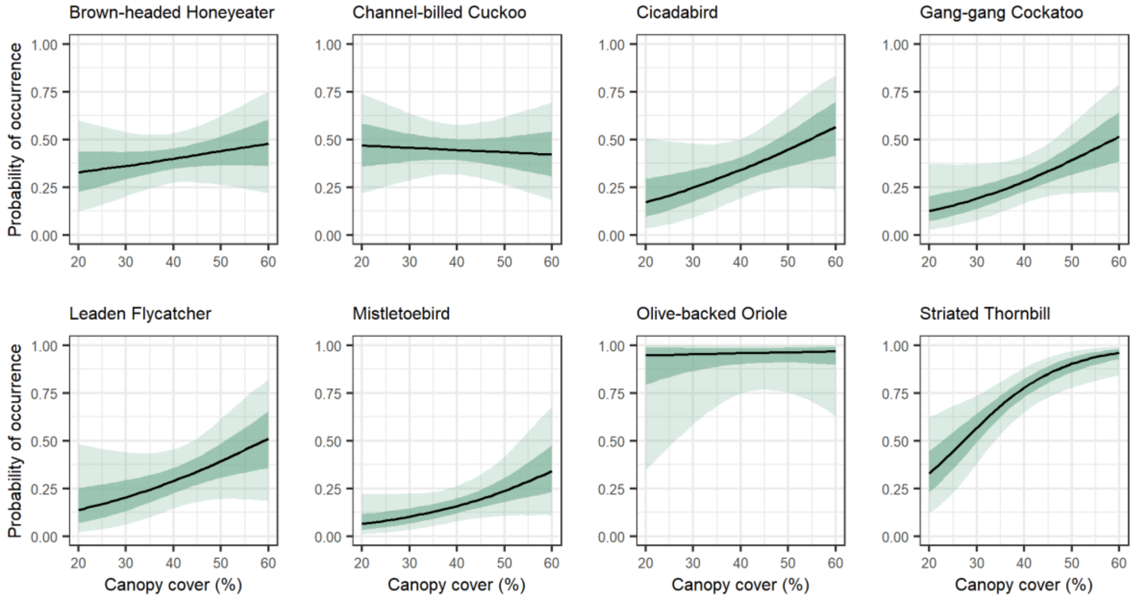

Fig. 6.4. The probability of occurrence of canopy-foraging species in relation to canopy cover in montane dry sclerophyll forest. Lines are medians with bands representing the central 50% and 90% of distributions of Bayesian complete mediation model predictions. Results for canopy-foraging species recorded in < 20% and > 80% of sites are not shown. See Appendix E.1 for species scientific names.

6.5 Discussion

The effects of time since fire were strongly mediated through canopy cover for the total number of species, number of canopy species, and occurrence of individual canopy species. Avian responses to canopy cover were mostly positive, and there were no negative responses to increased cover. The inclusion of time since fire as a direct predictor of any of the bird responses did not increase the predictive accuracy of mediation models. These results suggest that the direct effects of an increase in time since fire from five to 16 years on these species were slight or negligible. Most of the canopy species investigated were nomads and/or migrants, which are relatively mobile in fire-prone landscapes of the region (Franklin et al. 2021b). As such, populations may have had the capacity to avoid substantial direct mortality through emigration to refugia, and to recolonise burnt habitat fairly rapidly once in a suitable state. Furthermore, as canopy species, some of these species may have avoided direct mortality by moving to canopies where fire was only burning, or had recently burnt, the understory, thereby obtaining vertical refuge in forest burnt at low severity (Robinson et al. 2014).

6.5.1 Time since fire and canopy structure

In the montane dry sclerophyll forests of the region, canopy cover increased substantially from five to 16 years after fire. Similar positive trends have been recorded for the total canopy (Haslem et al. 2016) or mid-canopy (Sitters et al. 2014b) in other eucalypt forests of south-eastern Australia. However, regeneration of the canopy may not have been complete at 16 years since fire, so the habitat was potentially suboptimal for animals that require the most complex canopy structures possible in these communities. The longest time since fire used in the present study was 16 years, so it is likely that further small increases in canopy structure would accrue after this time, given results obtained in similar systems. In other dry sclerophyll forests of the region, upper canopy cover (> 15 m) continued to gradually increase beyond 16 years since fire, while lower canopy cover (4-15 m) increased up to ~ 30 years post-fire then began to decline (Price & Gordon 2016). Ongoing post-fire increases in canopy cover were predicted for temperate dry eucalypt forests at higher latitudes, albeit at a reduced rate after 16 years since fire (Haslem et al. 2016).

6.5.2 Canopy structure and bird occurrence

The responses of most canopy species to canopy cover were positive, and there were no negative responses. Similarly, in a range of coastal vegetation communities of the region, only positive responses to percentage cover of the midstory were recorded among the species for which both direct and indirect effects of time since fire could be distinguished (Lindenmayer et al. 2016). In varied eucalypt forests at higher latitudes, mostly positive links were established among time since fire, vegetation structure and bird species occurrence, but vegetation structure had better predictive capacity than time since fire for most species (Sitters et al. 2014b). Of the eight canopy species that were recorded in > 20% and < 80% of sites in the present study, six species consumed fruit, seeds, or both as part of their diet. Four of these granivorous/frugivorous species responded positively to canopy cover, which is consistent with increasing availability of fruit and seeds as the canopy regenerates over time since fire.

6.5.3 Management implications

Birds perform essential ecosystem functions, including regulation of canopy herbivory by insects, pollination, and seed dispersal (Sekercioglu 2006), so a management focus on maintaining the long-term viability of their populations is necessary. There is potential for increased effectiveness of fire management of fauna in fire-prone forests if their structural habitat preferences are included and considered as complementary to species fire responses (Kelly et al. 2017). Our findings are supportive of forest fire management for avian diversity that includes consideration of canopy cover as some function of time since fire (Sitters et al. 2014b). Because there is not a perfect correspondence between canopy cover and time since fire, spatial data for these attributes could be overlaid to refine habitat suitability assessment in the management of natural landscapes for fire-sensitive bird species. Recent processing tools and readily available LiDAR or satellite data products can be used to infer structural attributes of forests (e.g., Queinnec et al. 2021), which increases options for achieving biodiversity objectives in fire planning and management.

6.5.3.1 Threatened species case study

Wildfires burnt vast areas of forest during the 2019-2020 fire season in south-eastern Australia, which directly impacted populations of many bird species and substantially reduced the amount of habitat within their distributions (Legge et al. 2021). One such species was the Gang-gang Cockatoo (*Callocephalon fimbriatum*), which had been declining in numbers over preceding decades (Cameron et al. 2021). Because their population had been in decline for some time leading up to the recent extensive loss of habitat, in 2022 the Gang-gang Cockatoo was listed as Endangered under the federal Environmental Protection and Biodiversity Conservation Act 1999. We found that the probability of occurrence of the gang-gang Cockatoo increased from 0.13 where canopy cover was 20%, to 0.52 where cover was 60%. This result suggests that the management of montane dry sclerophyll forests to support this species would include provision of substantial areas of forest with denser canopy, and consequently older forest, given the positive relationship between canopy cover and time since fire in these communities.

6.5.3.2 Further research

This study has increased understanding about the relationships among time since fire, canopy cover and canopy bird occurrence, thereby providing options for the application of a range of analytical approaches in subsequent investigations of the topic. We recognise that simpler model structures than those we employed can be used to predict canopy cover using time since fire, or bird species richness/occurrence using canopy cover. However, it was more appropriate to use the components of our mediation models to generate predictions, given that they were used to make inferences about direct and indirect effects of time since fire. Subsequent work could measure a range of resources used by birds that may be associated with canopy structure, then map causal relationships in structural equation models of greater complexity to potentially elucidate increasingly nuanced avian responses to fire regimes. Recent remote sensing methods accompanied by ground validation provide options to increase specificity of fire management for canopy birds by enabling estimates of avian resources associated with canopy cover, such as nectar from flowering trees, to be obtained (Law & Chidel 2008, Dixon et al. 2021). For logistical reasons the shortest time since fire included in this study was five years, but the direct effects of fire on birds are presumably stronger in the years immediately following a wildfire. An investigation of the response of canopy birds and canopy structure commencing shortly after fire would fill out our understanding of the relative strength of direct and indirect effects of time since fire.

6.6 Conclusion

The total number of species, the number of canopy species, and the occurrence of individual canopy species were positively influenced by the effects of time since that were mediated through forest canopy structure. There was little, if any, direct effect of increasing time since fire from five to 16 years on these birds. This suggests that for these canopy species, at five years since wildfire the forest is accessible to colonisers, and numbers of breeding individuals are adequate to support further population recovery, given ongoing increases in canopy structure. The increased canopy structure at longer time since fire is clearly of vital importance for avian diversity in montane dry sclerophyll forest. Fire management of these forests is faced with the challenge of reconciling the requirements of much of the avifauna for older habitat, with increasing proportions of recently burnt forest, driven by escalating fire activity under climate change.

6.7 Acknowledgements

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Chapter 7. Research Synthesis

Avian responses to fire regimes are context specific (Rainsford et al. 2021), and the processes and mechanisms that underpin the fire responses of most bird species are not fully understood (Driscoll et al. 2010, Clarke 2020). The research in this thesis addressed knowledge gaps pertaining to avian responses to both separate and combined components of fire regimes in montane dry sclerophyll forests of south-eastern Australia. Fire activity is increasing in high conservation value landscapes of the region under climate change (Abram et al. 2021), so fire histories representative of future fire regimes were included in the study design to gain understanding of the implications for birds.

This project has increased knowledge of avian fire ecology in several areas. Initially, a robust bird survey method using acoustic recorders was systematically produced (Chapters 2 and 3), then applied to obtain bird data for subsequent chapters. This method, and the processes used in its development, have broad applicability for future research. Through conceptualising and testing avian mobility as a mechanism that may influence species persistence, it was found that relatively mobile species may have better functional capacity to obtain required resources in fire-prone landscapes (Chapter 4). Using a novel approach, avian responses to historical high-severity fire, which was derived from consolidated spatial fire severity data for multiple fires through time, were investigated in Chapter 5. While both positive and negative responses to the extent of historical high severity fires were detected among species, responses did not change over time since fire, which implied incomplete regeneration of some avian resources. To gain insights into the processes driving avian responses to time since fire, structural equation modelling was used partition direct and indirect effects of time since fire on birds (Chapter 6). Once five years since fire had passed, birds responded primarily to ongoing regeneration of canopy structure. The fire responses of individual species were compared with their corresponding responses reported in other studies conducted in different habitats, and similarities were evaluated in the relevant sections of Chapters 4-6.

7.1 An acoustic bird survey method for montane dry sclerophyll forests

Prior to commencing the main investigation of avian responses to fire regimes, acoustic recorders were deployed in montane dry sclerophyll forest sites to collect data for a study that aimed to produce a robust acoustic bird survey method (Chapters 2 and 3). The resulting 9,000 minutes of recordings were manually processed to yield a data set of the detection/non-detection of species in 450 20-min samples. This species data was used in conjunction with results from observer-based surveys to develop, validate and refine an optimal acoustic bird survey method for subsequent use.

Three frameworks were presented and applied to systematically develop the optimal method, any of which may be used by other ecologists to produce their own context-specific method involving manually processed acoustic data. The first framework was to compare species detection probabilities obtained from a candidate acoustic method and an observer-based method using multispecies occupancy modelling (Furnas & McGrann 2018, Chapter 2). When both approaches were applied in the same sites with equal sampling effort, the selected acoustic method resulted in higher detection probabilities than those obtained from area searches conducted by an observer (Loyn 1986) for 73% of all species. The second framework was to compare a set of candidate acoustic survey protocols representing different levels of sampling effort and temporal configurations, on the basis of survey completeness, or the proportion of total species detected (Wimmer et al. 2013, Chapter 2). The third framework was to apply an unbiased results-based stopping rule (Watson 2004) to extensive acoustic data collected in each site, to establish a suitable amount of sampling effort per site survey in the study system (Chapter 3). The average amount of effort per site (200 minutes) was then used to set the level of sampling effort of a candidate set of different fixed-effort acoustic protocols for subsequent assessment. The optimal method was shown to be capable of detecting 69% of all species present (Chapters 2-3), including all common/moderately common species and a substantial proportion of uncommon/rare species (Chapter 3).

The multi-faceted development process yielded a reliable and well-understood acoustic bird survey method for the research in Chapters 4-6, that could also be applied in other projects requiring species data from dry sclerophyll forest bird assemblages. Following the development phase, the method was applied in 65 new sites to collect a total of 13,000-min of field recordings that were manually processed to obtain data for 79 diurnal, terrestrial bird species. The quality control processes built into the method ensured that the species data was accurate. Firstly, I conducted all processing to ensure consistency of the approach throughout. Secondly, the identification of species was rigorous, in that a library of species calls was built and referred to during sound file processing, published bird calls were used similarly, and other experts were consulted for their opinions on species responsible for atypical calls.

Varying detectability among species may lead to bias in the results of any bird survey method. This was accounted for in Chapter 4 by modelling individual species detectability in the Bayesian multispecies occupancy analysis. Most of the focus of the research in Chapters 5 and 6 was on individual species responses across fire history treatments and treatment combinations. Therefore, within-species variation in detectability among fire histories was more of a potential issue and required evaluation. Subsidiary multispecies occupancy modelling was conducted to address this matter in Chapter 5 (Appendix D.2). No systematic pattern of within-species differences in detectability among fire history combinations that could be explained by call attenuation owing to vegetation structure was found. For a small group of species there was a suggestion of a pattern of reduced detectability in more open habitats, but this could not be explained by structural habitat attributes. One possible explanation was that species vocalised less frequently where fires had been recent and/or severe (Mathers-Winn et al. 2018). However, it is more likely that these species were foraging more widely where resources may have been reduced, so individuals were beyond the detection range of the recorder for longer while the survey was underway (Chapter 5). Multispecies occupancy models rely on the assumption of a closed population (Iknayan et al. 2014), which is often accepted without testing, so associated research into the variation in daily avian movement patterns in contrasting disturbance histories would be valuable.

7.2 Mobility as an avian fire-response mechanism

Avian mobility is a recurrent theme in this thesis, because it influences patterns of species occurrence in relation to components of fire regimes and their effects on habitat. Through their stronger responses to fire history, relatively mobile species (migratory, nomadic, and/or large species) demonstrated their capacity to locate and access preferred dry sclerophyll forest habitats (Chapter 4). As such, mobility is a mechanism that may support population persistence to varying degrees as fire activity increases under climate change, because adequate levels of resources may become more widely distributed, or difficult to locate and access (Nimmo et al. 2019, Teitelbaum & Mueller 2019). To determine the consistency of fire responses among species with broadly similar movement strategies, species were allocated to groups of exclusively sedentary, migratory and nomadic species (Chapter 4). The only consistent group level response to fire history was shown by migrants, which were more likely to occur when long unburnt forest was present in the landscape surrounding the patch in which the species was detected. Mobile species such as migrants may have greater capacity to engage in landscape complementation (Nimmo et al. 2019), where a species accesses required resources in more than one type of habitat in fire-affected landscapes (Chapter 4).

