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Fire responses by bird guilds and species in heathy dry forests in central Victoria, Australia

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ABSTRACT

Predicted increases in fire frequency and extent are being realised across Australia, bringing changes to the fire regime which may influence the availability of essential resources required by birds. However, few studies have examined either the impacts of fire frequency on birds or the impacts from both wildfire and planned burns, combined. Birds were surveyed eight times across 84 sites in heathy dry forests in central Victoria, south-east Australia, from 2012 to 2014. Fire history records were retrieved from the 1970's onwards, the time from which accurate planned burn records were kept. We developed mixed models to investigate how birds responded to time-since-fire and fire frequency, analysing total bird abundance, ten foraging guilds and 30 individual species. We found distinct responses by all modelled guilds and species to time-since-fire, along with evidence for responses to fire frequency. The greatest shifts in species' abundances occurred during the first ten years post fire, with bird species commonly present across the stages greater than ten years since fire. For total bird abundance there was no statistically detectable difference between recently burnt forest (0-6 months) and other age classes. However, some guilds showed a significant drop in abundance in newly burnt vegetation (e.g. bark foragers, damp ground insectivores, those that feed on seeds close to the ground, tall shrub foragers). It is with guild and species' responses that more differences across vegetation age classes became apparent. Significant increases in abundance were apparent in both the regrowth and new growth vegetation age classes, compared with older habitat (e.g. canopy foragers, damp ground insectivores, tall shrub foragers); open ground foragers were especially common in post-fire regrowth but then significantly declined. Other responses were more complex, with species' preferences reflecting their foraging ecology. Some birds showed preferences across two age classes: sites that were young post-fire regrowth (6 months–2.5 years since fire) along with sites of old habitat (>35 years since fire), (e.g. Crimson Rosella, Scarlet Robin, Sulphur-crested Cockatoo), while some ground-foraging species became scarce in dense new-growth vegetation that appears 2.5–10 years post fire (e.g. Australian Magpie, Laughing Kookaburra and White-winged Chough). Such species may deserve specific management strategies to maintain populations in forests where substantial areas are burnt by wildfire or planned burns, over short periods of time. The model for total bird abundance showed a significant fire frequency response with birds preferring sites twice burnt within 35 years (e.g. bark and canopy-foraging guilds). Four guilds demonstrated a preference for sites frequently burnt, increasing in abundance as number of burns increased (nectarivores, open-ground foragers, seeds in trees foragers, tall shrub foragers). In contrast, two species appeared to prefer sites that had experienced low fire frequencies, a response not common to their guilds. Laughing Kookaburra (carnivore) and White-winged Chough (forages on open ground among trees) generally declined in abundance with increasing fire frequency.

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1. Introduction

Biodiversity loss is a global and expanding problem (Dirzo et al., 2014, Cowie et al., 2022) and birds are no exception to the trend (BirdLife International, 2022). Some of the greatest declines in bird populations are occurring across temperate zones (Ceballos et al., 2017), with the populations of several Australian bird species declining (Recher, 1999, Bennett and Watson, 2011, Ford, 2011, BirdLife Australia, 2015, Garnett and Baker, 2021). Such declines are manifesting as local population reductions, along with decreasing geographic ranges and regional extirpation (Franklin et al., 1989, Ford et al., 2009). It has been estimated that fifty percent of Australia's terrestrial birds may be at risk of extinction over the next one hundred years if factors impacting their decline, such as inappropriate fire regimes, are not addressed (Recher, 1999).

Anthropogenic climate change is driving an increase in fire frequency and extent (Bowman et al., 2020), contributing to global declines in flora and fauna populations and reduced extents of some ecological communities (Hobbs and Mooney, 1998, Ceballos et al., 2017). For example, the evidence from a study estimating fauna population losses resulting from the 2019–20 megafires in southeastern Australia resulted in recommendations for the listing or uplisting under national environmental protection legislation of 91 taxa (Legge et al., 2022). Authors suggested that over half the assessed taxa in their study are unlikely to recover within 10 years or three generations (Legge et al., 2022). Nevertheless, many species depend on resources that are influenced by fire, providing opportunities to use fire for conservation management (Kelly et al., 2017, Sitters and Di Stefano, 2020). For example, post-fire vegetation change can be linked to the abundance of ground vegetation, shrubs, bark and tree canopy (Haslem et al., 2016), and many bird species respond to these resources in fire-prone environments (Sitters et al., 2018, Swan et al., 2018). Of the bird species in decline in southeastern Australia, at least twenty are insectivorous (Watson, 2011), with fourteen of these being primarily ground foragers (Razeng and Watson, 2012). All these species can be expected to be affected by altered fire regimes. Consequently, understanding species' responses to time-since-fire can provide a useful framework for conservation management, particularly in systems where time-since-fire and resource abundance are closely correlated (Di Stefano et al., 2013, Sitters et al., 2014).

While knowledge gaps exist in our understanding of the influence of fire frequency on fauna, research into impacts of fire frequency on birds has increased in recent years (Garnett and Baker, 2021). In Australia, this increase in attention and research is driven by two principal factors: the need to better understand factors driving avifauna decline (Garnett and Baker, 2021); and also, concerns directly related to increases in fire frequency across the landscape – through planned burns (Teague, 2010), combined with megafires now occurring more than once a decade (Fairman et al., 2016). To this end, there exists a need to gather quantitative data on the response of fauna to fire frequency, combining the incidence of both wildfire and planned burns (Lindenmayer, 2007, Adams and Attwill, 2011).

In the temperate eucalypt forests of Australia, birds may be resilient to one-off, low-intensity fire events (Loyn, 1997, Loyn et al., 2003, Kuchinke et al., 2020), but they are more severely affected by higher-intensity fires (Loyn, 1997, Woinarski and Recher, 1997, Loyn and McNabb, 2015). In conifer-dominated forests in North America, repeated high-severity fires did not reduce bird species richness and bird densities were increased in sites subjected to repeat burns than in those burnt only once (Fontaine et al., 2009). However, in Australia, an increase in fire frequency may create conditions that limit vegetation recovery (Bradstock, 2010) and may threaten the persistence of species that have range distributions that evolved within a particular fire regime (Nimmo et al., 2018) and so challenge species' resilience to fire. For example, repeated, low intensity planned burns in temperate eucalypt forests have been found to reduce the abundance of coarse woody debris

and litter, and may simplify habitat structure (York, 1999, Aponte et al., 2014). Ground and shrub-level resources are essential for many ground-foraging bird species (Leonard et al., 2016). Further, increased fire frequency may result in a changed vegetation community (Kelly et al., 2017), or the complete removal of a plant species from a landscape (Morrison et al., 1995, Fairman et al., 2016), both of which may have important influences on birds.

Our primary objective was to determine the response of bird species and guilds to time-since-fire and fire frequency in the heathy dry forests of central Victoria, Australia. Heathy dry forests are fire-prone and extensively distributed throughout Victoria, representing around 18 % of native vegetation. Due to their flammability, they are susceptible to degradation from large wildfires, but are also amenable to management through the implementation of planned burns. Nevertheless, the influences of fire on birds in this vegetation type are essentially unstudied (Kuchinke et al., 2020), and given the variability of species' responses to fire in different ecosystems (Nimmo et al., 2014, Rainsford et al., 2021), quantifying species and guild responses to fire history in heathy dry forests will generate important new knowledge for species conservation.

Our study region has experienced extensive wildfires and planned burns since the 1970's, where patches within some wildfires burnt with low severity (Lindenmayer et al., 2013) and some planned burns have been of high severity (Kuchinke et al., 2020). While research across south-east Australia has been undertaken across foothills forests that contain wet gullies (Loyn et al., 2003, Robinson et al., 2014, Sitters et al., 2015, Loyn and McNabb, 2015, Haslem et al., 2016, Leonard et al., 2016, Kelly et al., 2017) and in the taller, wetter mountain ash (*Eucalyptus regnans*) forests in the Central Highlands of Victoria (Lindenmayer et al., 2014), there is a paucity of research on the responses by birds to multiple fires across the heathy dry forests, forests which are widespread in the lowlands of central and western Victoria.

Species responses to time-since-fire and fire frequency are likely related to (a) the way these fire history variables influence vegetation structure and composition, and (b) species traits (such as diet and nesting and foraging locations) that influence how species access important resources. In our study system, dominated by planned burns, we expected fire to alter the ground layer and understorey and have less influence on the sparse midstorey and canopy of <30 percent cover (both characteristic of heathy dry forests) (Penman et al., 2007, Cheal, 2010). Consequently, we expected species that gain important resources from the ground and understorey layers to respond more distinctly to fire history compared to species that acquire resources from the canopy.

This paper complements a previous allied investigation into the short-term responses of birds to fire severity in heathy dry forests (Kuchinke et al., 2020) using a Before-After-Control-Impact designed project. The current paper uses an expanded dataset, from a greater number of sites, across a broader region, allowing us to examine bird responses to both time-since-fire and fire frequency.

2. Material and methods

2.1. Study area and regional climate

The study was undertaken in the Central Victorian Uplands bioregion in south-east Australia (Fig. 1). The climate of the region is temperate (winter mean monthly temperature range of 3.2 °C–13.8 °C, summer mean monthly temperature range 8.8 °C–27.8 °C) (Bureau of Meteorology, 2017). Rainfall recorded at Durham Lead, central to the study area, is representative of the region with an annual mean of 830.5 mm from 2009 to 2012 (Bureau of Meteorology, 2017).

