

## **ORIGINAL RESEARCH**

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# Ecosystem type and species' traits help explain bird responses to spatial patterns of fire

Frederick W. Rainsford<sup>1,2\*</sup>, Katherine M. Giljohann<sup>1,3,4</sup>, Andrew F. Bennett<sup>1,2</sup>, Michael F. Clarke<sup>1,2</sup>, Josephine MacHunter<sup>5</sup>, Katharine Senior<sup>3,6</sup>, Holly Sitters<sup>6</sup>, Simon Watson<sup>7</sup> and Luke T. Kelly<sup>6</sup>

## Abstract

Background Understanding how temporal and spatial attributes of fire regimes, environmental conditions, and species' traits interact to shape ecological communities will help improve biodiversity conservation in fire-affected areas. We compared the influence of time since the last fire at a site, and the area and diversity of post-fire successional vegetation surrounding a site (i.e., the "spatial context" of fire), on bird species and functional groups in two ecosystems in south-eastern Australia. These ecosystems, semi-arid "mallee" woodlands and temperate "foothill" forests, differ in stand-regeneration patterns, climate, and topography. For 22 bird species in mallee woodlands, 33 species in foothill forests and four functional groups of birds in both ecosystems, we fitted non-linear models that differed in fire regime predictor variables.

**Results** In foothill forests, models that included both time since fire and a spatial context variable explained more variation in bird abundances than models that included only time since fire or a spatial variable. In mallee woodlands, the addition of spatial attributes of fire helped explain the occurrence of several species, but this finding was muted when measured across all species. There were key differences between ecosystems in functional group responses to fire regimes. Canopy/upper-midstorey foragers were positively associated with the amount of latesuccessional vegetation in mallee woodlands, but not in foothill forests. Lower-midstorev foragers showed a decline response to the amount of *late*-successional vegetation in mallee woodlands and a contrasting incline response in foothill forests. However, lower-midstorey foragers showed a similar response to the amount of surrounding *early*successional vegetation in both ecosystems—decreasing in abundance when > 50% of the surrounding vegetation was early-successional.

**Conclusions** The influence of fire regimes on birds varies among species within sites, across landscapes and between ecosystems. Species' foraging traits influence bird associations with fire regimes, and help to make sense of a myriad of relationships, but are usefully understood in the context of ecosystem types and the regeneration patterns of their dominant flora. The spatial context of fire regimes is also important—the amount of successional vegetation surrounding a site influences bird abundance. Fire management strategies that incorporate the spatial contexts of fire regimes, as well as the temporal and ecological contexts of fire regimes, will have the greatest benefits for biodiversity.

Keywords Birds, Fire management, Fire extent, Fire mosaic, Fire regime, Post-fire succession, Pyrodiversity, Southeastern Australia, Time since fire, Wildfire

\*Correspondence: Frederick W. Rainsford

f.rainsford@latrobe.edu.au

Full list of author information is available at the end of the article



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## Resumen

**Antecedentes** El entendimiento sobre cómo los atributos de la distribución espacial y temporal de los regímenes de incendios, las condiciones ambientales y las características de las especies interactúan para modelar las comunidades ecológicas, ayudará a mejorar la conservación de la diversidad en áreas afectadas por incendios. Comparamos la influencia del tiempo desde el último incendio en un sitio y área, y la diversidad sucesional de la vegetación post fuego alrededor de un sitio, sobre aves y grupos funcionales de especies en dos ecosistemas del sudeste de Australia. Estos ecosistemas, un matorral semiárido (mallee en Inglés Australiano), y un bosque pedemontano templado, difieren en los patrones de regeneración, clima, y topografía. Para 22 especies de aves en matorrales semiáridos (mallees de ahora en más), 33 especies en bosques pedementanos, y cuatro grupos funcionales de aves en ambos ecosistemas, ajustamos modelos no-lineales que difirieron en los predictores de regímenes de fuego.