The notion that relatively mobile species may be better equipped to locate and access resources in fire-prone landscapes is further supported by the findings in Chapters 5 and 6. Eight of the 10 species that responded strongly to the spatial extent of historical high-severity fire were partial or total migrants (Chapter 5). The pattern exhibited by less-mobile species in this chapter is also supportive of the mobility mechanism concept. Two-thirds of the species that were more likely to occur at longer time since fire were exclusively sedentary, which suggest that those species may have been responding positively to increased density of resources in the local habitat, such as vegetation structure (Catling et al. 2001). All but one of a set of moderately common/common canopy-foraging species (hereafter, canopy species) investigated in Chapter 6 was a partial or total migrant. Most of these species were more likely to occur in forest with higher levels of canopy structure, reflecting their capacity to occupy their preferred fire-affected habitat. Relatively mobile species may also use their capacity to move more widely to avoid the direct effects of wildfire, and to locate refugia more effectively in and external to a burning landscape (Nimmo et al. 2019).

Relatively mobile species numerically dominated the groups of species that responded strongly to particular fire regimes in this thesis, so less has been learnt about the threats posed by increasing fire activity in relation to small, exclusively sedentary species. For these species, targeted studies, i.e., where the design is dictated by what is known about individual species ecology (e.g., Brown et al. 2009), as distinct from designs optimised for sampling entire assemblages, are required to understand extinction risk posed by changing fire regimes. The findings of such studies would provide vital information for the evaluation of management options to support populations of species found to be at risk from fire regime change (Driscoll et al. 2010).

7.3 The importance of older forest for birds

The research in this thesis has raised awareness of the importance of montane dry sclerophyll forest at mid-range and longer time since fire for many species in the avian assemblages that occupy these habitats. The effects of three levels of time since fire on birds were investigated at either patch or landscape scales: short (five years; Chapters 5 and 6), mid-range (16 years; Chapters 4-6) and long (> 16 years; Chapter 4). Of the species that showed strong responses to time since fire, only two species were more likely to occur at short compared with mid-range time since fire (Chapter 5). No species were more likely to occur where long unburnt forest was absent in the surrounding landscape (Chapter 4). The presence of long unburnt forest in the surrounding landscape had much stronger effects on species occurrence than fire frequency (Chapter 4). The assessment of fire frequency effects focused on the difference in probability of occurrence of species in habitat burnt either once or four times in a 31-year period prior to and including the most recent fire, which occurred 16 years before bird surveys were conducted. Perhaps fire frequency effects on these birds would have been stronger at shorter time since fire, or where additional fires had occurred in mostly inaccessible locations during the period.

Five years after fire, montane dry sclerophyll forest is unsuitable for several species, and habitat at a more advanced state of regeneration is necessary to maintain low baseline levels of their occurrence. At the forest patch scale, at least 10% of total species were more likely to occur at mid-range compared with short time since fire (Chapter 5). The magnitude of the overall effect of time since fire was relatively small for some of these species, but most had occurrence probabilities of approximately zero at short time since fire. Regeneration of canopy structure as time since fire increased from five to 16 years was a primary driver of the occurrence of individual canopy species, and the richness of canopy and total species (Chapter 6). Other effects of a wildfire that may continue to influence birds through time, such as mortality and emigration (Whelan et al. 2002), were not apparent between five and 16 years since fire. Factors that may influence vegetation structure in addition to time since fire, including altered plant community composition owing to increased fire frequency (Fairman et al. 2016), or different precipitation patterns under climate change (Williamson et al. 2014), will be important for birds in dry sclerophyll forests. A space-for-time substitution design was implemented to study time since fire effects in Chapters 5 and 6, which enabled us to investigate avian responses to an increase in time since fire from five to 16 years since fire using bird data collected from multiple landscapes in a single season. However, sites may have differed in other (unmeasured) ways that could have reduced power to detect fire effects, despite care being taken to standardise sites in terms of elevation and broad vegetation community, (Driscoll et al. 2010).

An increase in time since fire from short to mid-range did not affect the responses of most species that were influenced by the extent of historical high-severity fire (Chapter 5). This suggests that some effects of high-severity fire on the resources used by these birds persist at least until mid-range time since fire. Approximately equal numbers of species responded either positively or negatively to the extent of historical high-severity fire, reflecting their individual preferences for habitat with particular structural attributes. This pattern is consistent with those in avian assemblages in other global forests (Hutto & Patterson 2016, Knaggs et al. 2020). In the montane dry sclerophyll forests of the region, canopy cover increased substantially from short to mid-range time since fire (Chapter 6), but regeneration was probably still incomplete, because positive trends have been shown to continue well beyond that time in broadly similar forests (Haslem et al. 2016, Price & Gordon 2016). Furthermore, levels of associated structural and other resources used by birds continue to increase over multiple decades in other systems, including nest hollows (Haslem et al. 2012), and food such as seeds (Valentine et al. 2014).

Individuals of many species require long unburnt forest in their home ranges. At the landscape scale, at least 12% of total species detected in forest at mid-range time since fire were more likely to occur where long unburnt forest (> 16 years) was present in the surrounding landscape (Chapter 4). Similarly, in north-east Australian woodlands, the extent of long unburnt habitat (> 10 years) in the landscape was the most important attribute for landscape-scale richness of frugivores, insectivores and canopy species (Burgess & Maron 2016). Long unburnt forest in the landscape is used by relatively mobile species to obtain required resources (Chapter 4). In addition, older forest can provide refugia from subsequent fires in the landscape for many species (Robinson et al. 2014). However, the size and spatial configuration of unburnt patches determines their utility as refugia from wildfire and as post-fire habitat for birds, in combination with the capacity and propensity of individual species to move in fire-affected landscapes (Nimmo et al. 2019, Chapter 4). Unburnt habitat external to or within the spatial extent of a wildfire represents a base from which particular species may exploit resources in burnt areas, and source habitat for delayed recolonisation contingent on sufficient regeneration (Watson et al. 2012b).

7.4 Changing fire regimes

Forecast increases in fire activity in the dry sclerophyll forests of south-eastern Australia (Bradstock et al. 2009, Bradstock 2010, Clarke et al. 2011) have occurred rapidly (Abram et al. 2021), amplifying the need to better understand the implications for fauna and their habitats. The responses of birds to fire histories representative of future fire regimes under climate change, including short time since fire, high fire frequency, and extensive high-severity fire, were investigated using a space-for-time substitution design incorporating multiple landscapes. Of the 79 total species studied in relation to fire, 18% were averse to forest where time since fire was short (Chapter 5), and/or where there was an absence of long unburnt forest in the surrounding landscape (Chapter 4). These species are exposed to risk from larger, more frequent fires that will increase the proportion of forest at short fire-ages in landscapes. Several species were less likely to occur where historical high-severity fire had been extensive (Chapter 5), which identifies them as potentially vulnerable to future fire regimes. The negative response shown by these species was temporally sustained, suggesting at least some persistent effects of high-severity fires on their habitat. The direct effects of wildfire on birds, such as mortality and emigration, were minimal once five years since fire had passed (Chapter 6). However, fires are becoming larger (Abram et al. 2021), with increases in the area burnt at high severity (Tran et al. 2020, Collins et al. 2021). Therefore, direct fire effects may impact more widely across bird species distributions in the region (Legge et al. 2021, Jolly et al. 2022). These threats would be exacerbated if the size of montane dry sclerophyll forest patches burnt homogeneously at high severity was found to have increased, as they have in particular North American forests (Steel et al. 2021).

7.5 Fire management for avian diversity

Fire management and planning for montane dry sclerophyll forests now needs to retain long unburnt forest strategically, with proportions burnt infrequently and at low severity, for biodiversity conservation. The 2019-2020 mega-fires in the forests of south-eastern Australia were evidence of increased fire activity driven by climate change (Abram et al. 2021). As a result of these fires, vast areas of forest estate in the region currently have a fire-age of less than three years, which presents challenges for management that aims to support species populations and biodiversity (Legge et al. 2022). Forest canopy structure is less complex at short time since fire, but many forest bird species require the denser canopies associated with longer time since fire (Chapter 6). Furthermore, many species responded to the effects of time since fire on canopy structure instead of time since fire *per se*, so spatial definition of both canopy structure and fire history would enhance specificity of avian fire management. Increases in fire activity will provide substantial areas for species with requirements for early successional, and frequently or severely burnt habitat, that could also be actively managed.

In light of the trend of increasing fire activity, the results of this research do not support a management approach that maintains a mosaic of balanced fire age classes in landscapes dominated by montane dry sclerophyll forests. Such an approach acknowledges that fire responses vary widely among flora and fauna but assumes that provision of habitat at a range of successional states will suffice to support biological populations (Parr & Andersen 2006). The need to additionally consider the complexity of the effects of multiple fires through time on species and their communities in fire management was raised early in the 21st century (Bradstock et al. 2005). Since that time, much research has been conducted and knowledge gained about responses of biota to the effects of separate or combined components of fire regimes at a range of temporal and spatial scales (e.g., Kelly et al. 2017). Some forest bird species may respond positively to increased levels of one or more components of a fire regime, and negatively to greater levels of others (Chapter 4), so attempting to characterise species as either fire-loving or fire-averse may be too general. There is much that is still unknown about the implications of changing fire regimes for birds (Clarke 2020), and more options for resource provision are available to management with long unburnt vegetation than there are with recently burnt habitat (Gosper et al. 2019a). The research in this thesis has shown that mobility is a mechanism that can enable migratory and other relatively mobile species to access resources in long unburnt forest more effectively at landscape scales. Furthermore, avian species and functional groups that are potentially vulnerable to habitat loss through increased fire activity in dry sclerophyll forests have been identified.

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Appendix A. Supplementary material for Chapter 2

Appendix A.1. Estimates of the total number of species in each site.

Estimates were obtained using the complete acoustic data set with the incidence-based coverage estimator (ICE; Table A.1.1), which uses information about infrequently detected species to estimate unobserved species (Chazdon et al. 1998, Chao et al. 2000).

Table A.1.1. The number of species detected in the complete acoustic data set for each site and estimates of the total number of species in each site.

Site no.	No. species detected in the complete acoustic data set	Estimated total no. species (ICE)
1	29	32
2	28	30
3	23	24
4	30	31
5	29	42
6	21	22
7	34	37
8	28	30
9	26	42
10	20	21

Appendix A.2. Bird species detected in the study.

Overall, 57 bird species were recorded in the study. Of these, 48 were detected by survey methods used to obtain data for modelling species detection probabilities (Table A.2.1). Six additional diurnal species were detected in the complete acoustic data set (Table A.2.2). Nocturnal species (n = 3) were excluded from all data analyses in the study (Table A.2.3).

Table A.2.1. The number of 20-min samples in which species were detected by the two survey methods that were used to obtain data for modelling species detection probabilities.

Scientific name	Common name	Species code	No. detections (samples) Acoustic protocol	 Standardised searches
Acanthorhynchus tenuirostris	Eastern Spinebill	EASB	96	83
Strepera graculina	Pied Currawong	PCUR	90	34
Platycercus elegans	Crimson Rosella	CROS	81	57
Cacatua galerita	Sulphur-crested Cockatoo	SCCT	76	26
Cormobates leucophaea	White-throated Treecreeper	WTTC	74	46
Colluricincla harmonica	Grey Shrike-thrush	GRST	71	18
Acanthiza pusilla	Brown Thornbill	BRTB	69	39
Lichenostomus chrysops	Yellow-faced Honeyeater	YFHE	63	26
Alisterus scapularis	Australian King-Parrot	AUKP	53	7
Menura novaehollandiae	Superb Lyrebird	SLYB	44	7
Lichenostomus leucotis	White-eared Honeyeater	WEHE	42	12
Phylidonyris novaehollandiae	New Holland Honeyeater	NHHE	41	15
Acanthiza lineata	Striated Thornbill	STTB	40	8
Rhipidura albiscapa	Grey Fantail	GRFT	37	32
Cracticus tibicen	Australian Magpie	AUMP	37	11
Psophodes olivaceus	Eastern Whipbird	EAWB	35	7
Pachycephala pectoralis	Golden Whistler	GLDW	34	11
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	YTBC	33	6
Anthochaera carunculata	Red Wattlebird	REDW	23	10
Cracticus torquatus	Grey Butcherbird	GRBB	14	3
Pycnoptilus floccosus	Pilotbird	PLTB	14	1
Dacelo novaeguineae	Laughing Kookaburra	LKKB	10	1
Ptilonorhynchus violaceus	Satin Bowerbird	SBOW	10	0
Zosterops lateralis	Silvereye	SEYE	9	0
Leucosarcia melanoleuca	Wonga Pigeon	WONP	8	0
Pardalotus punctatus	Spotted Pardalote	SPAR	5	0
Callocephalon fimbriatum	Gang-Gang Cockatoo	GGCT	4	4
Meliphaga lewinii	Lewin's Honeyeater	LEHE	4	0
Corvus coronoides	Australian Raven	AURV	3	5
Phylidonyris pyrrhopterus	Crescent Honeyeater	CRHE	3	1
Rhipidura rufifrons	Rufous Fantail	RUFT	2	1
Melithreptus brevirostris	Brown-headed Honeyeater	BHHE	2	0
Macropygia amboinensis	Brown Cuckoo-Dove	BRCD	2	0
Smicrornis brevirostris	Weebill	WBIL	2	0

Sericornis citreogularis	Yellow-throated Scrubwren	YTSW	2	0
Sericornis frontalis	White-browed Scrubwren	WBSW	1	2
Accipiter fasciatus	Brown Goshawk	BRGH	1	0
Falcunculus frontatus	Crested Shrike-tit†	CRST	1	0
Eopsaltria australis	Eastern Yellow Robin‡	EAYR	0	15
Microeca fascinans	Jacky Winter	JWNT	0	8
Petroica rosea	Rose Robin	ROSR	0	6
Lichmera indistincta	Brown Honeyeater†	BHON	0	1
Artamus cyanopterus	Dusky Woodswallow†	DUWS	0	1
Falco peregrinus	Peregrine Falcon†	PFCN	0	1
Myiagra cyanoleuca	Satin Flycatcher†	SAFC	0	1
Malurus lamberti	Variegated Fairy-wren‡	VAFW	0	1
Gerygone olivacea	White-throated Gerygone†	WTGY	0	1
Acanthiza nana	Yellow Thornbill‡	YETB	0	1

†Detected only once in the study.