The natural vegetation in the study area is dry temperate eucalypt forest. All sites were within vegetation classified as Grassy/Heathy Dry Forests (Cheal, 2010) (termed heathy dry forest herein), a forest that supports a low, relatively open understorey dominated by tussock grasses (Poaceae), with low- to medium- height sclerophyllous shrubs (e. g. Epacridaceae, Fabaceae). Eucalypt canopy trees have a maximum 30

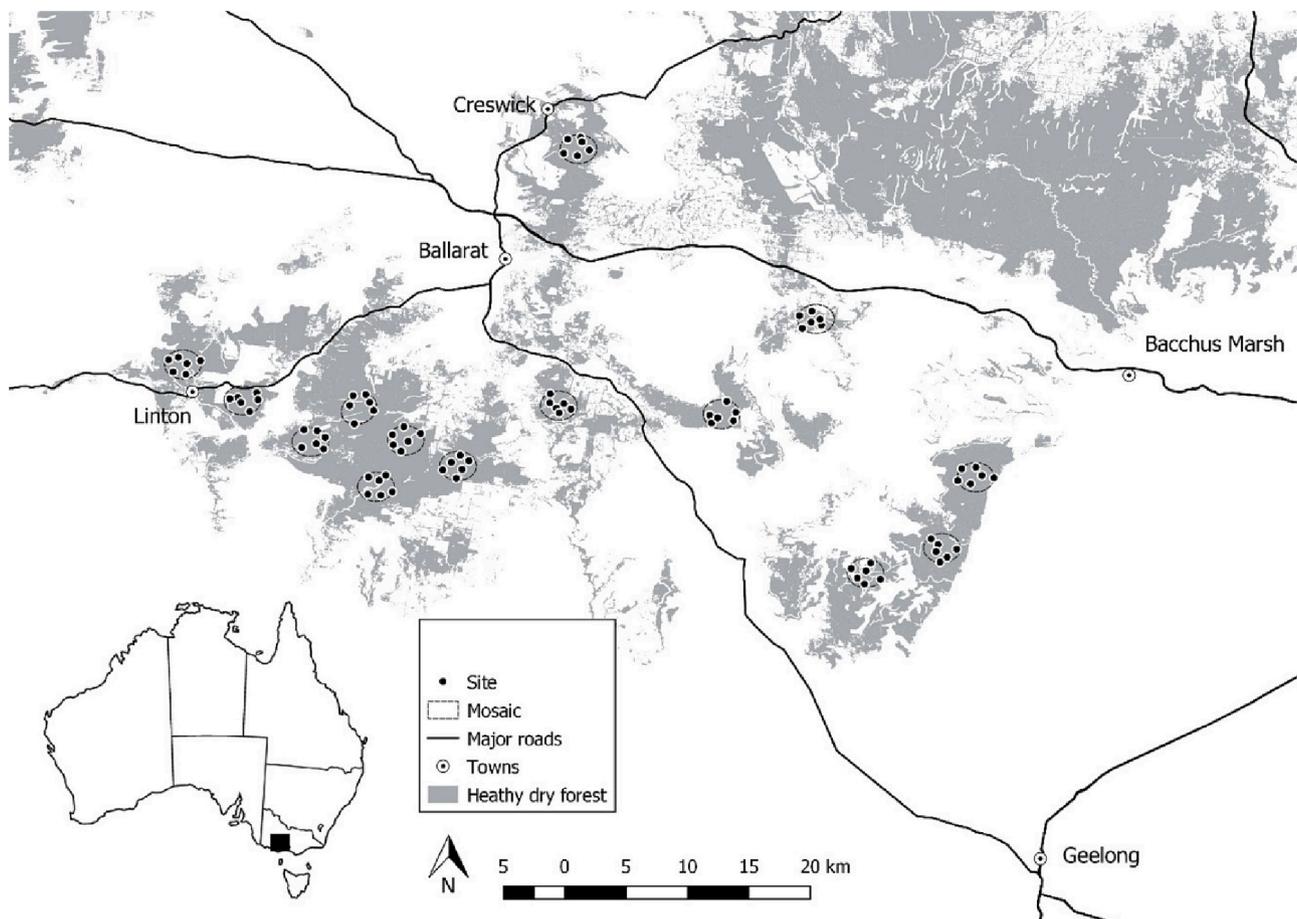


Fig. 1. Site locations in Victoria, Australia showing 84 sites in 14 groups comprising six sites each.

percent canopy cover and a characteristic height of approximately 25 m. Overstorey species include stringybark (e.g. Messmate *Eucalyptus obliqua* and Brown Stringybark *E. baxteri*) and peppermint species (Narrow-leaved Peppermint *E. radiata* and Broad-leaved Peppermint *E. dives*), as well as gum-barked species such as Manna Gum (*E. viminalis*).

Several large wildfires (>3000 ha burnt area, high intensity fires) have occurred across the region over the past 80 years and planned burns are applied broadly across the landscape to achieve fuel reduction goals (Department of Sustainability and Environment, 2004; see Supplementary Material Table S1).

2.2. Site selection

Fourteen groups of six heathy dry forest sites (84 sites) were selected within areas of three km diameter (Fig. 1). Sites were two ha in size, a minimum of 600 m apart and selected to be at least 50 m from roads and burn edges, and at least 100 m from drainage lines and major clearings. Sites were located in intact patches of native vegetation embedded within substantial areas of forested public land (Fig. 1).

2.3. Fire history variables

Two categorical variables were chosen to measure bird responses to fire: time-since-fire (TSF), and fire frequency (FF).

The time-since-fire classes used were based on an established protocol, intended to reflect major successional changes in the structure of heathy dry forests (Cheal, 2010). The classes distinguished between five regeneration stages post fire, in terms of obvious structural features (Table 1, Fig. 2). For example, the second and third classes distinguish the period of peak epicormic growth 6 months–2.5 years after fire

(sprouting from buds in surviving tree trunks), and the 2.5–10 year age class, where a more dominant feature is dense new growth of young trees growing from seed or submerged rootstock. The time-since-fire classification of 31 sites changed during the course of the study, due to either fire events or increasing time-since-fire. For these sites, observations made from the date that moved them into the new classification were pooled with data in the new classification. Time-since-fire was based on the last recorded fire at the site, regardless of whether it was a wildfire or a planned burn. The nature of the last recorded fire was a planned burn at 47 sites and a wildfire at 20 sites, while 17 sites had no recorded fire since the 1970's (Supplementary Material Table S1).

The second variable examined was fire frequency. This was classified into four levels (Table 2) based on the number of fires recorded at the site in the previous 35 years (1979–2014), regardless of whether those fires were wildfires or planned burns (Supplementary Material Table S1).

The fire history for each site was determined by reference to the Department of Land Water and Planning, Firemap GIS overlays (<https://services.land.vic.gov.au/SpatialDatamart/>) and from historical hardcopy maps. The records include all fires known to have burned since 1979 (Supplementary Material Table S1). Fire history was corroborated on ground, using an assessment of fire signs (e.g. bark char, blackened stumps, coarse woody debris, trunks and key fire response species) to determine their consistency across each two-hectare site.

2.4. Bird surveys

The 20 minute search method (Loyn, 1986) was used to survey birds. Sites were traversed on foot for 20 minutes and all birds seen or heard were counted and identified to species level. Birds flying overhead and

Table 1

Post-fire age classes for heathy dry forest vegetation (Cheal, 2010). There was a total of 84 sites, of which 31 sites changed category during the course of the study.

Code	Description	Fire-age range	Number of sites
TSF1	Renewal. Most of the ground bare, bradysporous species releasing seed, soil-stored seed germinating, resprouting species have buds activating, eucalypt coppice evident at end of stage, species not flowering, little or no litter.	0–6 mths	20
TSF2	Juvenility. Most of the ground is bare, fire ephemerals common, bradysporous species germinating, tree seedlings evident, resprouting species vigorously growing, herbaceous fire ephemerals and annuals with first seeds set, little to no litter.	6 mths–2.5 yrs	22
TSF3	Adolescence. Bare soil less common, fire ephemerals in decline with longer lived fully reproductive, earlier germinants and resprouting shrubs and sedges vigorously growing, some litter accumulation. Referred to within the text as ‘regrowth’.	2.5–10 yrs	35
TSF4	Maturity. Canopy cover at maximum, all fire ephemerals retreated to soil seed store, no further germination of bradysporous species, resprouting species growing, sedges common but not vigorous, canopy eucalypts flowering, herbaceous species appearing, litter accumulating and lichen establishing	10–35 yrs	24
TSF5	Waning – Senescence. Canopy opening, canopy eucalypts flowering, annual species more common, no further germination of bradysporous species, resprouting shrubs growing but growth rate decreasing, litter cover re-established with lichen and bryophyte cover well established	35+ yrs	14

those considered to be outside the two-hectare perimeter of the plot were not recorded. All surveys were carried out in mild weather conditions with no monitoring was undertaken on days of extreme heat (>30 °C) or when wind was >20 km/hr.

A total of 672 surveys were undertaken, across two winter and two spring/summer seasons from June 2012 (winter) to February 2014 (summer). Two surveys were conducted at each site in each of the four sampling periods (one in the morning and one in the afternoon) yielding a total of eight.

Bird species observed were classified into one of twelve foraging guilds based on the classification used by Loyn et al. (2007) (Table 3). Two guilds, frugivores and waterbirds, had too few bird observations for each guild and were not modelled (Supplementary Material Table S2).

2.5. Statistical methods

Three response variables were used in the analyses: an index of total bird abundance (counts across species), counts pooled across foraging guilds and counts of individual bird species. Variables were constructed as means per survey as, at some sites, the eight surveys were associated with more than one time-since-fire or fire frequency class. All detected species were used to construct the first two response variables, while 30 species were modelled individually. The remaining 26 species occurred at <15 % of sites and the data were deemed too sparse for reliable inference. For each response variable, time-since-fire and fire frequency were modelled separately as they were correlated in our data set. At recently burnt sites fire frequency tended to be high, and at long-unburnt sites fire frequency tended to be low. A Fisher's exact test confirmed that the two variables were statistically associated ($p < 0.001$).

We used generalised linear mixed models (GLMMs) with random

intercepts to determine the influence of time-since-fire and fire frequency on our three response variables. Mixed effects models were necessary to account for a nested data structure due to repeated sampling through time and clustering of sites around the location of prescribed burns (Zuur et al., 2009); sites within each group of six were not independent. The analysis proceeded in two stages.