**Resultados** En los bosques pedemontanos, los modelos que incluyeron tanto el tiempo desde el último incendio y un contexto espacial variable, ayudaron a explicar la ocurrencia de varias especies, aunque este patrón fue mutando cuando fue medido para todas las especies. Hubo algunas diferencias clave entre ecosistemas en las respuestas de grupos funcionales a los regímenes de incendio. Los forrajeadores de doseles altos y medios estuvieron positivamente asociados con la vegetación en estado seral tardío en mallees, pero no en bosques pedemontanos. Los forrajeadores de doseles bajos mostraron una respuesta declinante al incremento de vegetación seral tardía en los mallees, y una tendencia al aumento en los bosques pedemontanos. En cambio, los forrajeadores de doseles medios mostraron una respuesta similar a la cantidad de vegetación en estadios serales tempranos en ambos ecosistemas, decreciendo en abundancia cuando > 50% de la vegetación de los alrededores estaba en etapas sucesionales tempranas.

**Conclusiones** La influencia de los regímenes de fuego sobre las especies de aves varía entre especies dentro de los sitios, entre paisajes y entre ecosistemas. Las características de forrajeo de las especies influencian las relaciones entre regímenes de fuego de manera diferencial dependiendo de los patrones de regeneración de la vegetación. Las respuestas de las aves al fuego se entienden de manera útil en el contexto de tipos de ecosistema y su flora dominante. El contexto espacial de los incendios es también importante. La vegetación en estado sucesional tardío es más importante para las aves que forrajean en los doseles cuando la vegetación se recupera lentamente luego de in incendio, y aun los taxones que están asociados positivamente en sitios con vegetación en estados sucesionales tempranos, pueden ser afectados negativamente por grandes incendios que queman reservas enteras. Las estrategias de manejo del fuego que incorporan los contextos espaciales, temporales y también los ecológicos de los regímenes de fuego, tendrán los mejores beneficios para la biodiversidad.

## Introduction

Spatial and temporal patterns of fire shape Mediterranean-type ecosystems worldwide (Chalmandrier et al. 2013, Puig-Gironès et al. 2017, Clarke et al. 2021, Saab et al. 2022). Fire changes vegetation by altering the survival, reproduction, and dispersal of plants (Smith et al. 2016) and, in turn, the availability of food and shelter resources used by animal species such as birds (Jacquet and Prodon 2009, Hutto and Paterson 2016, Rainsford et al. 2021a). Shifts from historic fire regimes due to climate change and human activities have been implicated in the decline of many bird species (Kelly et al. 2020; Stephens et al. 2019). A better understanding of how spatial and temporal components of fire regimes affect bird species is crucial for bird conservation in fire-affected areas.

Some key temporal and spatial attributes of fire regimes that influence birds include the time since the last fire (Watson et al. 2012a, Hutto and Patterson 2016), the spatial extent of fire (Lindenmayer et al. 2014), and the diversity and configuration of successional states (Tingley et al. 2016; Stillman et al. 2019) and fire severity classes (Nappi and Drapeau 2011; Puig-Gironès et al. 2022). The relative importance of these attributes in shaping bird communities may vary in different locations and under different conditions. A spatial mosaic of diverse post-fire successional states can promote biodiversity in some situations, such as in mixed Eucalyptus forests (Sitters et al. 2014a), conifer forests (Tingley et al. 2016), and African savannas (Beale et al. 2018). However, the relationship is not straightforward in others, such as semi-arid woodlands (Taylor et al. 2012), where there are important tradeoffs between critical habitat provided by long-unburnt vegetation and positive influences of fire-driven variation over time (Clarke et al. 2021). In addition, the relative importance of fire-influenced elements, such as the proportion of early, mid, or late-successional vegetation, can differ among ecosystems (Kelly et al. 2017a; Rainsford et al. 2021a; Jones and Tingley 2022). Consequently, a challenge for land, fire and conservation managers is to understand where generalities of fire-driven patterns may or may not be applicable among ecosystems.

Differing responses of birds to fire within and across landscapes may stem from extrinsic factors (e.g., climate, topography) or intrinsic factors (e.g., species traits), or the interactions between them. For example, water availability (an extrinsic factor) influences the post-fire recovery of vegetation (Puig-Gironès et al. 2017), which can lead to variation in bird species' responses to fire within ecosystems over time (Connell et al. 2022; Puig-Gironès et al. 2022). Responses to fire may also vary spatially due to differences in flammability or productivity among vegetation types. For example, Watson et al. (2012a, b) showed that bird species' responses to time since fire differed between semi-arid vegetation types which have differing understorey compositions and capacities for vegetation to carry fire. Interactions between fire and plant species traits are also important for birds. Plant regeneration patterns differ among ecosystems: systems may be dominated by basal (ground) or epicormic (stem) resprouters or by obligate seeders (Pausas & Keeley 2017). These differences have implications for the rate and form of post-fire habitat change for fauna (Rainsford et al. 2020) and potentially for how species respond to the temporal and spatial attributes of the fire regime.