‡Detected in the complete acoustic data set.

Table A.2.2. Diurnal species recorded in the complete acoustic data set that were not detected in surveys used to obtain data for multi-species occupancy modelling.

Scientific name	Common name
Gerygone mouki	Brown Gerygone
Myiagra rubecula	Leaden Flycatcher
Dicaeum hirundinaceum	Mistletoebird
Pardalotus striatus	Striated Pardalote
Hirundo neoxena	Welcome Swallow†
Melithreptus lunatus	White-naped Honeyeater

†Detected only once in the study.

Table A.2.3. Nocturnal species recorded during surveys.

Scientific name	Common name
Aegotheles cristatus	Australian Owlet-nightjar
Ninox boobook	Southern Boobook
Podargus strigoides	Tawny Frogmouth

Appendix A.3. Detection probabilities for species (Fig. A.3.1) and foraging stratum guilds (Fig. A.3.2) estimated using data that includes species heard calling from outside the 2-ha sampling area during 20-min standardised searches.

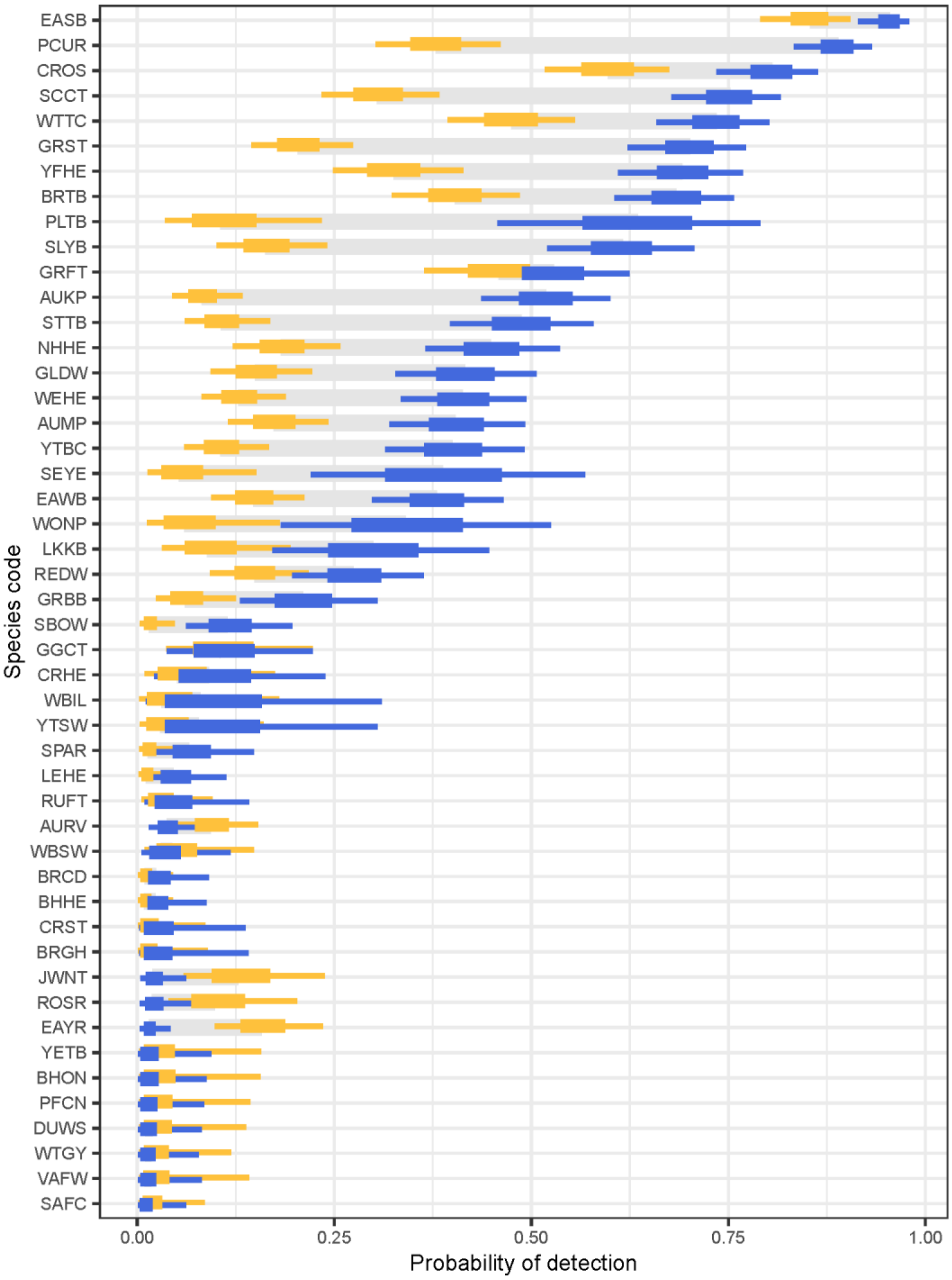


Fig. A.3.1. The probability of detection of bird species for the acoustic survey protocol (blue) and standardised searches (gold). Bars represent the interquartile range and central 90% of posterior distributions. Species common and scientific names are provided against species codes in Table A.2.1.

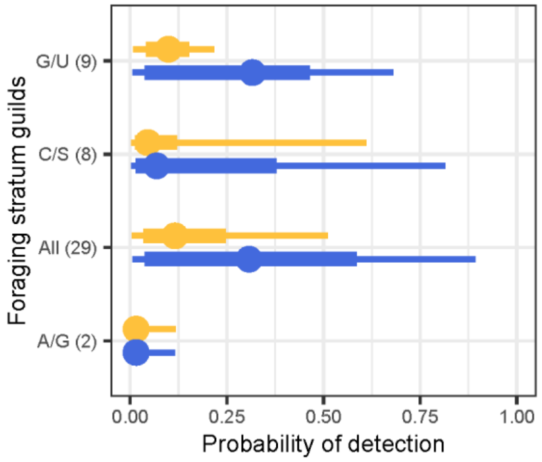


Fig. A.3.2. The probability of detection of species members of foraging stratum guilds for the acoustic survey protocol (blue) and standardised searches (gold). The median value is shown as a circle in the bars, which represent the interquartile range and central 90% of posterior distributions. Guild category abbreviations are: All (all strata), G/U (ground/understorey), C/S (canopy/subcanopy), A/G (aerial/ground). The number of species belonging to each guild category are shown in brackets. Species membership of foraging stratum guilds are provided in Table A.2.1.

Appendix B. Supplementary material for Chapter 3

Appendix B.1. Incidence rates for species observed in the study.

Table B.1.1. The incidence (proportion of 20-min samples in which the species was detected) of 47 diurnal species observed in the study based on 1) complete acoustic data (n = 450 samples), 2) the three-sample stopping rule (n = 91 samples), and 3) the optimal method (n = 100 samples).

Scientific Name	Common name	Complete data	3-survey rule	Optimal method
Acanthorhynchus tenuirostris	Eastern Spinebill	0.969	0.967	0.960
Strepera graculina	Pied Currawong	0.753	0.945	0.900
Acanthiza pusilla	Brown Thornbill	0.718	0.703	0.690
Platycercus elegans	Crimson Rosella	0.711	0.835	0.810
Cormobates leucophaea	White-throated Treecreeper	0.660	0.703	0.740
Cacatua galerita	Sulphur-crested Cockatoo	0.656	0.802	0.760
Colluricincla harmonica	Grey Shrike-thrush	0.627	0.758	0.710
Lichenostomus chrysops	Yellow-faced Honeyeater	0.613	0.648	0.630
Phylidonyris novaehollandiae	New Holland Honeyeater	0.391	0.473	0.410
Lichenostomus leucotis	White-eared Honeyeater	0.362	0.473	0.420
Alisterus scapularis	Australian King-Parrot	0.358	0.549	0.530
Menura novaehollandiae	Superb Lyrebird	0.342	0.418	0.440
Acanthiza lineata	Striated Thornbill	0.336	0.374	0.400
Cracticus tibicen	Australian Magpie	0.329	0.429	0.370
Pachycephala pectoralis	Golden Whistler	0.296	0.396	0.340
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	0.293	0.330	0.330
Anthochaera carunculata	Red Wattlebird	0.269	0.209	0.230
Rhipidura albiscapa	Grey Fantail	0.262	0.418	0.370
Psophodes olivaceus	Eastern Whipbird	0.247	0.319	0.350
Pardalotus punctatus	Spotted Pardalote	0.153	0.044	0.050
Pycnoptilus floccosus	Pilotbird	0.089	0.088	0.140
Zosterops lateralis	Silvereye	0.084	0.088	0.090
Dacelo novaeguineae	Laughing Kookaburra	0.065	0.088	0.100
Ptilonorhynchus violaceus	Satin Bowerbird	0.058	0.110	0.100
Phylidonyris pyrrhopterus	Crescent Honeyeater	0.056	0.033	0.030
Corvus coronoides	Australian Raven	0.049	0.033	0.030

Cracticus torquatus	Grey Butcherbird	0.049	0.143	0.140
Leucosarcia melanoleuca	Wonga Pigeon	0.040	0.077	0.080
Callocephalon fimbriatum	Gang-Gang Cockatoo	0.033	0.033	0.040
Dicaeum hirundinaceum	Mistletoebird	0.029	0	0
Meliphaga lewinii	Lewin's Honeyeater	0.024	0.044	0.040
Melithreptus brevirostris	Brown-headed Honeyeater	0.020	0.011	0.020
Accipiter fasciatus	Brown Goshawk	0.013	0.011	0.010
Smicrornis brevirostris	Weebill	0.011	0.022	0.020
Pardalotus striatus	Striated Pardalote	0.009	0	0
Sericornis frontalis	White-browed Scrubwren	0.009	0.022	0.010
Eopsaltria australis	Eastern Yellow Robin	0.007	0	0
Rhipidura rufifrons	Rufous Fantail	0.007	0.022	0.020
Malurus lamberti	Variegated Fairy-wren	0.007	0	0
Sericornis citreogularis	Yellow-throated Scrubwren	0.007	0.022	0.020
Macropygia amboinensis	Brown Cuckoo-Dove	0.004	0.022	0.020
Gerygone mouki	Brown Gerygone	0.004	0	0
Myiagra rubecula	Leaden Flycatcher	0.004	0	0
Melithreptus lunatus	White-naped Honeyeater	0.004	0	0
Acanthiza nana	Yellow Thornbill	0.004	0	0
Falcunculus frontatus	Crested Shrike-tit	0.002	0.011	0.010
Hirundo neoxena	Welcome Swallow	0.002	0	0
	Total no. species:	47	38	38

Appendix C. Supplementary material for Chapter 4

Appendix C.1. Species information.

The general level of incidence of each species in the Greater Blue Mountains World Heritage Area (Smith et al. 2019) was used as a basis for priors in Bayesian modelling. Smith et al. (2019) classified species as either rare, uncommon, moderately common or common in the region (Table C.1.1, GBMWHA prior incidence), then provided details of habitat preferences and seasonal incidence. Using these details, we applied a rule to convert general incidence to montane dry sclerophyll forest incidence for modelling (Table C.1.1, Habitat prior incidence), which was to drop species one level if they were specifically associated with habitat other than dry sclerophyll forest in spring/summer. For example, the Brown Gerygone (*Gerygone mouki richmondi*), a moderately common species that prefers rainforest and wet sclerophyll forest, tends to venture onto ridges only in winter (Smith et al. 2019), so it was reclassified as uncommon for the present study. Species allocation to movement groups and average body mass in Table C.1.1 were based on Garnett et al. (2015).

Table C.1.1. Species names, prior incidence, movement group membership and average body mass.

Scientific name	Common name	GBMWHA prior incidence	Habitat prior incidence	Movement group	Body mass (g)
Cacatua galerita	Sulphur-crested Cockatoo	Moderately common	Uncommon	Migratory	735
Scythrops novaehollandiae	Channel-billed Cuckoo	Moderately common	Moderately common	Migratory	684
Strepera versicolor	Grey Currawong	Uncommon	Uncommon	Migratory	388
Strepera graculina	Pied Currawong	Common	Common	Migratory	308

Callocephalon fimbriatum	Gang-Gang Cockatoo	Moderately common	Uncommon	Migratory	257
Eudynamys orientalis	Eastern Koel	Uncommon	Uncommon	Migratory	243
Alisterus scapularis	Australian King-Parrot	Moderately common	Moderately common	Migratory	207
Macropygia amboinensis	Brown Cuckoo-Dove	Uncommon	Rare	Migratory	202
Falco cenchroides	Nankeen Kestrel	Moderately common	Uncommon	Migratory	179
Coracina novaehollandiae	Black-faced Cuckoo-shrike	Moderately common	Moderately common	Migratory	115
Oriolus sagittatus	Olive-backed Oriole	Moderately common	Moderately common	Migratory	97
Colluricincla harmonica	Grey Shrike-thrush	Common	Common	Migratory	67
Coracina tenuirostris	Cicadabird	Moderately common	Moderately common	Migratory	65
Todiramphus sanctus	Sacred Kingfisher	Moderately common	Moderately common	Migratory	53
Cacomantis flabelliformis	Fan-tailed Cuckoo	Common	Common	Migratory	50
Pachycephala pectoralis	Golden Whistler	Common	Moderately common	Migratory	39
Cacomantis variolosus	Brush Cuckoo	Uncommon	Uncommon	Migratory	37
Pachycephala rufiventris	Rufous Whistler	Common	Common	Migratory	24
Chrysococcyx lucidus	Shining Bronze-Cuckoo	Moderately common	Moderately common	Migratory	24
Monarcha melanopsis	Black-faced Monarch	Moderately common	Uncommon	Migratory	23
Chalcites basalis	Horsefield's Bronze-Cuckoo	Uncommon	Uncommon	Migratory	23
Lichenostomus leucotis	White-eared Honeyeater	Moderately common	Moderately common	Migratory	22
Lichenostomus chrysops	Yellow-faced Honeyeater	Common	Common	Migratory	16
Phylidonyris pyrrhopterus	Crescent Honeyeater	Uncommon	Rare	Migratory	15
Melithreptus lunatus	White-naped Honeyeater	Common	Moderately common	Migratory	15
Myiagra rubecula	Leaden Flycatcher	Common	Common	Migratory	14