In stage 1 we used Akaike's Information Criterion, corrected for small sample size (AICc) (Akaike, 1973) to determine the most parsimonious random effect structure for determining the influence of time-since-fire and fire frequency on the three response variables (Zuur et al., 2009). For each separate analysis we tested four random effect structures: site, mosaic (a factor identifying groups of six sites clustered into 14 groups), site nested within a mosaic, and, no random effect. The purpose of this process was to find the most appropriate model for extracting extraneous variance potentially attributable to the clusters of sites or repeated sampling of the same site through time. Our aim was to model the variance attributable to these design factors, in order to clarify the influence of time-since-fire and fire frequency on our response variables. In all cases we applied a tweedie family as the response variables included zeros, fractional values, and their distributions were right skewed. For example, the model with the most complex random effect structure and a fixed effect of time-since-fire was specified as $\text{species} \sim \text{tsf} + (1 \mid \text{mosaic/site})$, family = tweedie. Residuals vs fitted values plots were generated for the final specification of each model (Zuur et al., 2009). No unusual patterns in residuals were identified.

As both time-since-fire and fire frequency were categorical variables, stage two of the analysis involved using ANOVA to test if the means of each group belong to the same population, followed by pairwise comparison tests to determine which levels of time-since-fire and fire frequency differed from others. Significant post-hoc tests were only interpreted as strong evidence of an effect if the overall response to time-since-fire and fire frequency through the ANOVA was statistically detectable at the 5 % level. For some analyses the ANOVA was not significant but the post-hoc tests showed significant pairwise differences. In these cases, we interpret these differences as indicative of potential true effects and use them as evidence supporting stronger, more distinct results. No adjustments were made for multiple comparisons (Stewart-Oaten, 1995).

All analyses were conducted in the R statistical environment (R Development Core Team, 2008). Model selection was conducted with the package MuMIn (Barton, 2016), models were built using the glmmTMB package (Brooks et al., 2017) and residual plots were generated using the DHARMA package (Hartig, 2021). The overall response to predictor variables was determined using the ANOVA function in the car package (Fox, 2009) and post-hoc tests were applied using the emmeans package (Lenth et al., 2018). Model predictions were plotted using ggplot2 (Wickham and Chang, 2016).

3. Results

In this study we investigated bird responses to fire at the site scale. Fifty-six species were observed and a total of 10,296 records of individuals were logged (Supplementary Material Table S2). Total abundance, ten foraging guilds and thirty species were modelled to detect responses to time-since-fire and fire frequency (Figs. 4–7, Tables 4–5). Tables detailing all significant contrasts between categories for both time-since-fire and fire frequency classes for individual species are included in Supplementary Material (Tables S3 and S4). Graphs of model predictions for all 30 species' responses to both time-since-fire and fire frequency are also included in Supplementary Material (Figs. S1, S2).

3.1. Successional changes in bird abundance

For total bird abundance there was no statistically detectable difference between recently burnt forest (TSF1) and other age classes (Fig. 4a,



TFS1, 0-6 months, Linton.



TFS2, 6 months-2.5 years, Linton.



TFS3, 2.5-10 years, Durham Lead.



TFS4, 10-35 years, Creswick.



TFS5, 35+ years, Brisbane Ranges.

Fig. 2. Typical vegetation in the five post-fire age classes in Victoria's heathy dry forests. TFS2 is referred to within the text as 'regrowth' and TFS3 is referred to as 'new growth'.

Table 4). Only some guilds showed a significant drop in abundance in newly burnt vegetation. A statistically significant decline in abundance in immediate post-fire vegetation was evident with: bark foragers (Fig. 4b), damp ground insectivores (Fig. 4e), those that feed on seeds close to the ground (Fig. 4i) and tall shrub foragers (Fig. 4k). With tall shrub foragers, there was a sixfold increase in regenerating vegetation (TFS2) compared to newly burnt sites, with abundances in the young post-fire vegetation (TFS2) approximately three times that of old habitat

(TFS5) (Fig. 4k).

Of individual species modelled, six were not observed at all across newly-burnt sites. Three of these species were nectarivores: Brown-headed Honeyeater (*Melithreptus brevirostris*), Red Wattlebird (*Anthochaera carunculata*) and White-naped Honeyeater (*Melithreptus lunatus*); one a bark forager, Varied Sitella (*Daphoenositta chrysoptera*); a damp ground insectivore, White-browed Scrubwren (*Sericornis frontalis*); and the last was the Sulphur-crested Cockatoo (*Cacatua galerita*) which feeds

Table 2

Fire frequency in heathy dry forest vegetation (FF). Fire history for 35 years (1979–2014) combining all wildfires and planned burns. There was a total of 84 sites, of which 6 sites burned during the course of the study (Supplementary Material Table S1).

Code	Number of fires between 1979 and 2014	Number of sites
FF1	0	18
FF2	1	42
FF3	2	20
FF4	3–4	10

Table 3

Foraging guilds considered in this study, adapted from Loyn et al. (2007). In our analyses one species (Grey Shrike-thrush) was classified as a carnivore (rather than the sole example of a generalist insectivore), reflecting its observed predilection for small vertebrates such as frogs when available, and its use of multiple strata for foraging. Total birds observed grouped into foraging guilds in Supplementary Material Table S2.

Foraging guild	Foraging habit
Bark	takes invertebrates from bark on trunks and branches
Canopy	takes invertebrates from foliage of eucalypts and other large trees
Carnivore	takes vertebrates as an important part of diet, often along with large invertebrates and other food such as fruit
Damp ground insectivore	takes invertebrates from damp ground below shrubs, among dense understorey or among damp litter
Frugivore	takes soft fruit along with other food such as nectar, invertebrates or seeds
Nectarivores	takes nectar along with other food such as fruit or invertebrates
Open ground	takes invertebrates from open ground, quite often far from tree or shrub cover
Open ground among trees	takes invertebrates from open ground among trees or scattered tall shrubs and does not usually venture far from woody vegetation
Seeds close to ground	takes seeds from ground or low plants such as grasses and herbs
Seeds from trees etc	takes seeds from trees and shrubs or wide range of strata, or other food in trees such as gall insects or insect larvae extracted from wood
Tall shrubs	takes invertebrates from foliage of tall shrubs, which may form middle storey of eucalypt forests
Waterbird	waterbird inhabiting inland waters

on seeds taken mainly on the ground (Supplementary Material Fig. S1). Two species had significantly lower abundances in newly burnt sites (TSF1) compared to regenerating vegetation (TSF2): Grey Shrike-thrush (*Colluricincla harmonica*) (carnivore; ANOVA, $p < 0.001$); and Brown Thornbill (*Acanthiza pusilla*) (tall shrub forager; ANOVA, $p < 0.001$) (Table 4). The Brown Thornbill response supported that of its guild as its abundance in young new growth (TSF2) was approximately eight times greater than in newly burnt vegetation (TSF1) and three times greater than in old habitat (TSF5) (Fig. 5a). Further support for a significant decline in immediate post-fire vegetation was evident with the post-hoc test for Buff-rumped Thornbill (*Acanthiza reguloides*), (open ground among trees forager), which showed a significant decline in abundance between newly burnt vegetation (TSF1) and each of the vegetation new growth age classes (TSF2, 3, 4) (Supplementary Material Fig. S1, Table S3).

A significant fire response for total abundance, was an increase in abundance in regenerating vegetation (6 months–2.5 years; TSF2) above both older regrowth sites (10–35 years; TSF4) and old habitat (35+ years; TSF5) (Fig. 4a, Table 4). For two of the guilds, significant increases were apparent in both the regrowth (TSF2) and new growth (TSF3) age classes, compared with older habitat: canopy foragers (Fig. 4c) and damp ground insectivores (Fig. 4e). Open ground foragers were especially common in post-fire regrowth (TSF2) but then significantly declined (Fig. 4g). Birds from both seed-eating guilds were as

abundant in post-fire regeneration (TSF2) as in long-unburnt forest (TSF5), with abundances significantly reduced in the older post-fire new growth (TSF4) (Fig. 4i, 4j). The preference for regenerating vegetation (TSF2) and new growth vegetation (TSF3) was evident for individual species, such as the canopy forager, Spotted Pardalote (*Pardalotus punctatus*), which showed a preference for regenerating vegetation (TSF2) approximately double that of older age classes (TSF4, 5; ANOVA, $p < 0.001$) (Table 4, Fig. 5b) and the carnivorous Australian Raven (*Corvus coronoides*) (ANOVA, $p = 0.04$) (Table 4). Further support for a significant increase in regenerating vegetation (TSF2) above older vegetation was evident with the post-hoc test for two more canopy foragers: Striated Thornbill (*Acanthiza lineata*) and Grey Fantail (*Rhipidura albiscapa*), (Supplementary Material Fig. S1, Table S3).

The nectarivore guild showed a preference for the dense new-growth vegetation that develops 2.5–10 years post-fire (TSF3), above all other classes. This response was supported by all six nectarivores modelled, to varying extents (Supplementary Material Fig. S1), significantly so with Eastern Spinebill (*Acanthorhynchus tenuirostris*) (ANOVA, $p = 0.01$). Species from other guilds that also displayed a preference for the dense vegetation age class (TSF3) were: Eastern Yellow Robin (*Eopsaltria australis*), (ANOVA, $p = 0.02$), a damp ground insectivore that increased in abundance threefold in dense new-growth (TSF3) compared with both young regenerating vegetation (TSF2) and old habitat (TSF5), and Superb Fairy-wren (*Malurus cyaneus*) that forages on open ground among trees (Fig. 5c). Similarly, the fairy-wren more than doubled in dense vegetation (TSF3) compared with younger (TSF2) and older (TSF4) post-fire regrowth. Further support for a significant increase in abundance in new growth vegetation (TSF3) above older vegetation was evident with the post-hoc tests for both nectarivore White-eared Honeyeater (*Nesoptilotis leucotis*) and Common Bronzewing (*Phaps chaloptera*), seeds close to ground forager (Supplementary Material Fig. S1, Table S3).