Behavioral traits (an intrinsic factor) of birds have also been linked to their responses to fire regimes (Pons et al. 2012, Chalmandrier et al. 2013, Gosper et al. 2019, Hutto et al. 2020). Recent studies in mixed-species *Eucalyptus* forests have highlighted how the foraging behavior of birds influences their post-fire occurrence. For example, birds that forage on open ground, like the scarlet robin *Petroica boodang*, were more abundant in the years soon after fire (Rainsford et al. 2022), whereas birds that depend on well-developed midstorey structure, like the golden whistler *Pachycephala pectoralis*, were more abundant in later successional vegetation (Rainsford et al. 2021b).

This study examines the responses of bird species and functional groups to a temporal attribute and several spatial attributes of fire regimes, and compares them between two Eucalyptus-dominated ecosystems in south-east Australia: semi-arid "mallee" woodlands and temperate "foothill" forests. These ecosystems differ in climate, topography, vegetation structure, plant and animal community composition; and, importantly, in the post-fire regeneration traits of the canopy trees. In mallee woodlands, trees regenerate by basal resprouting from lignotubers, whereas in foothill forests trees primarily recover via epicormic resprouting from tree trunks and branches. In mallee woodlands, time since fire at a site (Watson et al. 2012a) and the spatial context of fire in the landscape (i.e., the extent and diversity of surrounding successional vegetation) are important for bird communities (Taylor et al. 2012; Berry et al. 2015). In contrast, in temperate *Eucalyptus* forests, where tree stems survive fire and resprout epicormically, few bird species show strong associations with time since fire at a site (Sitters et al. 2014b; Kelly et al. 2017b), but evidence suggests bird species richness at a landscape scale is positively associated with the spatial diversity of fire age classes (Sitters et al. 2014a).

In both ecosystems, fire management is guided by models of post-fire temporal changes in vegetation structure, time to maturity, and senescence of key plant species (Cheal 2010; York and Friend 2016). Testing the relative influence of the spatial context of fire regimes on bird species in different ecosystems provides an opportunity to uncover commonalities and contrasts in the role of fire between ecosystems. This will help identify where generalizations in fire management may or may not be appropriate, and will build understanding of the interactions between fire, extrinsic and intrinsic ecosystem factors, and species' distributions in fire-affected areas.

Here, we address four main questions as they relate to bird species: (1) What is the relative influence of temporal and spatial attributes of the fire regime? (2) Does the influence of fire regime attributes differ between ecosystems? (3) Does the influence of fire regime attributes vary within ecosystems? (4) Is the influence of fire regime attributes on bird species explained by their foraging and nesting behavior? To address these questions, we modelled responses of species and functional groups of birds to fire regime attributes in each ecosystem while accounting for other environmental conditions.

## **Materials and methods**

### Study locations

The study areas cover as follows: (a) ~ 100,000 km<sup>2</sup> of mallee woodland vegetation, spanning parts of Victoria, South Australia and New South Wales, and (b) ~ 75,000 km<sup>2</sup> of foothill forests in Victoria, Australia (Fig. 1). Both ecosystems experience recurrent wildfires and are subject to fire management, including prescribed burning and wildfire suppression.

### Mallee woodlands

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



Fig. 1 A The extent of mallee woodlands vegetation (orange area) in south-east Australia and locations of survey sites. B Mallee woodlands vegetation (photo credit: MFBP). C The extent of foothill forests vegetation (green area) in Victoria, Australia, and locations of survey sites. D Foothill forests vegetation (photo credit: FR)

generally sparse understorey is dominated by sclerophyllous shrubs, including *Acacia* species, chenopod species and the hummock grass *Triodia scariosa* (Fig. 1A, B).

Mallee vegetation is flammable under suitable fire weather. Large wildfires (>10,000 ha) occur approximately decadally in the region (Clarke et al. 2021). Nevertheless, patches within large reserves can remain unburnt for many decades (>100 years, Clarke et al. 2010). Land managers undertake regular prescribed burning, mainly to reduce the extent and severity of wildfires to mitigate impacts on defined values (e.g., life and property, biodiversity, infrastructure) (Department of Environment, Land, Water and Planning [DELWP] 2022). Wildfires in mallee woodlands typically are "stand-replacing" in nature as tree stems are killed and regeneration happens from the ground up (Clarke et al. 2021).