Petroica phoenicea	Flame Robin	Uncommon	Uncommon	Migratory	13
Zosterops lateralis	Silvereye	Common	Common	Migratory	12
Acanthorhynchus tenuirostris	Eastern Spinebill	Common	Common	Migratory	10
Neochmia temporalis	Red-browed Finch	Common	Moderately common	Migratory	10
Rhipidura rufifrons	Rufous Fantail	Moderately common	Uncommon	Migratory	10
Dicaeum hirundinaceum	Mistletoebird	Moderately common	Moderately common	Migratory	9
Petroica goodenovii	Red-capped Robin	Rare	Rare	Migratory	9
Petroica rosea	Rose Robin	Moderately common	Uncommon	Migratory	9
Rhipidura albiscapa	Grey Fantail	Common	Common	Migratory	8
Pardalotus punctatus	Spotted Pardalote	Common	Common	Migratory	8
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	Moderately common	Moderately common	Nomadic	661
Phaps chalcoptera	Common Bronzewing	Moderately common	Uncommon	Nomadic	331
Cracticus tibicen	Australian Magpie	Moderately common	Uncommon	Nomadic	280
Ptilonorhynchus violaceus	Satin Bowerbird	Common	Moderately common	Nomadic	202
Trichoglossus haematodus	Rainbow Lorikeet	Uncommon	Uncommon	Nomadic	126
Philemon corniculatus	Noisy Friarbird	Common	Common	Nomadic	100
Anthochaera carunculata	Red Wattlebird	Moderately common	Moderately common	Nomadic	91
Artamus superciliosus	White-browed Woodswallow	Uncommon	Rare	Nomadic	35
Melithreptus brevirostris	Brown-headed Honeyeater	Moderately common	Moderately common	Nomadic	15
Alectura lathami	Australian Brush-turkey	Moderately common	Uncommon	Sedentary	2230
Menura novaehollandiae	Superb Lyrebird	Common	Common	Sedentary	1080
Corvus coronoides	Australian Raven	Moderately common	Moderately common	Sedentary	593

Leucosarcia melanoleuca	Wonga Pigeon	Moderately common	Uncommon	Sedentary	429
Dacelo novaeguineae	Laughing Kookaburra	Common	Common	Sedentary	312
Phaps elegans	Brush Bronzewing	Uncommon	Uncommon	Sedentary	203
Platycercus elegans	Crimson Rosella	Common	Common	Sedentary	126
Cinclosoma punctatum	Spotted Quail-thrush	Moderately common	Moderately common	Sedentary	112
Turdus merula	Common Blackbird†	-	Rare	Sedentary	105
Platycercus eximius	Eastern Rosella	Uncommon	Rare	Sedentary	104
Cracticus torquatus	Grey Butcherbird	Moderately common	Moderately common	Sedentary	91
Psophodes olivaceus	Eastern Whipbird	Common	Moderately common	Sedentary	59
Meliphaga lewinii	Lewin's Honeyeater	Common	Moderately common	Sedentary	33
Pycnoptilus floccosus	Pilotbird	Moderately common	Uncommon	Sedentary	30
Falcunculus frontatus	Crested Shrike-tit	Uncommon	Rare	Sedentary	26
Climacteris erythrops	Red-browed Treecreeper	Moderately common	Uncommon	Sedentary	23
Phylidonyris novaehollandiae	New Holland Honeyeater	Common	Common	Sedentary	21
Cormobates leucophaea	White-throated Treecreeper	Common	Common	Sedentary	21
Eopsaltria australis	Eastern Yellow Robin	Common	Common	Sedentary	19
Hylacola pyrrhopygia	Chestnut-rumped Heathwren	Uncommon	Uncommon	Sedentary	17
Sericornis frontalis	White-browed Scrubwren	Common	Common	Sedentary	13
Malurus cyaneus	Superb Fairy-wren	Moderately common	Uncommon	Sedentary	11
Sericornis magnirostra	Large-billed Scrubwren	Uncommon	Rare	Sedentary	10
Acanthiza pusilla	Brown Thornbill	Common	Common	Sedentary	9
Malurus lamberti	Variegated Fairy-wren	Moderately common	Moderately common	Sedentary	8

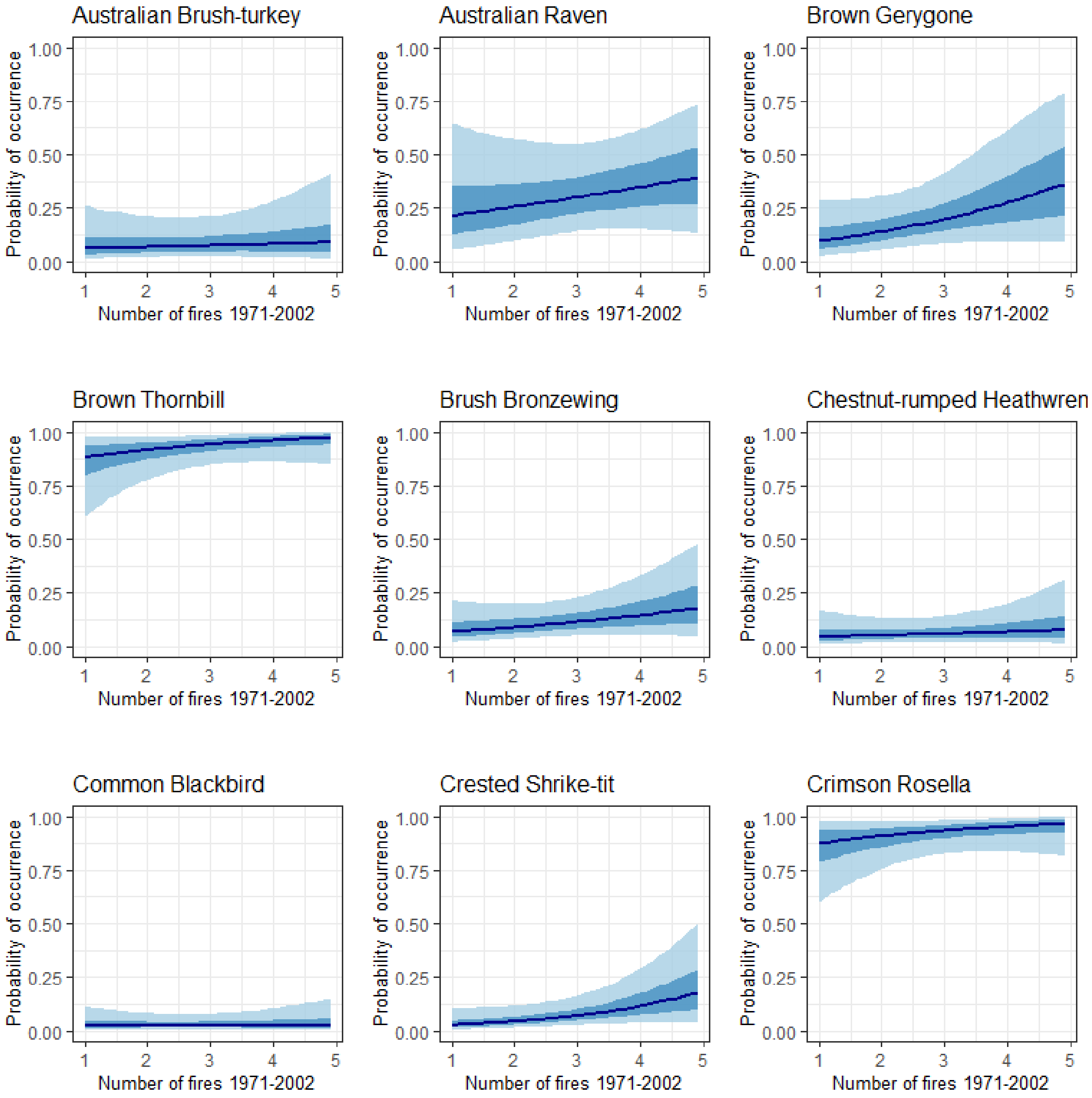
Stipiturus malachurus	Southern Emu-wren	Uncommon	Rare	Sedentary	7
Acanthiza lineata	Striated Thornbill	Common	Common	Sedentary	7
Smicrornis brevirostris	Weebill	Moderately common	Uncommon	Sedentary	6
Gerygone mouki	Brown Gerygone	Moderately common	Uncommon	Sedentary	5

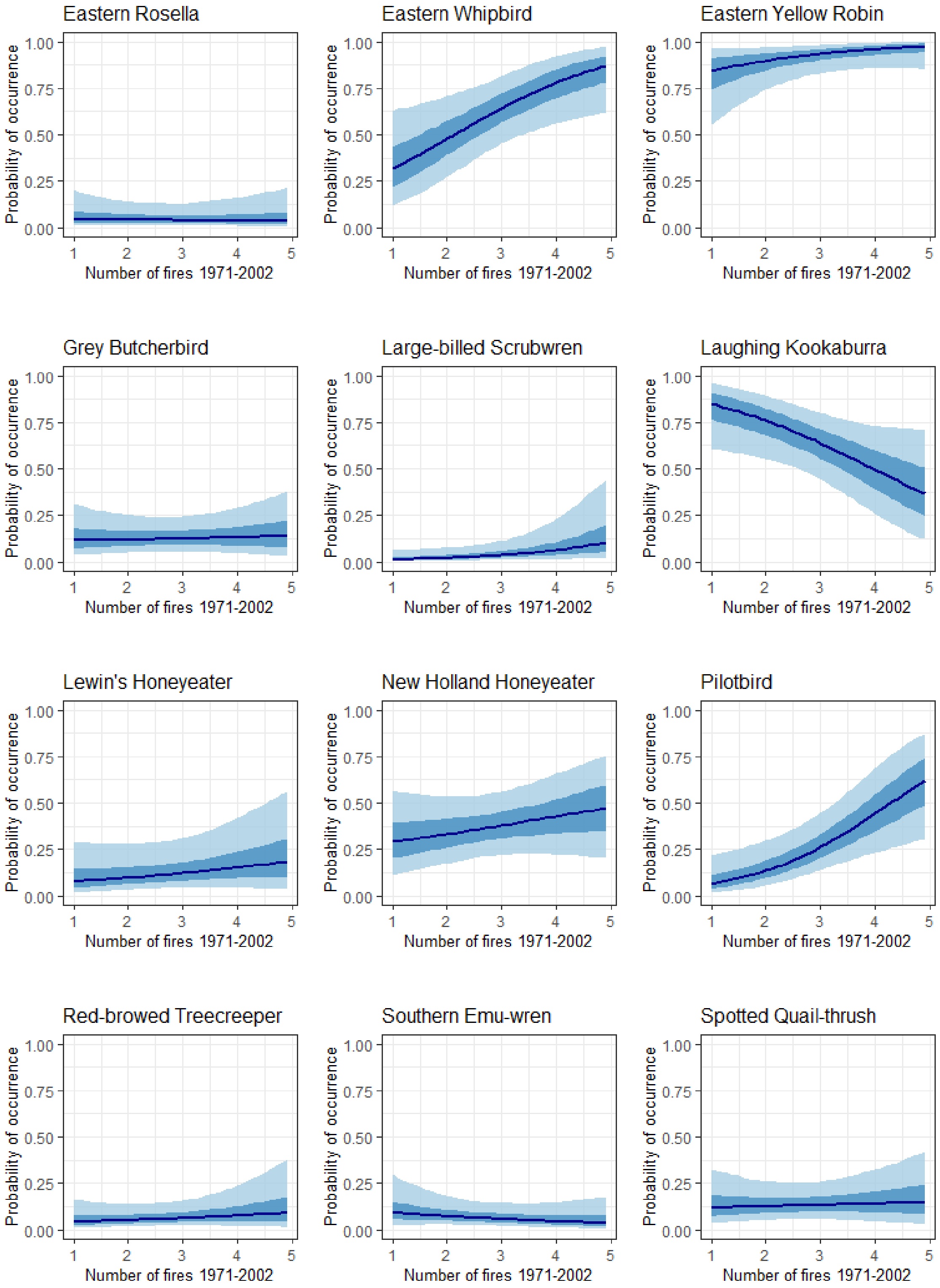
† The Common Blackbird was the only introduced species detected in the study and it was not included in Smith et al. (2019). The prior incidence of this species was assigned based on the description by Birdlife Australia (2021).

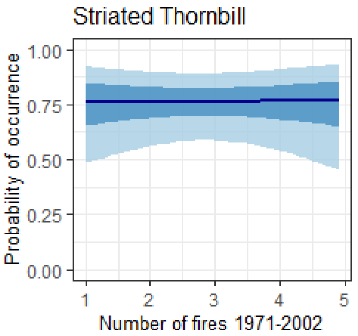
Appendix C.2. Modelled species occupancy in relation to fire frequency and long unburnt forest in the surrounding landscape.

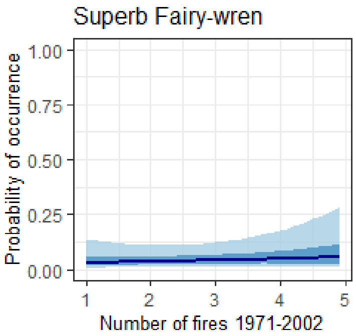
Fig. C.2.1. The probability of occurrence of species in relation to the area-weighted mean number of fires over a 31-year period. Median probabilities are indicated by lines, with bands representing the interquartile range and central 90% of distributions.