In contrast to the species mentioned above, post-hoc tests revealed that some species may have significantly lower abundances in the dense new-growth vegetation (TSF3). Both the carnivorous Laughing Kookaburra (*Dacelo novaeguineae*) (Fig. 5d); and White-winged Chough (*Corcorax melanorhamphos*), open ground among trees forager (Fig. 5e), returned to sites 6 month–2.5 years post fire but then declined by approximately 50 percent in abundance in denser new-growth vegetation (TSF3), then increased in abundance in the older new growth and old habitat (TSF4,5). Australian Magpie (*Gymnorhina tibicen*), significantly increased in abundance in epicormic regrowth vegetation (TSF2) and then declined in the dense growth stages (TSF3) by approximately 50 percent (Supplementary Material Fig. S1, Table S3).

For three species from three different guilds older habitat was favoured. Crimson Rosella (*Platycercus elegans*), which forages from seeds in trees, (ANOVA, $p < 0.01$) displayed preferences for the younger regenerating vegetation (TSF2) as well as older habitat (TSF5). Declines across the dense growth stage (TSF3) and older regrowth stage (TSF4) were significant, with a rebound in abundance in old habitat (TSF5) (Fig. 5f). Further support for a significant preference for regenerating vegetation (TSF2) and old habitat (TSF5) above denser vegetation classes (TSF3, 4) was evident with the post-hoc tests for Scarlet Robin (*Petroica boodang*), that forages on open ground among trees and Sulphur-crested Cockatoo (*Cacatua galerita*), which feeds on seed close to the ground (Supplementary Material Fig. S1, Table S3).

3.2. Total abundance, guild and species' responses to fire frequency

The model for total bird abundance showed a significant fire frequency response with birds preferring sites twice burnt (Fig. 6a, Table 5). This preference was supported by both bark and canopy-foraging guilds (Fig. 6b, c; Table 5). Within the bark-foraging guild, White-throated Treecreeper (*Cormobates leucophaea*) had a significant preference for a twice-burnt frequency (ANOVA, $p < 0.01$), as did the Grey Fantail (*Rhipidura albiscapa*) (ANOVA, $p < 0.01$) and Rufous

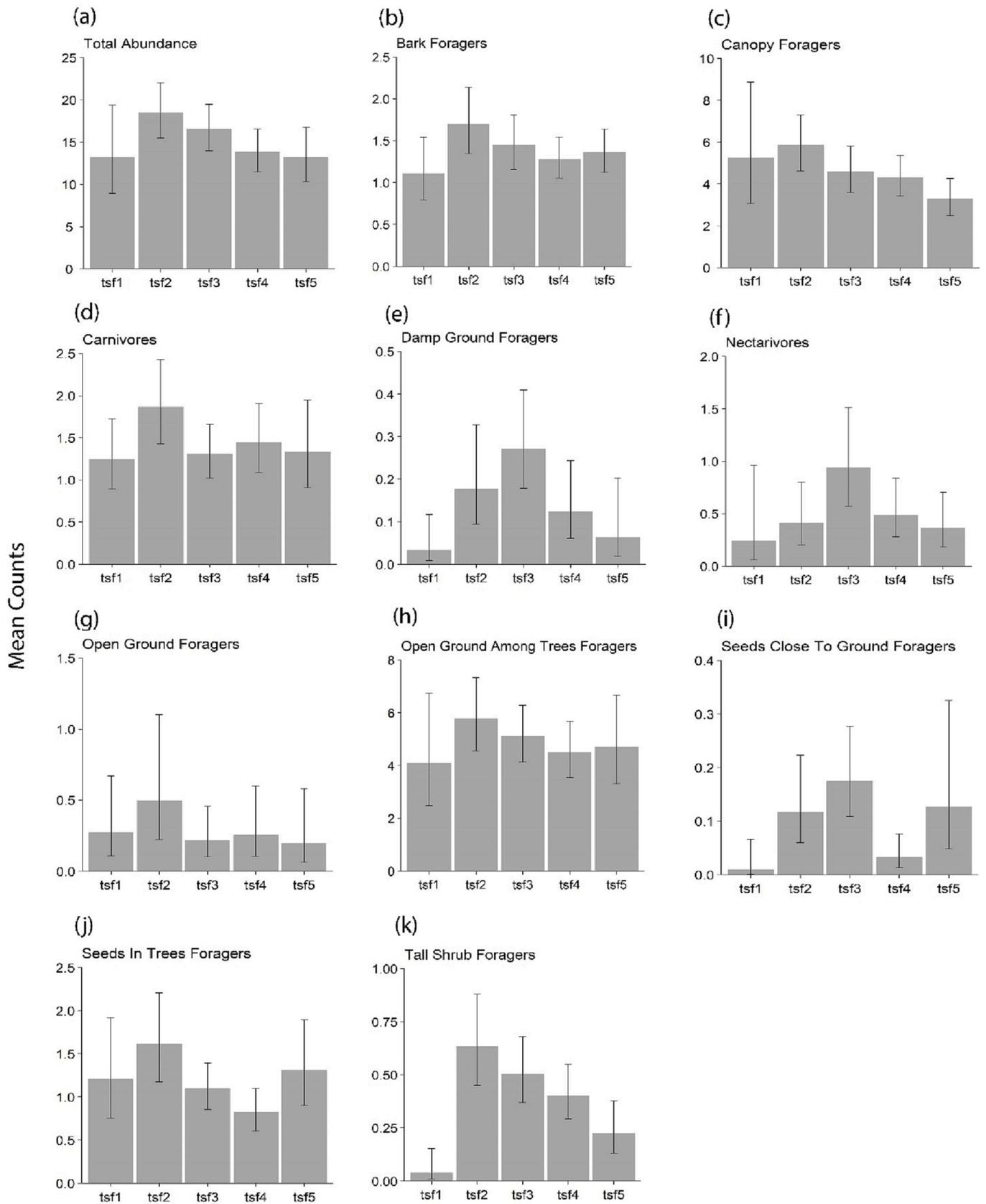


Fig. 4. Total bird abundance and foraging guild responses to time-since-fire (tsf). Y-axis represents mean counts per survey. Model selection based on 4 candidate models for random effect structure (site, mosaic, site within mosaic, no random effect) and ranked using Akaike’s Information Criteria (AICc). TSF categories: (tsf1) 0–6 months; (tsf2) 6 months–2.5 years; (tsf3) 2.5–10 years; (tsf4) 10–35 years; (tsf5) 35+ years, combined with last burn not recorded. Predictions are from generalized linear mixed models and errors are 95 % confidence limits.

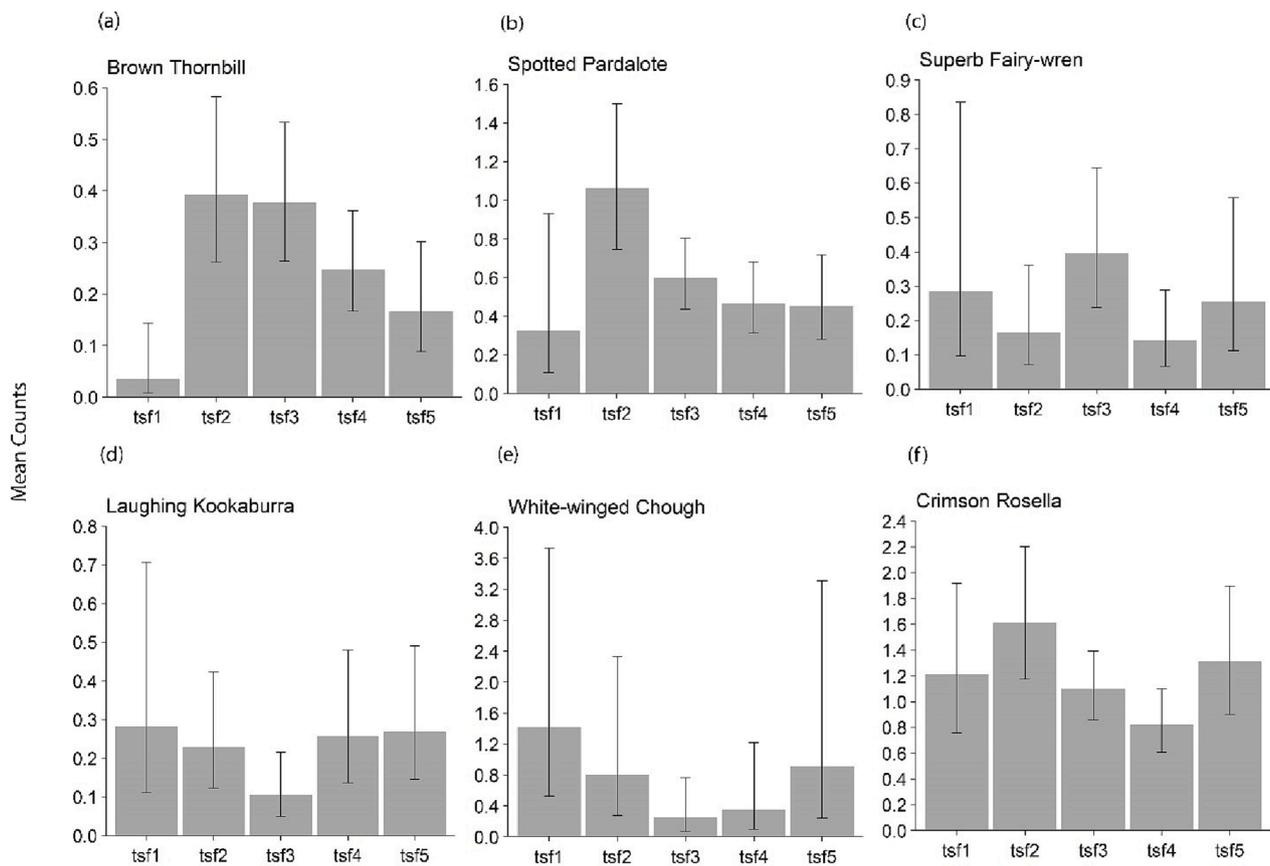


Fig. 5. Species' responses to time-since-fire (tsf). Y-axis represents mean counts per survey. Model selection based on 4 candidate models for random effect structure (site, mosaic, site within mosaic, no random effect) and ranked using Akaike's Information Criteria (AICc). Tsf categories: (tsf1) 0–6 months; (tsf2) 6 months–2.5 years; (tsf3) 2.5–10 years; (tsf4) 10–35 years; (tsf5) 35+ years, combined with last burn not recorded. Predictions are from generalized linear mixed models and errors are 95 % confidence limits.