## Foothill forests

Foothill forests are temperate dry forests that occur on the low- to mid-slopes (<900 m above sea level) of the Great Dividing Range in south-eastern Australia. Summers are hot, and winters are cool and wet (mean daily maxima January: 27 °C, July: ~13 °C [Willow Grove, Station 085283]; mean annual rainfall ranges from ~700 mm [Willow Grove] – 980 mm [Combienbar AWS, station no. 084143], http://www.bom.gov.au). The canopy (30–60 m) is dominated by thick-barked *Eucalyptus* species on drier slopes and ridges, and smooth-barked *Eucalyptus* species in more mesic areas, like gullies. The understorey consists of a diverse array of shrubs and herbs that ranges from dense in mesic areas to sparse on exposed slopes (Fig. 1C, D), leading to variation in broad vegetation type throughout the foothill forests study area.

The foothill forest ecosystem has typically experienced large wildfires (>10,000 ha) periodically (Haslem et al 2016). The frequency of large fires in the ecosystem, but not necessarily at a site, is increasing with multiple large fires occurring within a decade (Abram et al. 2021). Prescribed burns are regularly carried out mainly to reduce the extent and intensity of fires (Department of Environment, Land, Water and Planning 2022). Canopy trees typically persist through fire and trees resprout from protected epicormic buds along the trunk and branches (Collins 2019). Fire also triggers *Eucalyptus* recruitment though seed germination.

Throughout the text, we use the term "ecosystem" to refer to the broadest level of classification (i.e., mallee woodlands, foothill forests) and the term "vegetation type" to refer to within-ecosystem vegetation classifications.

## Bird data

To determine the responses of diurnal bird species and functional groups of birds to fire regimes and other environmental conditions (climate, topography, vegetation type), we used relative abundance data collated during two multi-institutional research projects: Mallee Fire and Biodiversity Project (Taylor et al. 2012; Watson et al. 2012a) and Foothills Fire and Biota Project (Kelly et al. 2017b). In both projects, bird data were obtained from sites stratified along a time-since-fire gradient. We included only sites where >60% of the area within a 900 m ×900 m (81 ha) area centered on the site was either mallee woodland or foothill forest. This resulted in 555 sites in mallee woodlands and 458 sites in foothill forests.

Bird data were collected during systematic surveys that used either timed point counts or timed area searches (Watson et al. 2012a; Kelly et al. 2017b). All individuals heard or seen by an experienced observer within the defined survey area were identified to species level. Mallee woodlands were surveyed during 2006 and 2007, and foothill forests between 2009 and 2012. Surveys were conducted during the austral spring and autumn in each survey year. The relative abundances of species were calculated for each site by summing the total number of detections over all survey rounds (range 2–4). We accounted for differences in survey effort among foothill forest sites by including total survey time and survey area in analyses. Details of bird survey methods can be found in Additional file 1.

For functional groups, we pooled relative abundance values for all recorded species within four groups based on behavioral traits plausibly related to species' fire responses (Rainsford et al. 2022): (1) ground foragers birds that forage mostly on the ground, (2) lower-midsto-rey foragers—birds that forage mostly in vegetation < 3 m height, (3) canopy/upper- midstorey foragers—birds that forage mostly in vegetation > 3 m height, (4) hollow nesters—birds that nest exclusively in tree hollows. Classifications are based on Garnett et al. (2015), BirdLife Australia species profiles (www.birdlife.org) and expert knowledge of the authors. Species lists, foraging, and nesting groups are provided in Additional files 2 and 3 for mallee woodlands and foothill forests, respectively.

### Fire data

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

### Fire regime attributes

We investigated the influence of four fire regime attributes in each ecosystem (Table 1). These included one temporal attribute, time since fire at the site, and three spatial attributes calculated within a 900 m×900 m window (81 ha) (see below) centered on the site; (i) the amount of early-successional vegetation ("amount early"), (ii) the amount of late-successional vegetation ("amount late"), and (iii) the spatial diversity of successional vegetation ("spatial diversity").