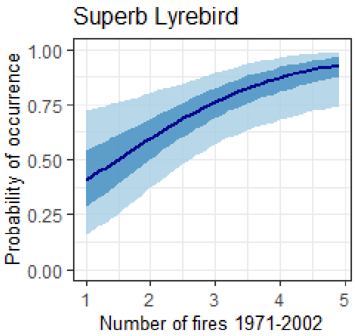
Sedentary species

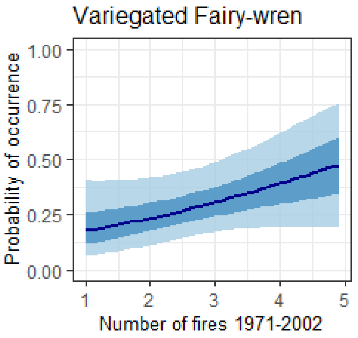


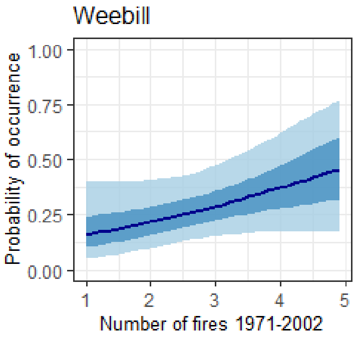

Eastern Rosella
Eastern Whipbird
Eastern Yellow Robin
Grey Butcherbird
Large-billed Scrubwren
Laughing Kookaburra
Lewin's Honeyeater
New Holland Honeyeater
Pilotbird
Red-browed Treecreeper
Southern Emu-wren
Spotted Quail-thrush
Probability of occurrence
1.00
0.75
0.50
0.25
0.00
1
2
3
4
5
Number of fires 1971-2002

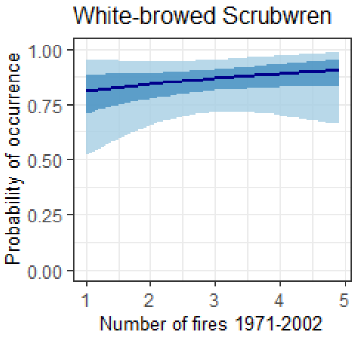


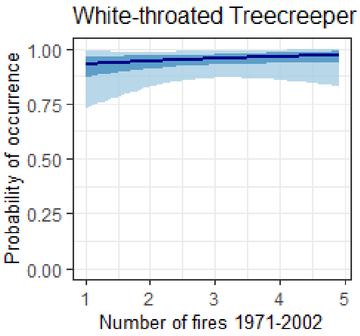


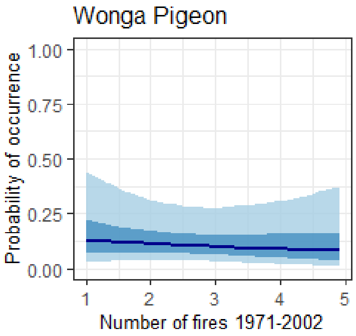




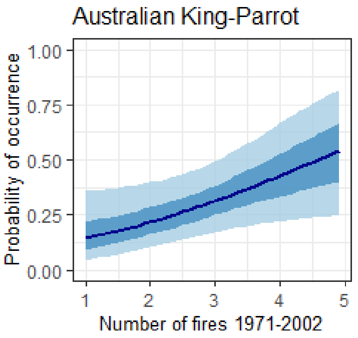


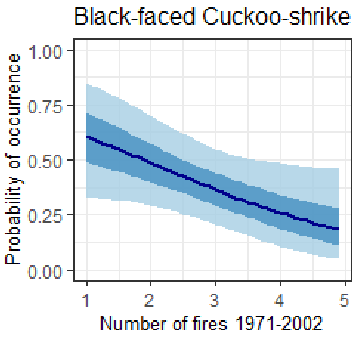


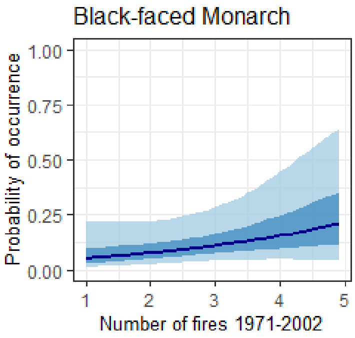


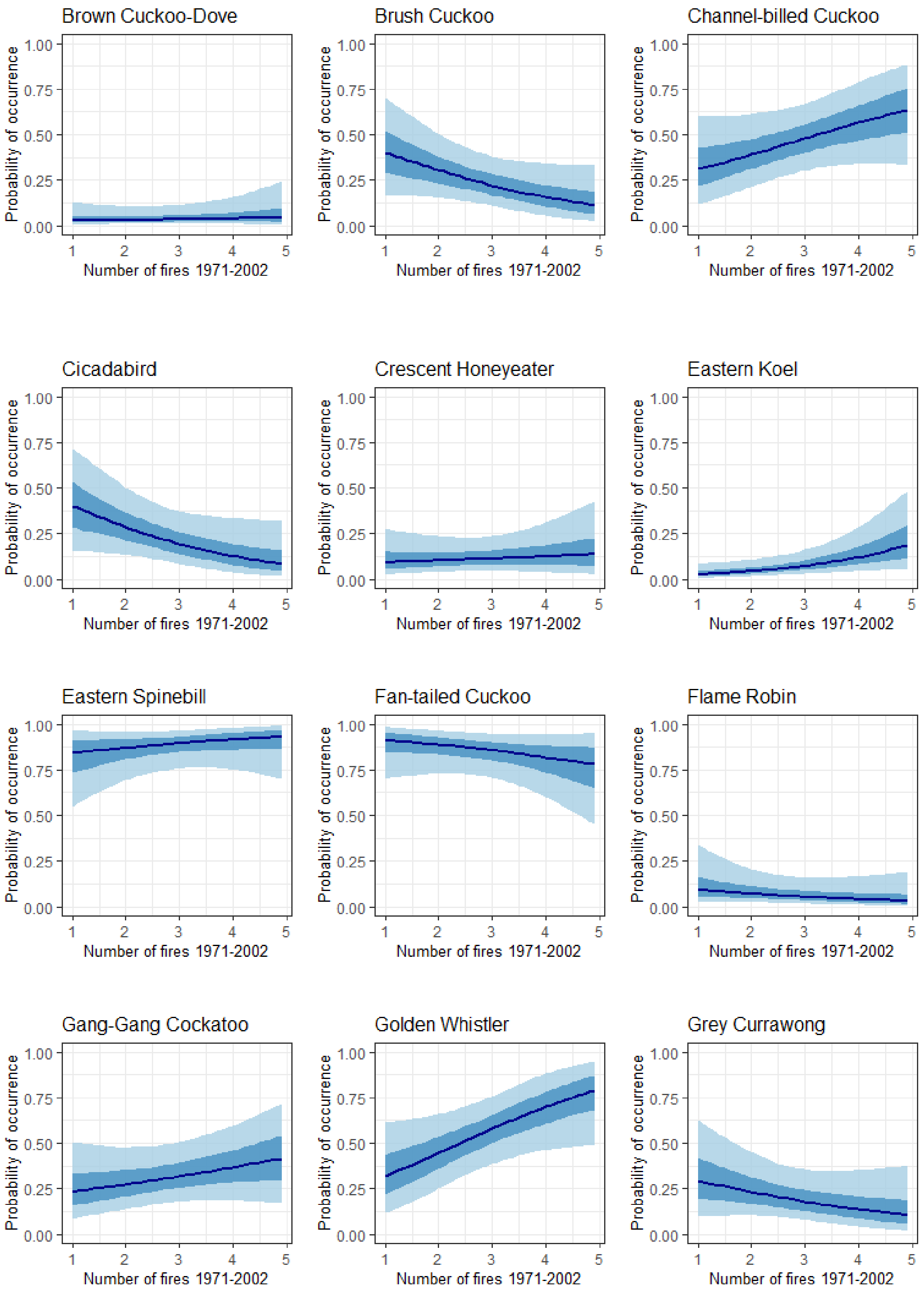


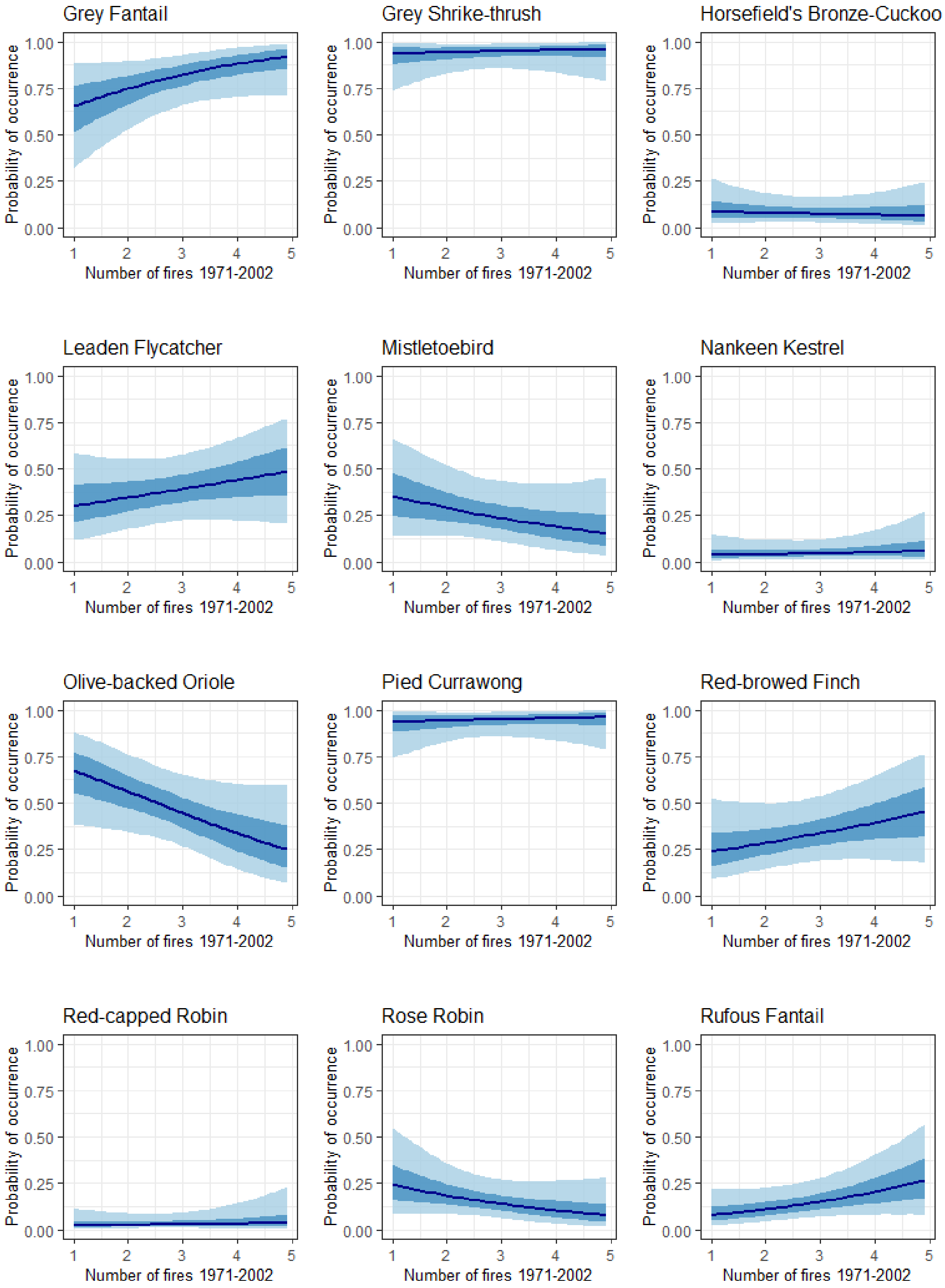
Migratory species

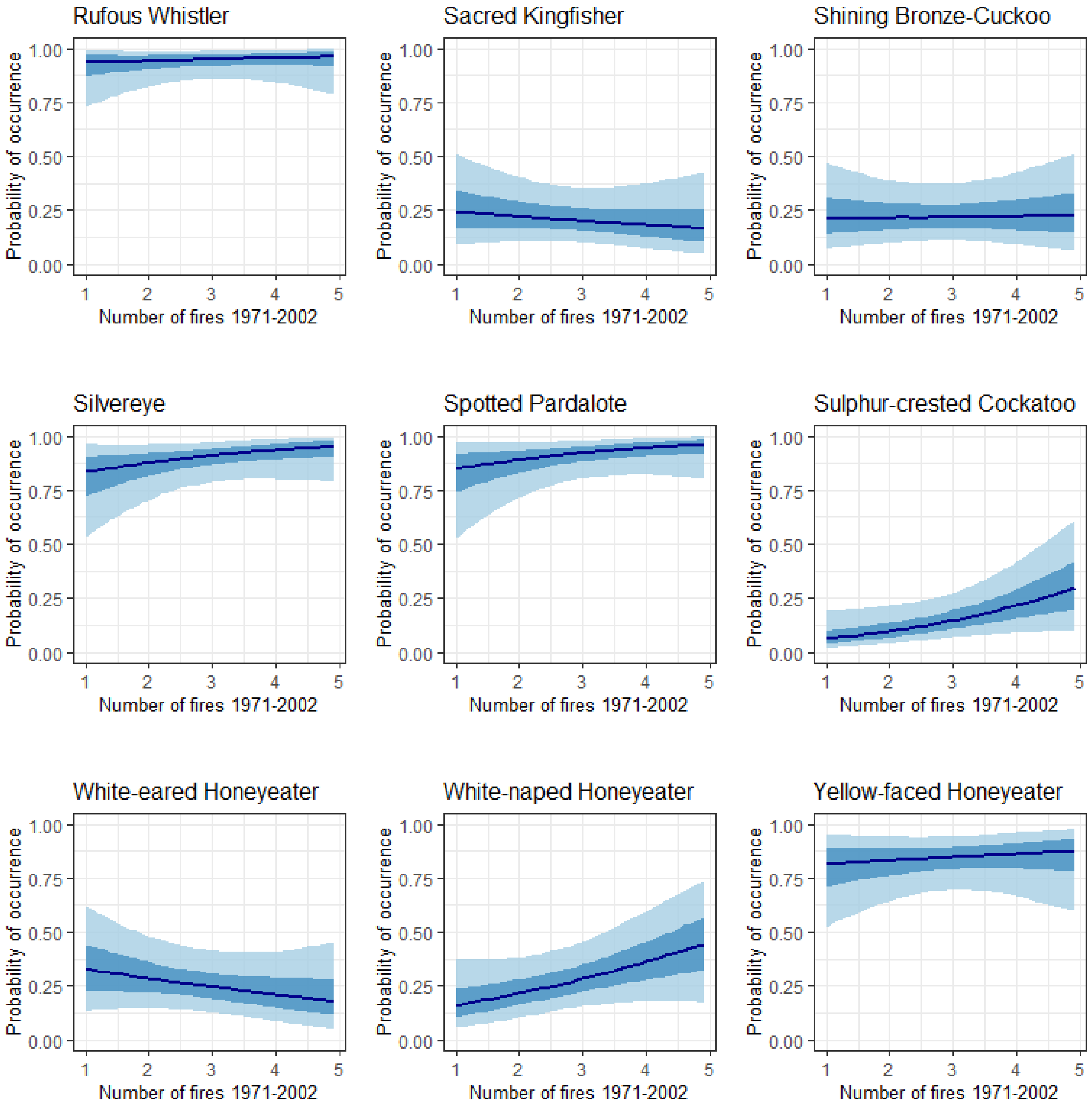




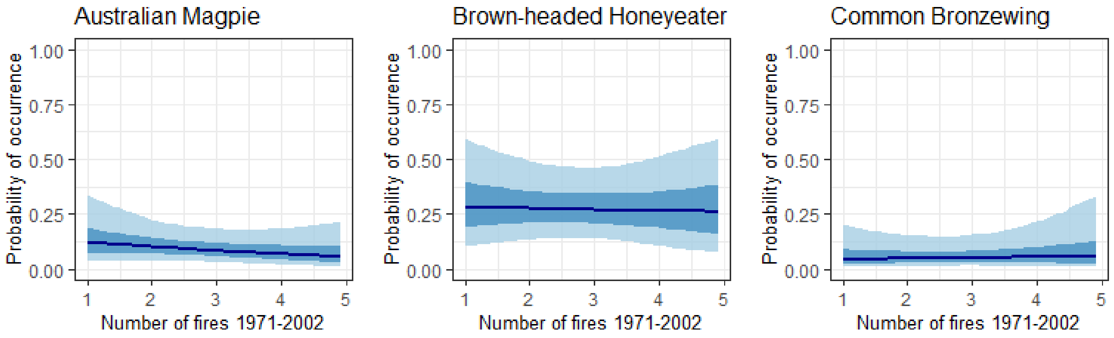



Brown Cuckoo-Dove
Brush Cuckoo
Channel-billed Cuckoo
Cicadabird
Crescent Honeyeater
Eastern Koel
Eastern Spinebill
Fan-tailed Cuckoo
Flame Robin
Gang-Gang Cockatoo
Golden Whistler
Grey Currawong
Probability of occurrence
0.00
0.25
0.50
0.75
1.00
Number of fires 1971-2002
1
2
3
4
5