Whistler (*Pachycephala rufiventris*) (ANOVA, $p < 0.001$) (Fig. 7a), both canopy foragers (Table 5). Rufous Whistler had a fourfold increase from unburnt sites to those burnt twice, declining significantly on sites frequently burnt (3–4 times) (Fig. 7a).

Analyses for four guilds demonstrated a preference for sites frequently burnt, with birds increasing in abundance as number of burns increased. Nectarivores (Fig. 6f), open-ground foragers (Fig. 6g), seeds in trees foragers (Fig. 6j) and tall-shrub foragers (Fig. 6k), each displayed significant differences between low-level frequency (unburnt or once burnt), to twice burnt and three to four times burnt (Table 5). For tall shrub foragers this represented an increase of approximately 100 % (Fig. 6k). This preference was observed for four species within those guilds: Eastern Spinebill (*Acanthorhynchus tenuirostris*), (nectarivore; ANOVA, $p = 0.03$); Australian Magpie (*Gymnorhina tibicen*), (open ground forager; ANOVA, $p < 0.01$); Crimson Rosella (*Platycercus elegans*), (seeds in trees; ANOVA, $p < 0.01$); and Brown Thornbill (*Acanthiza pusilla*), (tall shrub forager; ANOVA, $p < 0.01$) (Table 5; Supplementary Material, Fig S2, Table S4). Brown Thornbill displayed a threefold increase between unburnt sites compared with sites burnt 3–4 times (Fig. 7b). A further three species also displayed this preference, though it was not typical of their guilds as a whole. Those species were: Striated Thornbill (*Acanthiza lineata*) (canopy feeder; ANOVA, $p = 0.01$); Grey Currawong (*Strepera versicolor*) (carnivore; ANOVA, $p < 0.001$); open ground among tree forager, Superb Fairy-wren (*Malurus cyaneus*) (ANOVA $p < 0.001$) (Table 4). Further support for a significant preference for sites frequently burnt was evident with the post-hoc tests: Spotted Pardalote (*Pardalotus punctatus*) (canopy forager); Pied Currawong (*Strepera graculina*) (carnivore); and damp ground insectivore, White-browed Scrubwren (*Sericornis frontalis*). Each increased in

abundance with an increase in fire frequency (Supplementary Material Fig S2, Table S4).

In contrast, one species displayed a negative response to fire frequency, that was not common for its guild. Laughing Kookaburra (carnivore; ANOVA, $p < 0.001$) generally declined in abundance with increasing fire frequency (Fig. 7c). While Laughing Kookaburra showed a preference for sites burnt twice, they declined significantly on sites burnt more frequently. Further support for a significant decline on sites frequently burnt was evident with the post-hoc test for White-winged Chough (forages on open ground among trees), which showed an eightfold decline between sites burnt twice and sites burnt 3–4 times (Fig. 7d).

4. Discussion

This study highlights distinct responses by all modelled guilds and individual species to both time-since-fire and fire frequency. Many species declined in abundance immediately after fire and then increased in abundance in the dense, new post-fire vegetation. Eucalypt forests have few immediate post-fire specialists (Loyn and McNabb, 2015, Sitters et al., 2015, Kuchinke et al., 2020) and the forests rapidly regenerate after fire (Loyn, 1997, Lindenmayer et al., 2008, Kuchinke et al., 2020). Furthermore, patterns of increase after immediate post-fire declines differed among species; some species peaked in abundance in long unburnt habitat (>35 years since fire), while others became more abundant in the sparse juvenile regrowth stage of healthy dry forest vegetation (6 months–2.5 years) or the dense new-growth adolescent stage (2.5–10 years). However, at least three common species - Australian Magpie, White-winged Chough and Laughing Kookaburra -

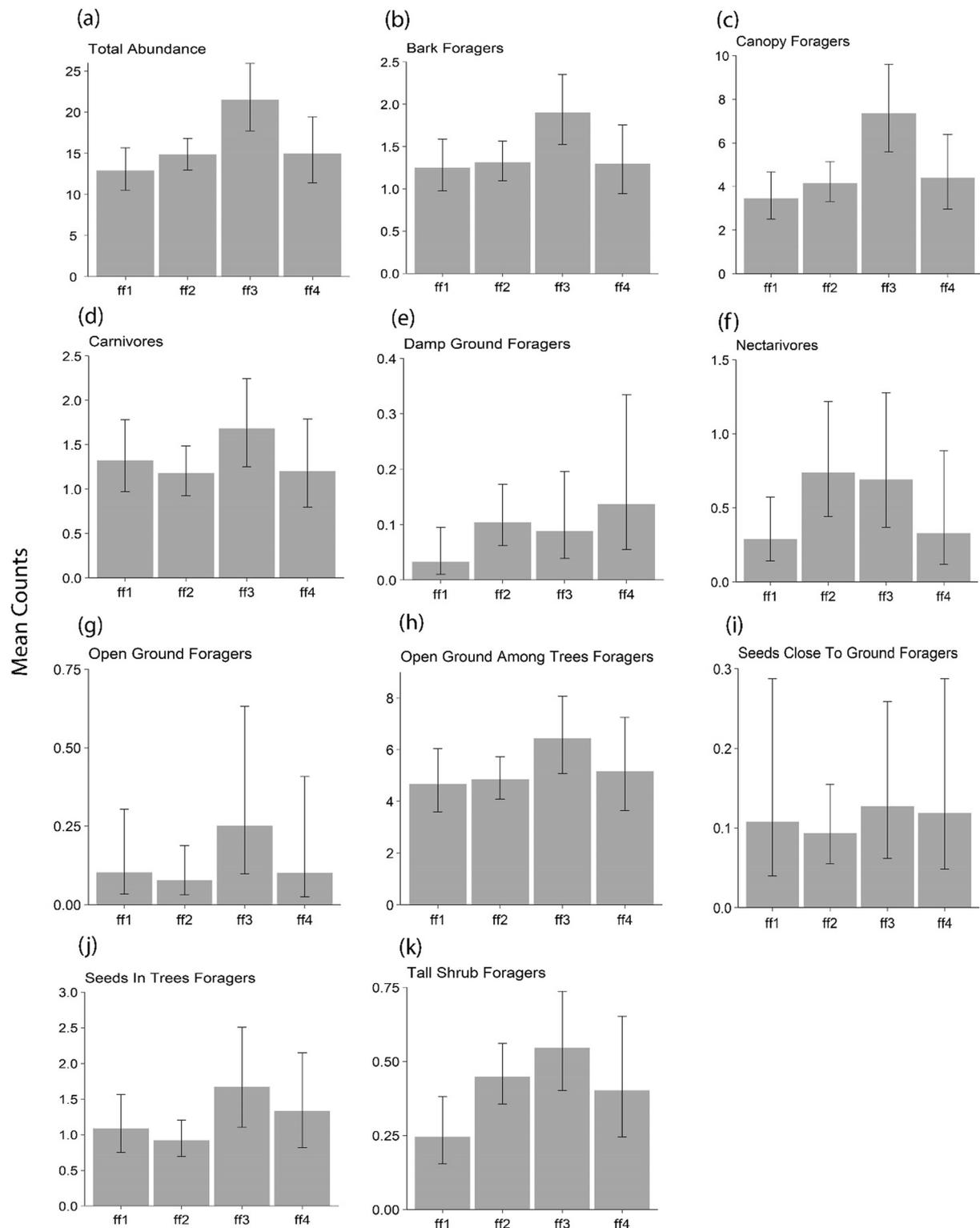


Fig. 6. Total bird abundance and foraging guild responses to fire frequency (ff). Y-axis represents mean counts per survey. Model selection based on 4 candidate models for random effect structure (site, mosaic, site within mosaic, no random effect) and ranked using Akaike's Information Criteria (AICc). Fire frequency categories: (ff1) 0 fires; (ff2) 1 fire; (ff3) 2 fires; (ff4) 3–4 fires, in 35 years (1979–2014). Predictions are from generalized linear mixed models and errors are 95 % confidence limits.

showed a markedly different trend, with abundances temporarily decreasing in the 2.5–10 year post-fire stage, where ground cover was densest. These species all feed from open ground, with varying degrees of tree cover, but they generally avoid areas with dense shrub cover. Similar aversions to dense shrub cover have been reported for a range of

bird species in regrowth after logging (Kavanagh et al., 2004) or fire (MacHunter et al., 2009), but their needs have not been given as much attention as those of species that need elements of old-growth, such as tree hollows. The effects of climate change are a drying landscape combined with an increase in both the frequency and extent of large-