Time since fire was calculated as the number of years between the date of the bird survey and the most recent preceding mapped fire at the site. To represent the spatial context of fire regimes, we categorized the vegetation into post-fire successional states based on the time since last fire. For mallee woodlands, these categories were calculated following Kelly et al. (2012): early: 0–10, mid: 11–35, and late:>35 years since fire. For foothill forests, successional states were based on Cheal (2010): early: 0–3, mid 1: 4–10, mid 2: 11–40, late:>40 years since fire. "Amount early" and "amount late" were calculated using ArcGIS 10.3.1 as the summed area in each respective successional state. Spatial diversity was calculated using the Shannon diversity index of all successional states.

To select the window size for these spatial attributes, we first ran a set of three exploratory models for all species in which we varied the window size used (i.e.,  $300 \times 300$  m,  $900 \times 900$  m,  $1900 \times 1900$  m windows). As the explanatory power of species models did not differ substantially among the three window sizes, we used a window size of  $900 \times 900$  m. A 900-m<sup>2</sup> window was large enough to cover a range of values of spatial attributes and large relative to the home range size of many common birds in these ecosystems.

### Environmental data

We selected environmental variables representing three gradients that influence important ecological processes for birds: temperature, elevation, and vegetation type (Table 1) (Kelly 2017b). We used the average annual

Category	Variable	Mean (range) of values		Description	Scale
		Mallee woodlands	Foothill forests		
Fire regime	Time since fire (years)	34 (0–106)	37 (0–107)	Number of years between the date of the bird survey and the most recent mapped fire at the site that preceded the survey	Site
	Amount early (ha)	15 (0–81)	35 (0–81)	The amount (ha) of vegetation classified as "early- successional" [0–10 years since fire (MW), 0–3 years since fire (FF)] within a $900 \times 900$ m window, cen- tered on the bird survey site	Landscape
	Amount late (ha)	31 (0–81)	16 (0–81)	The amount (ha) of vegetation classified as 'late- successional' [> 35 years since fire (MW), > 40 years since fire (FF)] within a 900×900 m window, cen- tered on the bird survey site	Landscape
	Spatial diversity of succes- sional vegetation (index)	0.38 (0–1.13)	0.30 (0–1.33)	Shannon's diversity index of post-fire successional states within a 900 × 900 m window, centered on the bird survey site. Successional states were: Mallee woodlands: 0–10, 11–35, > 35 years since fire. Foothill forests: 0–3, 4–10, 11–40, > 40 years since fire	Landscape
Environmen- tal condi- tions	Temperature (°C)	16.6 (15.4–17.4)	23.7 (19.4–28.5)	MW: annual average daily temperature; FF: average daily maximum temperature for January (hottest month)	Site
	Elevation (m)	66 (32–104)	397 (33–954)	Meters above sea level based on digital elevation model (DEM)	Site
	Vegetation type (categorical)	Triodia Mallee Chenopod Mallee Heathy Mallee	Driest Dry Mesic	Groups of vegetation classes with similar floristic and structural characteristics	Site

**Table 1** Summary of explanatory variables included in generalized additive models for birds in mallee woodlands (MW) and foothills forests (FF). The range of values in each ecosystem and a description of variables are given

temperature for mallee woodlands and the average daily maximum temperature in January (hottest month) for foothill forests. Different metrics were used to better represent the different gradients in each ecosystem: north– south in mallee, elevation + latitude in foothills. Elevation data were based on a 1-s SRTM Digital Elevation Model (DEM) (Geoscience Australia, 2011), resampled to a 100-m grid using bilinear resampling in ArcGIS 10.3.1.

Mallee vegetation types were classified according to Haslem et al. (2010) as either Chenopod Mallee, Heathy Mallee, or Triodia Mallee. These vegetation types differ mainly in their dominant understorey species— Triodia mallee: Hummock grass, Chenopod mallee: Chenopodiaceae species Heathy mallee: heathy shrub species. Foothill forest vegetation was classified following Haslem et al. (2016) as Driest (Grassy/Heathy Dry Forest, Tall Mixed Forest), Dry (Foothills Forest, Forby Forest), or Mesic (Moist Forest). These vegetation types were derived from a spatial data layer of native vegetation (Department of Environment, Land, Water and Planning 2005).

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

All fire and environmental variables were calculated using ArcMap 10.3.1 (ESRI 2016) and the raster package

(Hijmans and van Etten 2016) in the R statistical environment (R Development Core Team 2020).