Grey Fantail
Grey Shrike-thrush
Horsefield's Bronze-Cuckoo
Leaden Flycatcher
Mistletoebird
Nankeen Kestrel
Olive-backed Oriole
Pied Currawong
Red-browed Finch
Red-capped Robin
Rose Robin
Rufous Fantail
Probability of occurrence
0.00
0.25
0.50
0.75
1.00
Number of fires 1971-2002
1
2
3
4
5



Nomadic species



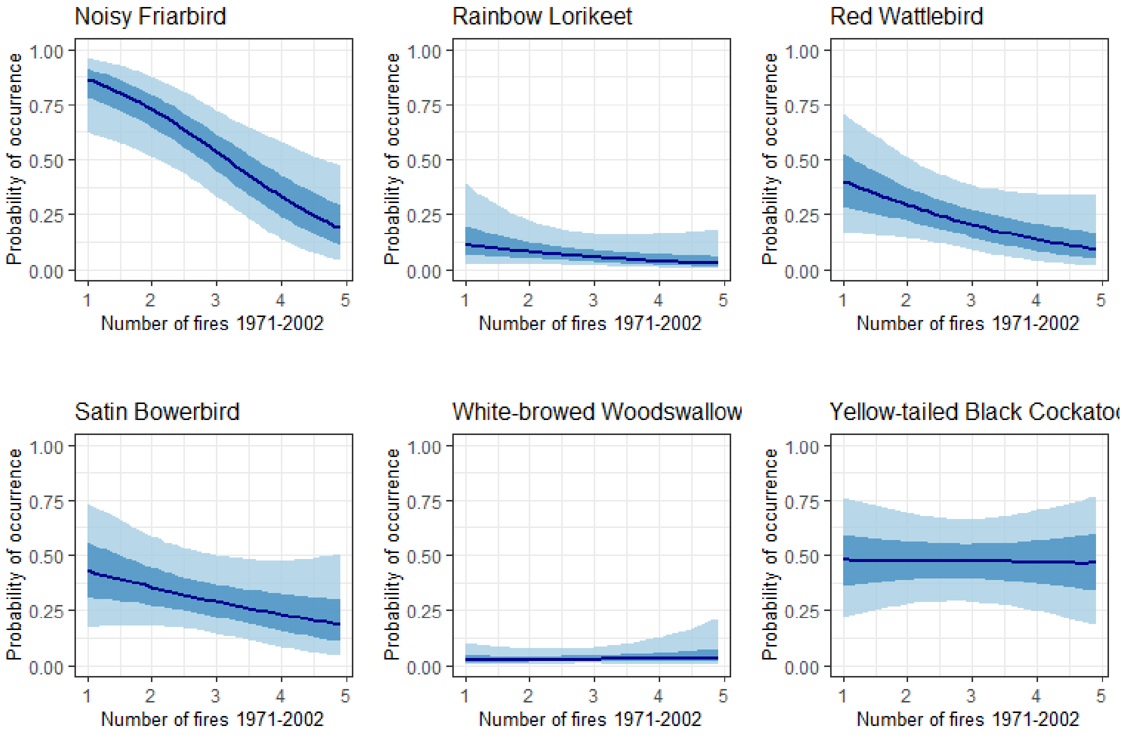
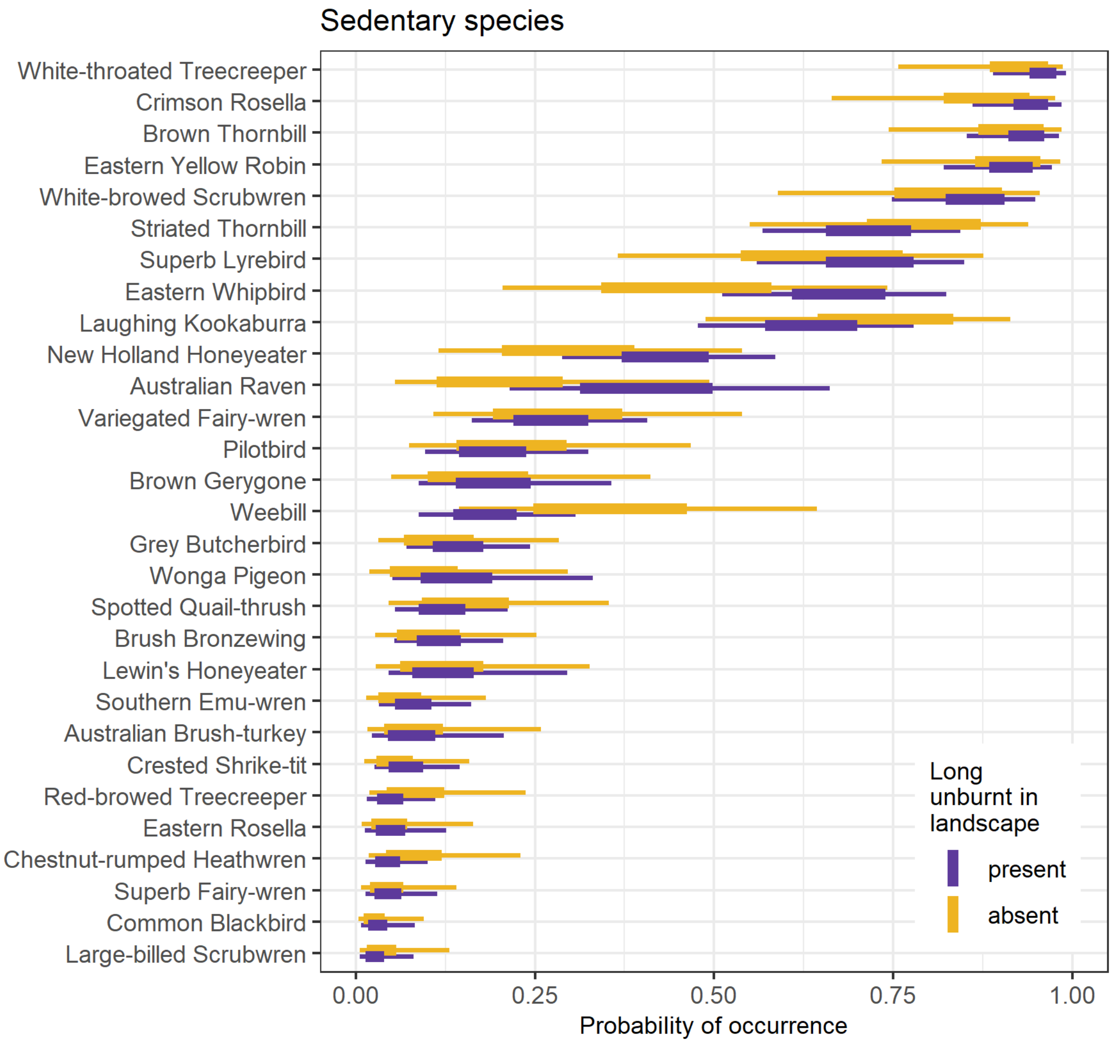
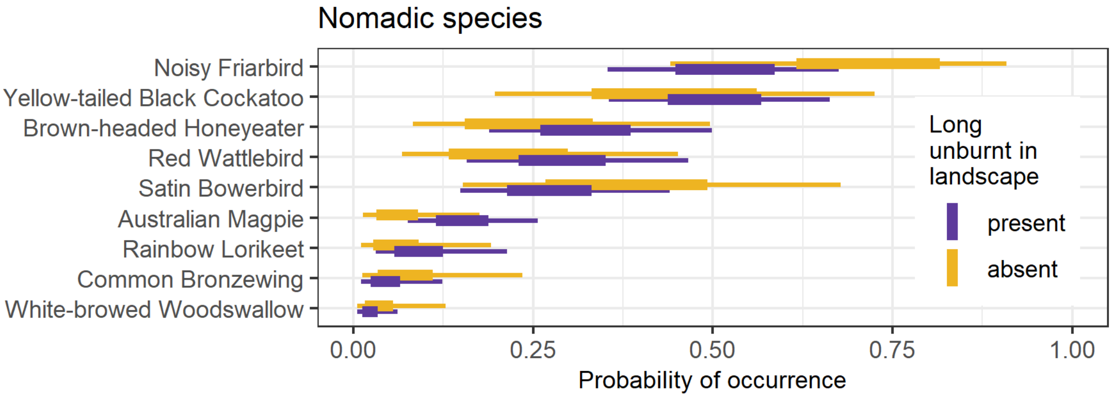
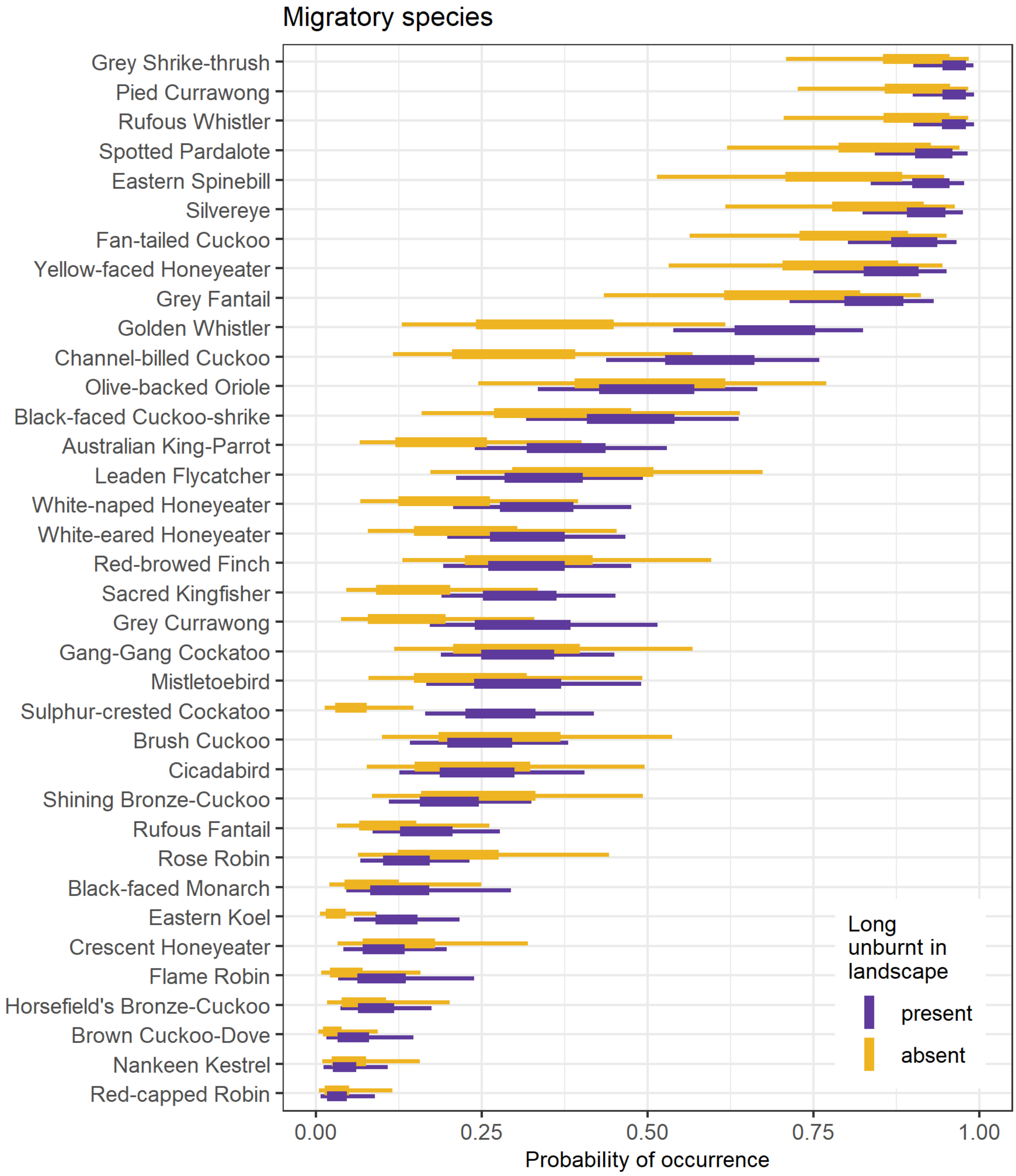

Noisy Friarbird
Rainbow Lorikeet
Red Wattlebird
Satin Bowerbird
White-browed Woodswallow
Yellow-tailed Black Cockato
Probability of occurrence
0.00
0.25
0.50
0.75
1.00
1
2
3
4
5
Number of fires 1971-2002

Fig. C.2.2. The probability of occurrence of species when long unburnt forest was present or absent in the surrounding landscape (10 km^2). Bars represent the interquartile range and central 90% of distributions.






Migratory species
Grey Shrike-thrush
Pied Currawong
Rufous Whistler
Spotted Pardalote
Eastern Spinebill
Silvereye
Fan-tailed Cuckoo
Yellow-faced Honeyeater
Grey Fantail
Golden Whistler
Channel-billed Cuckoo
Olive-backed Oriole
Black-faced Cuckoo-shrike
Australian King-Parrot
Leaden Flycatcher
White-naped Honeyeater
White-eared Honeyeater
Red-browed Finch
Sacred Kingfisher
Grey Currawong
Gang-Gang Cockatoo
Mistletoebird
Sulphur-crested Cockatoo
Brush Cuckoo
Cicadabird
Shining Bronze-Cuckoo
Rufous Fantail
Rose Robin
Black-faced Monarch
Eastern Koel
Crescent Honeyeater
Flame Robin
Horsefield's Bronze-Cuckoo
Brown Cuckoo-Dove
Nankeen Kestrel
Red-capped Robin
0.00
0.25
0.50
0.75
1.00
Probability of occurrence
Long unburnt in landscape
present
absent

Appendix D. Supplementary material for Chapter 5

Appendix D.1. Ordination plots from Bayesian latent variable models.