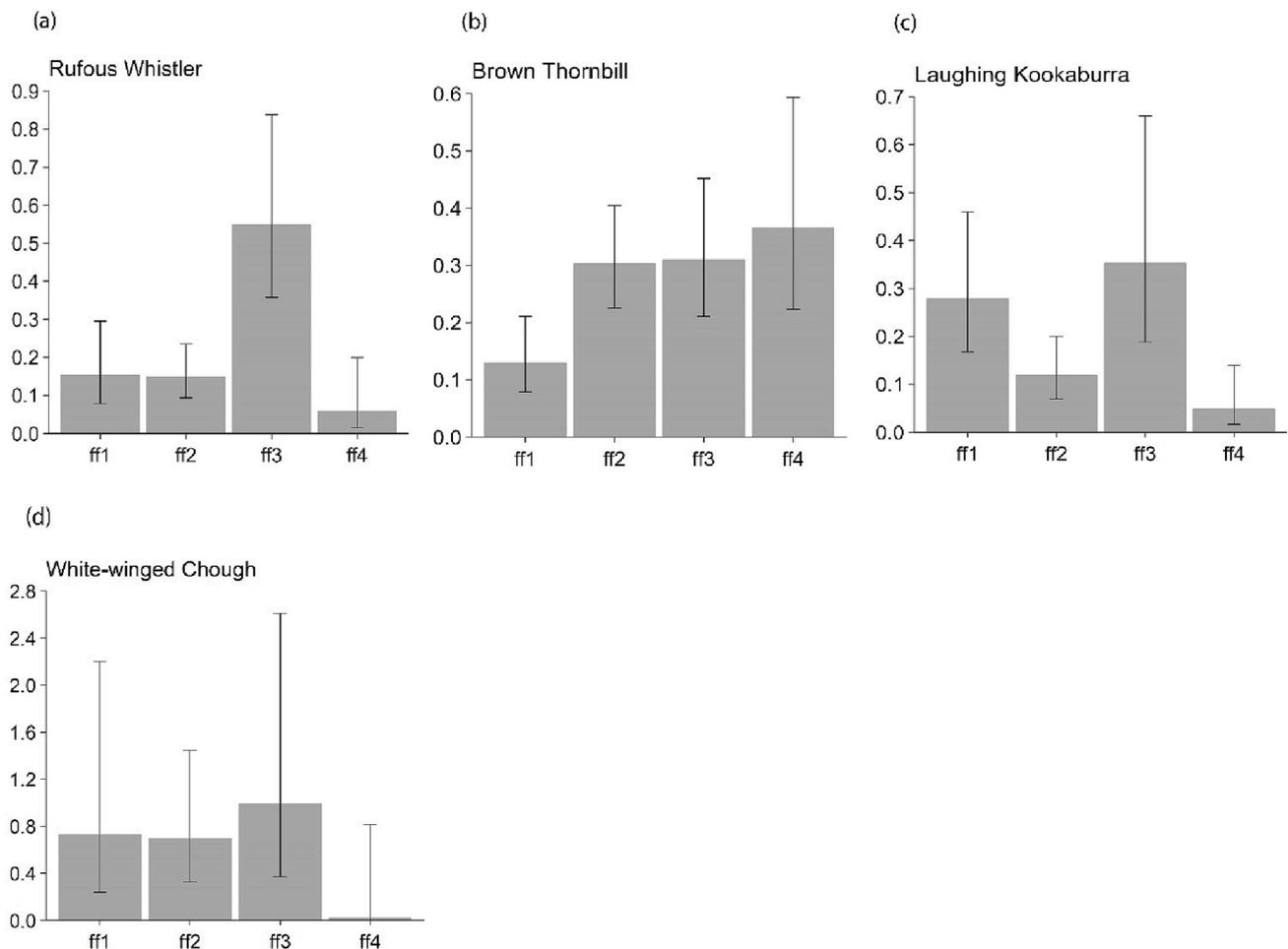


Fig. 7. Species' responses to fire frequency (ff). Y-axis represents mean counts per survey. Model selection based on 4 candidate models for random effect structure (site, mosaic, site within mosaic, no random effect) and ranked using Akaike's Information Criteria (AICc). Fire frequency categories: (ff1) 0 fires; (ff2) 1 fire; (ff3) 2 fires; (ff4) 3–4 fires, in 35 years (1979–2014). Predictions are from generalized linear mixed models and errors are 95 % confidence limits.

scale fires. Combine this with an increase in the application of planned burns and this will likely mean more of the landscape will be burnt each year. Depending on the nature of fire in the future, this may have important consequences for forest birds in general, including those that forage on open ground, if shifts in the fire regime produce extensive areas of dense ground cover for longer periods.

4.1. Heathy dry forest bird abundances recover rapidly post fire

The evidence for a substantial, but short duration, post-fire decrease in bird abundance, likely occurring in response to the loss of suitable foraging habitat, is consistent with results presented in other vegetation types across Australia (Loyn, 1997, Woinarski and Recher, 1997, Loyn and McNabb, 2015, Kelly et al., 2017). However, within six months, in the spring after an autumn fire in heathy dry forest, epicormic growth was observed to be dense on tree trunks. While new growth may begin developing from seed, ground cover is still sparse during the early post-fire stages (6 months–2.5 years). At this stage, most species had returned to the sites (Fig. 4a). As many birds display strong site fidelity, this rapid vegetation regrowth allows the populations of resident birds to recover quickly from surrounding populations (Lindenmayer et al., 2014). Habitat changes post fire that impact bird populations may vary significantly between vegetation types, with habitats varying in recovery rates and total bird abundance reductions in the order of 60 % in some habitats, while recovering within three years (Loyn, 1997). Similarly, in Booderee National Park (southern coast of New South Wales, south-east Australia), Lindenmayer et al. (2008), also found that bird

assemblages had recovered in three years in sites of varying vegetation complexity. The results in heathy dry forests here suggest an even more rapid rate of recovery.

4.2. There is no evidence for immediate post-fire specialists in heathy dry forests

No species in our study showed post-fire responses that would identify them as post-fire specialists. This result aligns with evidence from shrubby dry, foothills and damp forest vegetation sites of central Victoria (Loyn et al., 2003) where, while there was evidence for some increases in open ground foragers and seed eaters on burnt areas, there was little evidence of immediate post-fire specialists. In sites further east, Loyn (1997) observed a small influx of carnivores post wildfire, and various studies showed that a few uncommon passerine species were found mainly in areas that had been recently logged or burned (Emison et al., 1987, Kavanagh et al., 2004, Loyn and McNabb, 2015). However, this was not evident in the heathy dry forest bird assemblages in the current study. Similarly, immediately after the wildfire events of Black Saturday (across Victoria in 2009), Lindenmayer et al. (2014) concluded that there are few if any species in the Central Highlands montane-ash forests that specialise on early successional vegetation. The current evidence from heathy dry forests, broadly reflects the conclusion from other investigations on major vegetation types across southeastern Australia (Lindenmayer et al., 2008, Sitters et al., 2014, Sitters et al., 2015, Lindenmayer et al., 2022), that most bird species do not specialise at inhabiting early successional stages after fire.

Table 4

Summary of significant responses to time-since-fire (TSF) for total abundance and by foraging guilds and 30 individual species. Foraging guild responses are in italics. ANOVA results for generalized linear mixed models based on Wald chi-square. All models with 4 degrees of freedom. Potential random effects: mosaic, site, site within mosaic, no random effect. TSF categories: (TSF1) 0–6 months, (TSF2) 6 months–2.5 years, (TSF3) 2.5–10 years, (TSF4) 10–35 years, (TSF5) 35+ years, combined with last burn not recorded. Favoured TSF and disfavoured TSF have significant differences in abundances (Supplementary Material Table S3). Graphed outputs of all individual species' models are supplied (Supplementary Material Fig. S1).

Foraging guild	Common name	Chi squared	P	Random effect	Favoured	Disfavoured
					Time-since-fire	Time-since-fire
Total abundance		12.35	0.01	mosaic	TSF2	TSF4,5
<i>Bark foragers</i>		8.63	0.07	<i>mosaic</i>	<i>TSF2</i>	<i>TSF1,4</i>
	Varied Sitella	3.67	0.45	site		
	White-throated Treecreeper	4.89	0.30	mosaic		
<i>Canopy foragers</i>		13.43	<0.01	<i>mosaic</i>	<i>TSF2</i>	<i>TSF4,5</i>
					<i>TSF3</i>	<i>TSF5</i>
	Grey Fantail	8.31	0.08	no random effect	TSF2,3	TSF4
	Rufous Whistler	7.04	0.13	no random effect	TSF1,2	TSF4
	Spotted Pardalote	19.83	<0.001	mosaic	TSF2	TSF1,3,4,5
	Striated Pardalote	7.33	0.12	no random effect	TSF1	TSF4
	Striated Thornbill	7.56	0.11	mosaic	TSF5	TSF1,2,4
<i>Carnivores</i>		3.62	0.46	<i>mosaic/site</i>		
	Australian Raven	9.99	0.04	site	TSF2	TSF1,4,5
					TSF4	TSF3
	Grey Currawong	8.37	0.08	site	TSF2	TSF3,4
	Grey Shrike-thrush	22.07	<0.001	mosaic	TSF2,3,4	TSF1
					TSF2,3	TSF5
	Laughing Kookaburra	5.97	0.20	site	TSF4,5	TSF3
	Pied Currawong	1.55	0.82	no random effect		
<i>Damp ground insectivores</i>		14.82	<0.01	<i>no random effect</i>	<i>TSF3</i>	<i>TSF1,5</i>
					<i>TSF2</i>	<i>TSF1</i>
	Eastern Yellow Robin	12.33	0.02	site	TSF3	TSF1,2,4
<i>Nectarivores</i>		2.81	0.59	site		
	White-browed Scrubwren	13.59	<0.01	<i>mosaic</i>	<i>TSF3</i>	<i>TSF2,4,5</i>
	Brown-headed Honeyeater	2.55	0.64	site		
	Eastern Spinebill	12.53	0.01	site	TSF1,3,5	TSF4
	Red Wattlebird	2.93	0.57	mosaic/site		
	White-eared Honeyeater	9.06	0.06	site	TSF3	TSF1,2,4
	White-naped Honeyeater	2.84	0.58	mosaic		
	Yellow-faced Honeyeater	4.09	0.39	mosaic		
<i>Open ground foragers</i>		4.85	0.30	<i>mosaic</i>		
<i>Open ground among trees</i>	Australian Magpie	5.43	0.25	mosaic	TSF2	TSF3
		3.76	0.44	<i>mosaic</i>		
	Buff-rumped Thornbill	9.08	0.06	mosaic	TSF2,3,4	TSF1
	Scarlet Robin	4.89	0.30	no random effect	TSF2	TSF4
	Superb Fairy-wren	10.29	0.04	mosaic	TSF3	TSF2,4
	White-winged Chough	6.61	0.16	no random effect	TSF1	TSF3
<i>Seeds close to ground</i>		19.05	<0.001	<i>mosaic/site</i>	<i>TSF2, 3, 5</i>	<i>TSF1,4</i>
	Common Bronzewing	14.71	<0.01	site	TSF3	TSF2,5
	Sulphur-crested Cockatoo	7.69	0.10	mosaic	TSF2,5	TSF4
<i>Seeds in trees</i>		14.03	<0.01	<i>mosaic</i>	<i>TSF2</i>	<i>TSF3, 4</i>
					<i>TSF5</i>	<i>TSF4</i>
	Crimson Rosella	14.03	<0.01	mosaic	TSF2	TSF3,4
					TSF5	TSF4
<i>Tall shrubs</i>		28.11	<0.001	<i>mosaic</i>	<i>TSF2,3,4,5</i>	<i>TSF1</i>
					<i>TSF2,3,4</i>	<i>TSF5</i>
	Brown Thornbill	21.36	<0.001	mosaic	TSF2	TSF4
					TSF2,3,4,5	TSF1
					TSF2,3	TSF4,5
	Fan-tailed Cuckoo	4.77	0.31	no random effect	TSF4	TSF5

Elsewhere in the world, studies from mixed-conifer forests reveal post-fire vegetation stands to be suitable for specific foraging guilds and fire specialist species (Hutto, 1995, Nappi and Drapeau, 2009). Conifer forests may have a higher level of canopy tree loss immediately post fire, so evidence of structure and resource shifts may be much greater than what is evident in an Australian heathy dry forest. These distinctive communities are not apparent in heathy dry forests, where no species or foraging guilds displayed a preference for newly-burnt vegetation. Conifer forests will host higher numbers of 'early stage' species, along with those species that appear on burn sites only (Smucker et al., 2005).

4.3. Birds in heathy dry forests respond to the temporal vegetation patterns post fire

The greatest shifts in species' abundances occurred during the first ten years post fire in heathy dry forest, with bird species commonly present across the stages greater than ten years since fire.

Many of the modelled species had low abundances (or were absent) in the newly burnt vegetation, and many had returned in high abundances in one or both of the regrowth (6 months–2.5 years) and new-growth (2.5–10 year) age classes.

In heathy dry forests, early-stage regrowth (6 months–2.5 years) supports epicormic growth on trunks, but the ground may remain bare. Canopy feeding birds such as Spotted Pardalote, Rufous Whistler and Grey Fantail, were found to be most abundant in this age class. While the

Table 5

Summary of significant responses to fire frequency (FF) in 35 years (1979–2014), for total abundance and by foraging guilds and 30 individual species. Foraging guild responses are in italics. ANOVA results for generalized linear mixed models based on Wald chi-square. All models with 4 degrees of freedom. Potential random effects: mosaic, site, site within mosaic, no random effect. (FF1) 0 fires; (FF2) 1 fire; (FF3) 2 fires; (FF4) 3–4 fires. Favoured FF and disfavoured FF have significant differences in abundances (Supplementary Material Table S4). Graphed outputs of all individual species' models are supplied (Supplementary Material Fig. S2).

Foraging guild	Common name	Chi squared	P	Random effect	Favoured	Disfavoured
					Fire frequency	Fire frequency
Total abundance		19.14	<0.001	mosaic/site	FF3	FF1,2,4
<i>Bark foragers</i>		13.11	<0.01	mosaic	FF3	FF1,2,4
	Varied Sitella	3.08	0.38	no random effect		
	White-throated treecreeper	14.92	<0.01	mosaic/site	FF3	FF1,2,4
<i>Canopy foragers</i>		19.77	<0.001	mosaic	FF3	FF1,2,4
	Grey Fantail	14.45	<0.01	mosaic	FF3	FF1,2,4
	Rufous Whistler	31.06	<0.001	site	FF3	FF1,2,4
	Spotted Pardalote	4.34	0.23	mosaic	FF3	FF1
	Striated Pardalote	4.00	0.26	site		
	Striated Thornbill	11.05	0.01	mosaic	FF3	FF1,2
<i>Carnivores</i>		5.96	0.11	mosaic	FF3	FF2
	Australian Raven	2.49	0.48	mosaic/site		
	Grey Currawong	23.30	<0.001	mosaic/site	FF3,4	FF2
	Grey Shrike-thrush	4.00	0.26	mosaic		
	Laughing Kookaburra	18.30	<0.001	site	FF1,3	FF2,4
	Pied Currawong	5.44	0.14	site	FF3	FF2
<i>Damp ground insectivores</i>		5.01	0.17	site	FF2,4	FF1
	Eastern Yellow Robin	2.49	0.48	no random effect		
	White-browed Scrubwren	4.05	0.26	no random effect	FF3	FF1
<i>Nectarivores</i>		12.12	<0.01	mosaic	FF2,3	FF1
	Brown-headed Honeyeater	3.66	0.30	site		
	Eastern Spinebill	8.66	0.03	site	FF3	FF2
	Red Wattlebird	1.63	0.65	mosaic/site		
	White-eared Honeyeater	3.33	0.34	mosaic/site		
	White-naped Honeyeater	2.53	0.47	mosaic/site		
	Yellow-faced Honeyeater	2.76	0.43	mosaic		
<i>Open ground foragers</i>		13.19	<0.01	mosaic/site	FF3	FF2
	Australian Magpie	15.17	<0.01	mosaic/site	FF3	FF2
<i>Open ground among trees</i>		4.48	0.21	no random effect		
	Buff-rumped Thornbill	2.47	0.48	no random effect		
	Scarlet Robin	4.13	0.25	site		
	Superb Fairy-wren	17.47	<0.001	site	FF3	FF1,2
	White-winged Chough	4.02	0.26	no random effect	FF3	FF4
<i>Seeds close to ground</i>		0.72	0.87	site		
	Common Bronzewing	5.43	0.14	mosaic		
	Sulphur-crested Cockatoo	2.29	0.52	no random effect		
<i>Seeds in trees</i>		11.82	<0.01	mosaic	FF3	FF2
	Crimson Rosella	11.82	<0.01	mosaic	FF3	FF2
<i>Tall shrubs</i>		8.60	0.04	no random effect	FF2, 3	FF1
	Brown Thornbill	13.76	<0.01	mosaic	FF2,3,4	FF1
	Fan-tailed Cuckoo	2.80	0.42	no random effect		

responses of insects to fire events vary across species (Elia et al., 2011), evidence from heathy dry forests suggests the Spotted Pardalote responded to an increase in the abundance of psyllid insects, observed among the developing epicormic growth (Loyn and McNabb, 2015). Low shrubs and tall herbs interspersed with bare ground, the preferred habitat of Superb Fairy-wrens (Emison et al., 1987), feature widely in regrowth (6 months–2.5 years post fire) and new-growth vegetation (2.5–10 years post fire). While evidence elsewhere shows Superb Fairy-wrens avoid dense regrowth after wildfire (Loyn, 1997), in heathy-dry forests Superb Fairy-wrens had a significant preference for the denser new growth, suggesting that shrub cover was a limiting factor for the species at other successional stages in this forest type. Superb Fairy-wrens are common in some urban park settings (Harrisson et al., 2013) and their persistence in many landscapes altered by humans indicates a resilience to landscape changes (Trollope et al., 2009). However, as they are territorial, sedentary and weak fliers, Superb Fairy-wrens may be vulnerable to fire events.

In contrast to the early post-fire vegetation age class in heathy dry forest, the ground layer of the older regrowth and shooting new growth vegetation (2.5–10 years post fire) had serotinous seedlings sprouting, and grasses were regenerating. Trees in this time-since-fire class were in flower, providing eucalypt nectar, an important primary food source for nectarivorous birds (Ford and Paton, 1977) and for many invertebrate

prey species (Horskins and Turner, 1999). White-eared Honeyeaters favoured this class because it provides a rich source of psyllids and other associated honeydew on the foliage and bark, while Eastern Spinebills depend more strongly on nectar from eucalypts, mistletoe or favoured shrub species such as Common Correa (*Correa reflexa*) or Victorian Heath (*Epacris impressa*).

Three species that primarily feed from open ground, decreased in abundance in the dense vegetation, 2.5–10 years post fire: Laughing Kookaburra (classified as a carnivore), Australian Magpie (open-ground insectivore sometimes far from cover) and White-winged Chough (open-ground insectivore among trees). This was likely caused by the inability of these species to forage effectively in dense regenerating vegetation. For example, dense vegetation may not be suitable for a broad range of reptiles, as these ectothermic animals need sunny environments for basking (Michael et al., 2011) and some lizards prefer unburnt sites (Davis and Doherty, 2015). As lizards are a major component of a Laughing Kookaburra's diet (Higgins et al., 1999), not only does the denser ground cover potentially impede vision of prey, but a component of the kookaburra's diet may be rare or absent from these habitats. Australian Magpies feed mainly in open country and it is not surprising that they also avoided dense vegetation. They are generally common in lightly treed farmland and scarce in forests (Higgins et al., 2006), so they arguably deserve little attention in the forest environment. In contrast,

White-winged Choughs inhabit a range of forests and woodlands (Higgins et al., 2006), where flocks forage for invertebrates and other foods (including tubers of plants such as orchids, Orchidaceae) from open ground among trees, or less often in nearby pasture. These foraging strategies and their communal social behaviour may inhibit them from using areas with dense shrub cover, and some of their food sources (including orchids) may be scarce in such situations. White-winged Choughs are highly mobile and flocks were often found foraging from open ground in newly burnt areas. White-winged Choughs and Laughing Kookaburras were both as common in long-unburnt forest (TSF5) as they were in newly burnt and young post-fire vegetation. For species such as these it is clearly important to manage fire to limit the development of extensive dense vegetation, especially in patches of remnant forest that can be important habitats for these and other species.