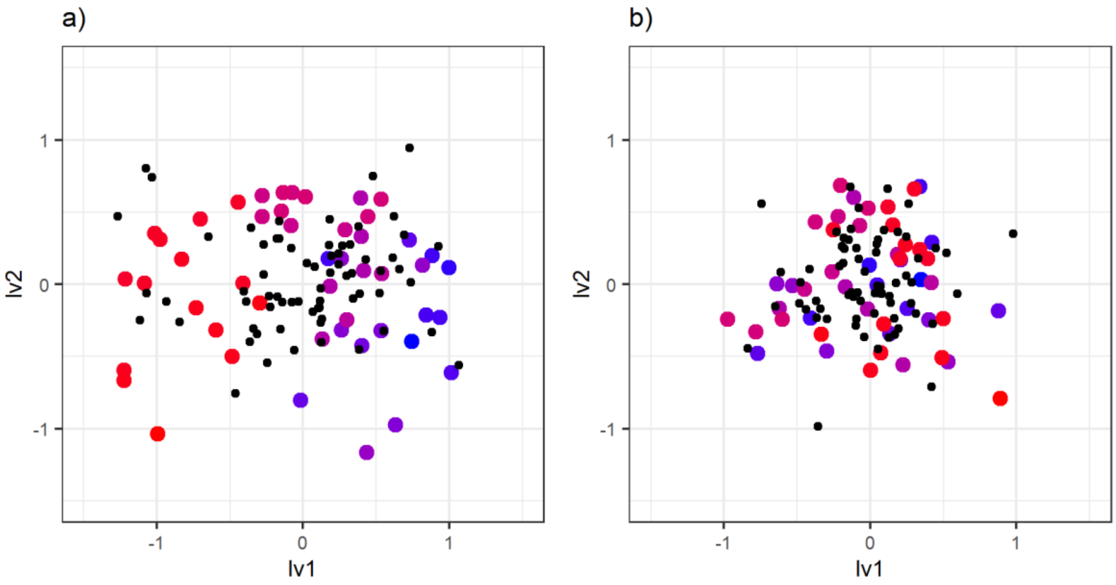
To visualise relationships among sites in terms of their species composition, we fitted an unconstrained ordination via Bayesian latent variable modelling using the boral package (Hui 2016) in R (R Core Team 2021). The resulting plot is analogous to a multi-dimensional scaling ordination plot and can be interpreted similarly (Hui et al. 2015). Response data was in the form of species detection/non-detection (1/0) in each site. The occurrence of species *i* in site *j* was modelled as:

$$\text{probit}(\mu_{ij}) = \alpha_j + \beta_{0i} + z_j^{T}\theta_i \qquad \text{Equation D.1.1}$$

where α_j is a random effect for site *j*, β_{0i} is a species-specific intercept, z_j is a vector of two latent variables for $j = 1,\ldots,48$ sites and θ_i represents a vector of coefficients that relate species ($i = 1,\ldots,p$) responses to the latent variables (Hui et al. 2015, Hui 2016). Model priors and MCMC settings were the same as those used for the latent variable model specified in the main article.

The unconstrained ordination plot revealed that avian assemblages were structured according to latitude (Fig. D.1.1a), corresponding to the spatial distribution of sites (Fig. 2 main article). Consequently, we accounted for the effect of latitude by including it as a standardised covariate (LAT), along with fire variables, in the final latent variable model (Equation 1 main article, Fig. D.1.1b).

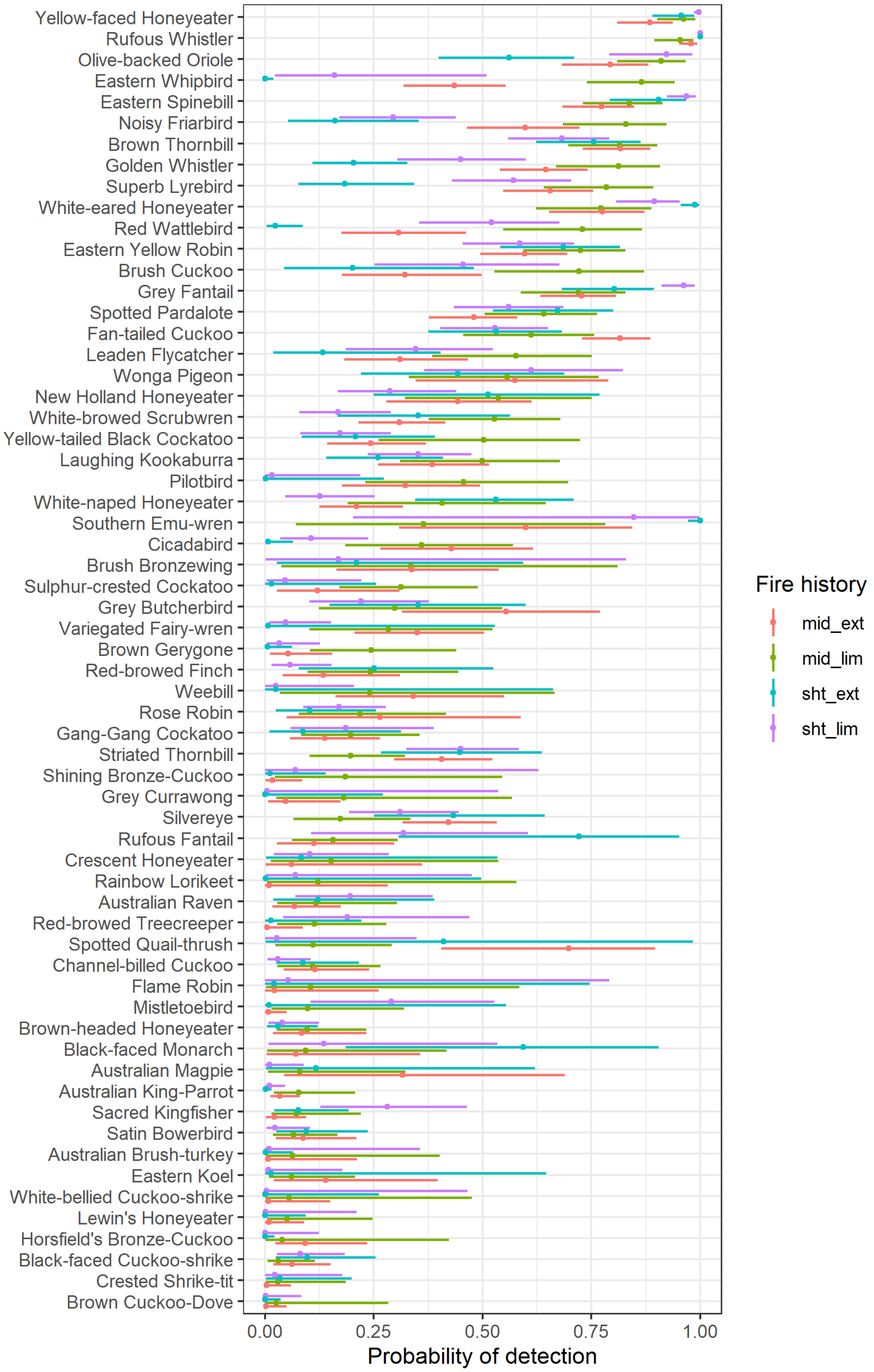
Fig. D.1.1. Ordination plots used to visualise relationships among sites and species, before and after the addition of explanatory variables to the model. Sites are shown as points on a colour gradient representing their location on a latitudinal gradient from south (blue) to north (red). Species are represented as black points. An unconstrained ordination plot (a) was generated from a preliminary model that included two latent variables, random site effects and no predictors (Equation D.1.1). A residual biplot (b) was produced from the final correlated response model that included two latent variables, random site effects and fire variables (Equation 5.1 main article).



Appendix D.2. Estimated species detection probabilities under different fire histories.

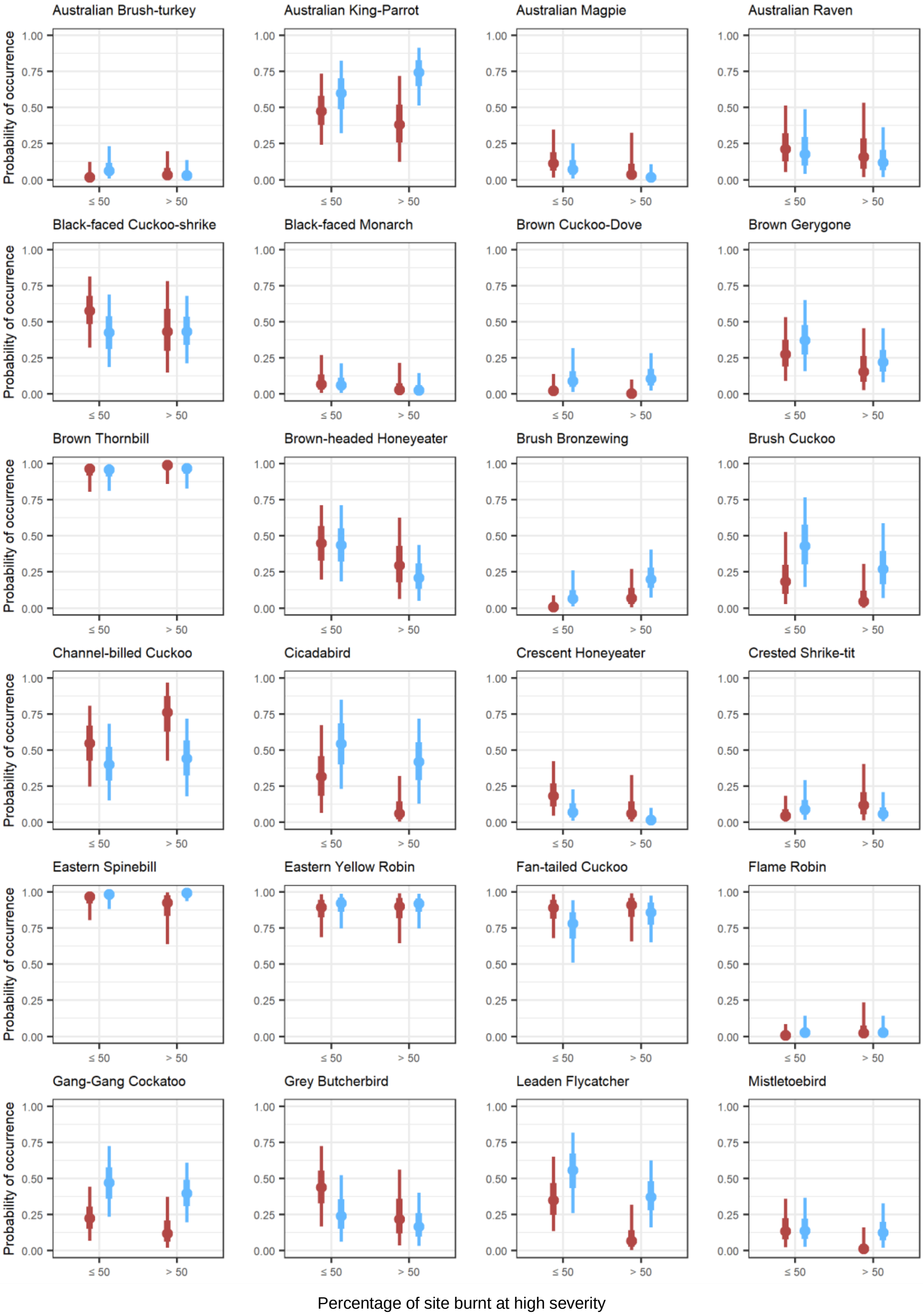
To assess the potential for the effects of different fire regimes on habitat to alter species detectability, we used a Bayesian multispecies occupancy model to estimate species detection probabilities (Furnas & McGrann 2018, Franklin et al. 2020) for each of the four fire history combinations used in the study.

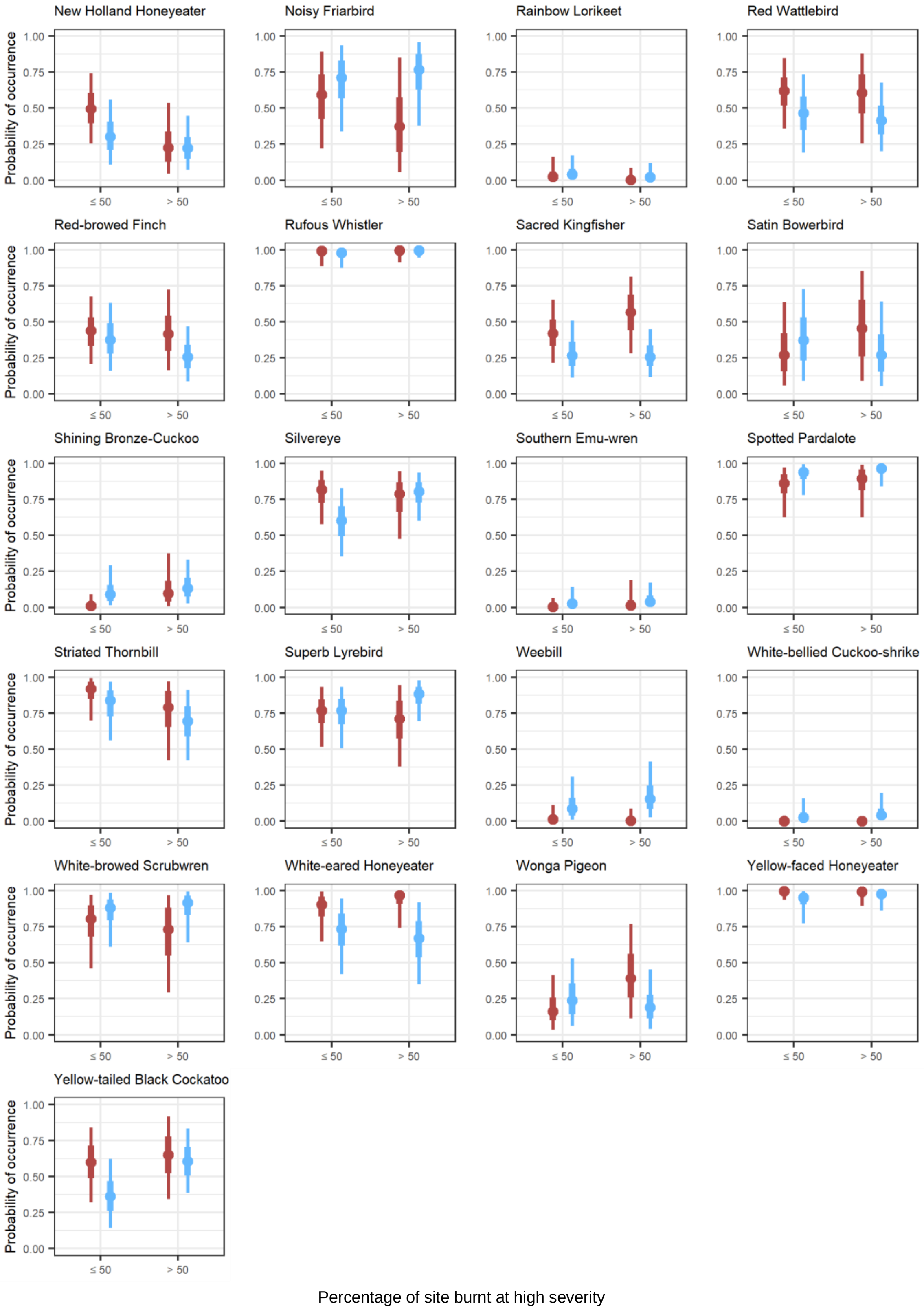
Fig. D.2.1. The probability of detecting species under the four fire histories used in the study. The fire histories shown represent combinations of mid-range (mid) or short (sht) time since fire, with either spatially extensive (ext) or limited (lim) historical high-severity fire. See the methods section in the article for further details. Bars around medians (circles) represent the central 90% of distributions of Bayesian multispecies occupancy model predictions. Species detected in less than three or more than 46 of the 48 total sites are not shown.


Yellow-faced Honeyeater
Rufous Whistler
Olive-backed Oriole
Eastern Whipbird
Eastern Spinebill
Noisy Friarbird
Brown Thornbill
Golden Whistler
Superb Lyrebird
White-eared Honeyeater
Red Wattlebird
Eastern Yellow Robin
Brush Cuckoo
Grey Fantail
Spotted Pardalote
Fan-tailed Cuckoo
Leaden Flycatcher
Wonga Pigeon
New Holland Honeyeater
White-browed Scrubwren
Yellow-tailed Black Cockatoo
Laughing Kookaburra
Pilotbird
White-naped Honeyeater
Southern Emu-wren
Cicadabird
Brush Bronzewing
Sulphur-crested Cockatoo
Grey Butcherbird
Variegated Fairy-wren
Brown Gerygone
Red-browed Finch
Weebill
Rose Robin
Gang-Gang Cockatoo
Striated Thornbill
Shining Bronze-Cuckoo
Grey Currawong
Silvereye
Rufous Fantail
Crescent Honeyeater
Rainbow Lorikeet
Australian Raven
Red-browed Treecreeper
Spotted Quail-thrush
Channel-billed Cuckoo
Flame Robin
Mistletoebird
Brown-headed Honeyeater
Black-faced Monarch
Australian Magpie
Australian King-Parrot
Sacred Kingfisher
Satin Bowerbird
Australian Brush-turkey
Eastern Koel
White-bellied Cuckoo-shrike
Lewin's Honeyeater
Horsfield's Bronze-Cuckoo
Black-faced Cuckoo-shrike
Crested Shrike-tit
Brown Cuckoo-Dove
0.00
0.25
0.50
0.75
1.00
Probability of detection
Fire history
mid_ext
mid_lim
sht_ext
sht_lim

Appendix D.3. The probability of occurrence of species not shown in the main article, in relation to fire predictors. Species detected in all sites, or less than three sites, (Appendix D.4) are not shown.

Fig. D.3.1. The probability of occurrence of species in relation to time since fire and the spatial extent of historical high-severity fire. Vertical bars around medians (circles) represent the interquartile range and central 90% of distributions, with colours indicating short (red) and mid-range (light blue) time since fire. See Appendix D.4 for species scientific names.


Australian Brush-turkey
Australian King-Parrot
Australian Magpie
Australian Raven
Black-faced Cuckoo-shrike
Black-faced Monarch
Brown Cuckoo-Dove
Brown Gerygone
Brown Thornbill
Brown-headed Honeyeater
Brush Bronzewing
Brush Cuckoo
Channel-billed Cuckoo
Cicadabird
Crescent Honeyeater
Crested Shrike-tit
Eastern Spinebill
Eastern Yellow Robin
Fan-tailed Cuckoo
Flame Robin
Gang-Gang Cockatoo
Grey Butcherbird
Leaden Flycatcher
Mistletoebird
Probability of occurrence
1.00
0.75
0.50
0.25
0.00
≤ 50
> 50
Percentage of site burnt at high severity


New Holland Honeyeater
Noisy Friarbird
Rainbow Lorikeet
Red Wattlebird
Red-browed Finch
Rufous Whistler
Sacred Kingfisher
Satin Bowerbird
Shining Bronze-Cuckoo
Silvereye
Southern Emu-wren
Spotted Pardalote
Striated Thornbill
Superb Lyrebird
Weebill
White-bellied Cuckoo-shrike
White-browed Scrubwren
White-eared Honeyeater
Wonga Pigeon
Yellow-faced Honeyeater
Yellow-tailed Black Cockatoo
Probability of occurrence
1.00
0.75
0.50
0.25
0.00
≤ 50
> 50
Percentage of site burnt at high severity

Appendix D.4. Species information.

Table D.4.1. Common and scientific names of the 74 species detected in the study, with the number of sites (total = 48) in which each species was detected.

Scientific name	Common name	No. sites
Platycercus elegans	Crimson Rosella	48
Colluricincla harmonica	Grey Shrike-thrush	48
Strepera graculina	Pied Currawong	48
Cormobates leucophaea	White-throated Treecreeper	48
Pachycephala rufiventris	Rufous Whistler	46
Rhipidura albiscapa	Grey Fantail	45
Lichenostomus chrysops	Yellow-faced Honeyeater	45
Acanthiza pusilla	Brown Thornbill	43
Acanthorhynchus tenuirostris	Eastern Spinebill	43
Pardalotus punctatus	Spotted Pardalote	42
Eopsaltria australis	Eastern Yellow Robin	41
Cacomantis flabelliformis	Fan-tailed Cuckoo	39
Pachycephala pectoralis	Golden Whistler	39
Acanthiza lineata	Striated Thornbill	35
Menura novaehollandiae	Superb Lyrebird	35
Zosterops lateralis	Silvereye	34
Sericornis frontalis	White-browed Scrubwren	34
Dacelo novaeguineae	Laughing Kookaburra	33
Lichenostomus leucotis	White-eared Honeyeater	32
Philemon corniculatus	Noisy Friarbird	29
Oriolus sagittatus	Olive-backed Oriole	28
Alisterus scapularis	Australian King-Parrot	26
Melithreptus lunatus	White-naped Honeyeater	26
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	26
Anthochaera carunculata	Red Wattlebird	24
Coracina novaehollandiae	Black-faced Cuckoo-shrike	23
Scythrops novaehollandiae	Channel-billed Cuckoo	23
Psophodes olivaceus	Eastern Whipbird	21
Ptilonorhynchus violaceus	Satin Bowerbird	20
Melithreptus brevirostris	Brown-headed Honeyeater	19
Coracina tenuirostris	Cicadabird	19
Myiagra rubecula	Leaden Flycatcher	18

Neochmia temporalis	Red-browed Finch	18
Petroica rosea	Rose Robin	18
Cacomantis variolosus	Brush Cuckoo	17
Phylidonyris novaehollandiae	New Holland Honeyeater	17
Todiramphus sanctus	Sacred Kingfisher	17
Callocephalon fimbriatum	Gang-Gang Cockatoo	16
Cracticus torquatus	Grey Butcherbird	16
Leucosarcia melanoleuca	Wonga Pigeon	15
Gerygone mouki	Brown Gerygone	14
Malurus lamberti	Variegated Fairy-wren	14
Corvus coronoides	Australian Raven	13
Cacatua galerita	Sulphur-crested Cockatoo	13
Rhipidura rufifrons	Rufous Fantail	10
Dicaeum hirundinaceum	Mistletoebird	9
Pycnoptilus floccosus	Pilotbird	9
Chalcites basalis	Horsfield's Bronze-Cuckoo	8
Strepera versicolor	Grey Currawong	7
Climacteris erythrops	Red-browed Treecreeper	7
Chrysococcyx lucidus	Shining Bronze-Cuckoo	7
Cracticus tibicen	Australian Magpie	6
Monarcha melanopsis	Black-faced Monarch	6
Falcunculus frontatus	Crested Shrike-tit	6
Stipiturus malachurus	Southern Emu-wren	6
Cinclosoma punctatum	Spotted Quail-thrush	6
Smicrornis brevirostris	Weebill	6
Phaps elegans	Brush Bronzewing	5
Phylidonyris pyrrhopterus	Crescent Honeyeater	5
Eudynamys orientalis	Eastern Koel	5
Macropygia amboinensis	Brown Cuckoo-Dove	4
Meliphaga lewinii	Lewin's Honeyeater	4
Alectura lathami	Australian Brush-turkey	3
Petroica phoenicea	Flame Robin	3
Trichoglossus haematodus	Rainbow Lorikeet	3
Coracina papuensis	White-bellied Cuckoo-shrike	3
Manorina melanophrys	Bell Miner	2
Sericornis magnirostra	Large-billed Scrubwren	2
Malurus cyaneus	Superb Fairy-wren	2
Hylacola pyrrhopygia	Chestnut-rumped Heathwren	1
Platycercus eximius	Eastern Rosella	1

Falco peregrinus	Peregrine Falcon	1
Myzomela sanguinolenta	Scarlet Honeyeater	1
Artamus superciliosus	White-browed Woodswallow	1

Appendix E. Supplementary material for Chapter 6

Appendix E.1. Species information.

Table E.1.1. Common and scientific names of the 74 species detected in the study and their primary foraging stratum (Marchant & Higgins 1994, Higgins & Davies 1996, Higgins & Davies 1996, Loyn 1997, Higgins 1999, Higgins et al. 2001, Higgins & Peter 2002, Higgins et al. 2006, Sitters et al. 2016, Smith et al. 2019).

Common name	Scientific name	Foraging stratum†
Falco peregrinus	Peregrine Falcon	A/G
Alisterus scapularis	Australian King-Parrot	All
Coracina novaehollandiae	Black-faced Cuckoo-shrike	All
Monarcha melanopsis	Black-faced Monarch	All
Macropygia amboinensis	Brown Cuckoo-Dove	All
Cacomantis variolosus	Brush Cuckoo	All
Gerygone mouki	Brown Gerygone	All
Phylidonyris pyrrhopterus	Crescent Honeyeater	All
Platycercus elegans	Crimson Rosella	All
Acanthorhynchus tenuirostris	Eastern Spinebill	All
Platycercus eximius	Eastern Rosella	All
Strepera versicolor	Grey Currawong	All
Pachycephala pectoralis	Golden Whistler	All
Cracticus torquatus	Grey Butcherbird	All
Colluricincla harmonica	Grey Shrike-thrush	All
Chalcites basalis	Horsfield's Bronze-Cuckoo	All
Sericornis magnirostra	Large-billed Scrubwren	All
Meliphaga lewinii	Lewin's Honeyeater	All
Phylidonyris novaehollandiae	New Holland Honeyeater	All
Philemon corniculatus	Noisy Friarbird	All
Strepera graculina	Pied Currawong	All
Climacteris erythrops	Red-browed Treecreeper	All
Anthochaera carunculata	Red Wattlebird	All
Trichoglossus haematodus	Rainbow Lorikeet	All

Petroica rosea	Rose Robin	All
Chrysococcyx lucidus	Shining Bronze-Cuckoo	All
Ptilonorhynchus violaceus	Satin Bowerbird	All
Zosterops lateralis	Silvereye	All
Artamus superciliosus	White-browed Woodswallow	All
Lichenostomus leucotis	White-eared Honeyeater	All
Melithreptus lunatus	White-naped Honeyeater	All
Cormobates leucophaea	White-throated Treecreeper	All
Lichenostomus chrysops	Yellow-faced Honeyeater	All
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	All
Manorina melanophrys	Bell Miner	C/S
Melithreptus brevirostris	Brown-headed Honeyeater	C/S
Scythrops novaehollandiae	Channel-billed Cuckoo	C/S
Coracina tenuirostris	Cicadabird	C/S
Falcunculus frontatus	Crested Shrike-tit	C/S
Callocephalon fimbriatum	Gang-Gang Cockatoo	C/S
Rhipidura albiscapa	Grey Fantail	C/S
Eudynamys orientalis	Eastern Koel	C/S
Myiagra rubecula	Leaden Flycatcher	C/S
Dicaeum hirundinaceum	Mistletoebird	C/S
Oriolus sagittatus	Olive-backed Oriole	C/S
Pachycephala rufiventris	Rufous Whistler	C/S
Myzomela sanguinolenta	Scarlet Honeyeater	C/S
Pardalotus punctatus	Spotted Pardalote	C/S
Acanthiza lineata	Striated Thornbill	C/S
Coracina papuensis	White-bellied Cuckoo-shrike	C/S
Smicrornis brevirostris	Weebill	C/S
Alectura lathami	Australian Brush-turkey	G/U
Cracticus tibicen	Australian Magpie	G/U
Corvus coronoides	Australian Raven	G/U
Phaps elegans	Brush Bronzewing	G/U
Acanthiza pusilla	Brown Thornbill	G/U
Hylacola pyrrhopygia	Chestnut-rumped Heathwren	G/U
Psophodes olivaceus	Eastern Whipbird	G/U
Eopsaltria australis	Eastern Yellow Robin	G/U
Petroica phoenicea	Flame Robin	G/U

Cacomantis flabelliformis	Fan-tailed Cuckoo	G/U
Dacelo novaeguineae	Laughing Kookaburra	G/U
Pycnoptilus floccosus	Pilotbird	G/U
Neochmia temporalis	Red-browed Finch	G/U
Rhipidura rufifrons	Rufous Fantail	G/U
Todiramphus sanctus	Sacred Kingfisher	G/U
Cacatua galerita	Sulphur-crested Cockatoo	G/U
Menura novaehollandiae	Superb Lyrebird	G/U
Stipiturus malachurus	Southern Emu-wren	G/U
Cinclosoma punctatum	Spotted Quail-thrush	G/U
Malurus cyaneus	Superb Fairy-wren	G/U
Malurus lamberti	Variegated Fairy-wren	G/U
Sericornis frontalis	White-browed Scrubwren	G/U
Leucosarcia melanoleuca	Wonga Pigeon	G/U

† Guild category abbreviations: All (all strata), G/U (ground/understorey), C/S (canopy/subcanopy), A/G (aerial/ground).

END