Three more species, from three different guilds, showed preferences for long-unburnt forest as well as young post-fire vegetation: Scarlet Robin, Crimson Rosella and Sulphur-crested Cockatoo. Each had a significant preference for vegetation with less ground cover than the adolescent, denser post-fire age class. All three spend time on the ground searching for food, whether it be insects or seeds (or plant tubers, often taken by Sulphur-crested Cockatoos), and so may be afforded greater opportunity in the open-ground conditions immediately after fire, and after the maturation of the regrowth herb and shrub layers. Crimson Rosellas are often attracted to take seeds from shrubs or herbs such as 'fireweeds' (native *Senecio* spp.) that proliferate after fire.

Many species listed as threatened in the Victorian Temperate Woodland Bird Community inhabit open woodlands with sparse understorey (Victorian State Government legislated listing of threatened communities, as per Flora & Fauna Guarantee Act 1988). They include some such as Scarlet Robin (*Petroica boodang*) that in other studies have been found to prosper initially after fire, before declining as shrubs regenerate and then reaching peak abundance at later successional stages (Loyn, 1997, Loyn and McNabb, 2015). This pattern of ecological succession has been recognised as one of the four main patterns of response to logging (Kavanagh et al., 2004) or fire (MacHunter et al., 2009).

4.4. There is evidence for bird responses to an increase in fire frequency

This study provided some evidence for a fire frequency response by birds in heathy dry forests, although it was clear that birds were principally responding to resource availability related to temporal vegetation changes. Similar conclusions were made in a study of multiple fires in patches of foothills forests (in central and eastern Victoria), where little evidence was found for post-fire vegetation succession being influenced by fire frequency (Haslem et al., 2016). Kelly et al. (2017) found various effects of fire frequency on flora and fauna, but most could be explained by the changed distribution of age classes. In other biomes, repeated burning in tropical forests of Kalimantan did not reduce bird species richness despite evidence for declines in abundances (Slik and Balen, 2005) and bird species richness was not impacted by repeated fires in the mixed evergreen forests of Oregon, USA (Fontaine et al., 2009). Coarse woody debris is an important resource for forest fauna (Haslem et al., 2016) and while repeated burns have the potential to significantly decrease coarse woody debris stocks in temperate eucalypt forests (Aponte et al., 2014), Haslem et al. (2016) found few effects from preceding fires on vegetation structure. Nevertheless, shorter inter-fire intervals and more severe fires may prevail in heathy dry forests in the future and both may potentially impact important resources for birds, such as coarse-woody debris and hollow-bearing trees (Haslem et al., 2016).

In this study some nectarivores responded negatively to increased fire frequency because frequent fires may reduce flowering opportunities for some species thus reduce the availability of nectar resources. Work elsewhere (Kavanagh et al., 2004, MacHunter et al., 2009) showed that nectarivores often favour mature forest (producing abundant nectar

from eucalypts and mistletoe) as well as from young regrowth as in the current study. So, their responses to fire frequency are complex.

In contrast, the positive response by the Brown Thornbill reflects its favouring of the shrubby young stages of regrowth where the species was observed feeding in young wattles and other shrubs that tend to proliferate in early stages after fire. Shrubs including wattles were generally most abundant at intermediate time-since-fire, and those conditions were most prevalent in sites that had been burnt twice in the last 35 years. Hence tall shrub foragers and insectivores that forage from damp ground below shrubs were found to be common in sites that had been burnt twice in the last 35 years. Fire frequency may promote plant species that regenerate and seed rapidly post fire, with wattles being a notable example.

While an increase in fire frequency in some vegetation types has resulted in a simplification of the vegetation structure with a reduction in the understorey (Albanesi et al., 2012), the structure of heathy dry forest tends to become simplified through time, naturally. As the vegetation matures, the structural diversity of the understorey greatly declines. By 35 years post fire, the heathy dry forest has a simple structure consisting largely of an open ground cover, bark and a canopy. In addition to a naturally simplified structure, results from an allied project on fire severity (on a subset of the sites that form this project) point to bird declines post fire on both burnt and unburnt sites, aligning with a decrease in rainfall that extended across the years of the Millennium Drought (1996 to 2010) through to 2014, when field observations were finished (Kuchinke et al., 2020). Woodlands with low complexity habitats support a lower abundance of species common in the heathy dry forests (e.g. Buff-rumped Thornbill, Spotted Pardalote, Grey Shrike-thrush, Scarlet Robin and White-winged Chough) (Watson et al., 2003), and so the role of fire in maintaining suitable habitat, in a drying climate, may be critical in maintaining populations.

Recent research has investigated fire frequency in dry sclerophyll forests of south-east Australia, with high frequency defined as four fires over a 31 year fire history period (Franklin et al., 2021). They investigated bird responses in terms of mobility (sedentary, migratory or nomadic) and found that fire responses within groups were unclear because responses by individual species were varied. However, they found evidence that the Laughing Kookaburra was one of three species, more likely to occur when fire frequency was low, as deduced in our study. (The other two were species not observed in this project).

While the evidence here for a limited response by birds to fire frequency is consistent with that elsewhere (Loyn et al., 2003), some recent research reveals that inter-fire interval can be an important driver of plant and animal populations (Kelly et al., 2017). With the predictions of an increase in fire frequency in the Australian landscape (Bradstock, 2010, Clarke et al., 2013) now being realised, and large scale wildfires occurring across south-east Australia more than once in a decade (Fairman et al., 2016), fire responses by birds may change as increases in fire frequency impact the fire sensitive (obligate seeders) and the fire tolerant (re-sprouting) trees in the landscape (Fairman et al., 2016). While re-sprouters display the greatest resilience to frequent fire, predictions are for plants with few seeds, potentially failing to regenerate, as fire frequency increases (Rodrigo et al., 2004). Further research has highlighted that plants take several years to establish pre-fire seed stocks, so subsequent fires occurring in the juvenile stages of obligate-seed regenerators can threaten species (Bowman et al., 2014).

Just as Victoria's heathy dry forest has an estimated tolerable fire interval requirement of 15 years post wildfire (Cheal, 2010), it was highlighted by Rodrigo et al. (2004) that fire intervals of <10 to 15 years may lead to the disappearance or reduction of plant species. As the climate in south-east Australia is drying, further investigations into the tolerable limits of fire tolerant vegetation species are required. What is already known is that these fire tolerant species have temperature tolerances that will likely result in site-location shifts as temperatures increase and rainfall decreases (Mok et al., 2012, Enright et al., 2015). The drying landscape and the increase in the frequency of large-scale fires,

both potentially impacting the persistence of fire-tolerant vegetation species, may have important consequences for forest birds. A threat to dense new-growth vegetation is a direct threat to bird biodiversity in heathy dry forests, or any other forest type.

4.5. Adaptive management must consider the responses of individual species to fire

If the trend of declining avian biodiversity in southeastern Australia is to be arrested, research needs to extend into the mechanisms behind species' responses to a changing fire regime. An adaptive management approach is required, to determine if present fuel reduction burns are influencing bird responses; and if so, how these can be manipulated to achieve asset protection, without threatening birds and other fauna. While there may now be evidence necessary to manage fire, an adaptive approach might refine the lessons available from this and other evidence. As wildfires increase in extent and frequency across the south-east Australian landscape, necessarily, levels of planned burning will increase (Teague, 2010) and more extensive ecological response analyses should become an increasingly important part of planned burning programmes.

Research in both arid Mallee woodlands (northern Victoria) and denser forests of the Otway Ranges (southern Victoria) showed that rates of resource development can be highly variable (Haslem et al., 2011, Sitters et al., 2014). Post-fire recovery of bird abundances will vary spatially, across most habitats, and some species will appear more vulnerable than others. Furthermore, management strategies promoting new-growth and regrowth vegetation will not necessarily benefit all species (Brown et al., 2009, Taylor et al., 2013, Connell et al., 2017).

While much research is currently, and necessarily, focused on the rarer and endangered birds heavily impacted by fires of unprecedented frequency and extent (Legge et al., 2022), it is prudent that, moving forward, plans reflect the needs of more common species that are also going to be impacted with range and abundance reductions, as fire increases in severity and extent over time. In our study in heathy dry forests, the common species made up 99 % of total abundance. But management plans incorporating the rare and cryptic 26 species that formed part of our dataset can prove challenging, when data are too few. However, if fire management fails to recognise and manage for the requirements of the common, as well as the rarer species, localised extinctions may result.

5. Conclusion

Our findings show that many bird species in the heathy dry forests of central Victoria are most numerous in relatively young new growth and regrowth vegetation after fire, and hence are likely to benefit from these classes being well represented across the landscape. However, findings also highlighted that there are exceptions to this pattern. Exceptions include species that favour older fire regrowth vegetation, that will require long fire intervals or effective protection of long-unburnt refuges, as is well recognised. The study also identified that at least three species that feed from open ground (and more from other studies) can be disadvantaged or excluded by the dense shrub regeneration that follows fire. That phenomenon deserves greater recognition in planning fire management. Most of those species favour older forest (which tends to be more open), reinforcing the need to protect and maintain suitable areas of long-unburnt forest.

CRedit authorship contribution statement

Diana Kuchinke: Conceptualization, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **Julian Di Stefano:** Methodology, Formal analysis, Writing – review & editing. **Richard Loyn:** Writing – review & editing. **Peter Gell:** Supervision, Writing – review & editing. **Grant Palmer:** Investigation, Writing – review &

editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Individual study sites were selected as experimental units for part of a wider research program (Fire in Temperate Forest Landscapes, Federation University), designed to investigate the relationship between fire mosaics and the status of native wildlife and their habitats.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120877>.

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