### Data analysis

We used generalized additive models (GAMs) to model the responses of bird species and functional groups to the fire and environmental variables. For individual species, we built models for species that occurred at  $\geq$  45 sites in each data set (10 and 8% of sites in foothill forests and mallee woodlands, respectively) so that all models converged.

For each species and functional group, we built six models that differed in the fire regime attributes included (Table 2). Four of the models included a single fire regime attribute: (1) time since fire, (2) amount late, (3) amount early, or (4) spatial diversity. The fifth model included two fire regime attributes: time since fire plus the spatial context attribute with the highest relative contribution (% deviance explained) for that species (from models 2 to 4). All models included temperature, elevation, and vegetation type to allow for detection of the influence of fire attributes while controlling for key aspects of environmental variation. An interaction between vegetation type and fire attributes was included in each model to detect variation in species' responses to fire regimes among vegetation types within each ecosystem (so two interaction **Table 2** Explanatory variables included in six generalized additive models to predict the relative abundance of bird species and functional groups in mallee woodlands and foothill forests. Models were built to test the influence of a single attribute of the fire regime (models 1–4), both time since fire and the spatial context of fire together (model 5), and environmental gradients without fire (model 6)

Model	Fire regime attribute	Other environmental variables
1	Time since fire	Temperature
		Elevation
		Vegetation type
2	Amount late	Temperature
		Elevation
		Vegetation type
3	Amount early	Temperature
		Elevation
		Vegetation type
4	Spatial diversity	Temperature
		Elevation
		Vegetation type
5	Time since fire	Temperature
	<sup>a</sup> Best spatial context variable	Elevation
		Vegetation type
6	None	Temperature
		Elevation
		Vegetation type

 $^{\rm a}$  The spatial context attribute with the highest relative contribution (% deviance explained) for the species

terms were included in model 5). A sixth model included the three environmental variables and no fire regime attribute.

Models were built using the mgcv package in R (Wood 2017). Highly correlated predictor variables (Pearson's coefficient > 0.6) were not included in the same model. For foothill forests, the variables log(survey duration) and log(survey area) were included in models to account for differences in survey effort between sites (following Kelly et al. 2017a, b). The number of knots of the smooth term of the fire regime variable was held at k=3 to prevent overfitting. Environmental and survey effort variables were included with no smooth term. Models were first built with a Poisson error distribution and checked for data overdispersion using the AER package in R (Kleiber & Zeileis 2008). Overdispersion was detected for most modelled species (43/55), so all models were built using a negative binomial error distribution (Linden and Mantyniemi 2011). Model checks, done using the "gam.check" function in the mgcv package, showed the negative binomial distribution was an appropriate fit. Modelling protocols for functional groups followed the same process as for individual species. Distance analyses performed on data from mallee woodlands and foothill forests showed that detectability was consistent among recently burnt and long-unburnt vegetation at different topographic positions (Watson et al. 2012a; Sitters et al. 2015); therefore, we modelled species' relative abundances without explicitly accounting for detectability. Models were built without explicitly accounting for potential spatial autocorrelation, but rather by accounting for environmental variables that would contribute to spatial autocorrelation.

To address our research questions, we first assessed models of each species that included a single fire regime attribute (models 1-4). Then, we assessed models that included time since fire and a spatial context of fire attribute (model 5). We compared the percent deviance explained (Zuur 2012) attributable to each fire regime attribute or combination of attributes for all modelled species within each ecosystem, by using notch plots built using the ggplot2 package (Wickham 2016) in R. Percent deviance explained is a measure of how much variation in the data is explained by a model (Zuur 2012) and has been used to compare the explanatory power of models and the variables included in them (e.g., Kelly et al. 2017b; Fusco et al. 2019). The "notches" on notch plots indicate 95% confidence intervals of the median (McGill et al. 1978). The deviance explained attributed to each fire regime attribute was calculated by subtracting the total deviance explained by the "no fire variable model" (model 6) from the total deviance explained by each of the five fire models. When the 95% confidence intervals for the deviance explained by the attributes did not overlap, we considered this to indicate substantial difference between attributes.

We then plotted the modelled (models 1-4) responses of species to (1) time since fire, (2) amount late, (3) amount early, and (4) spatial diversity of successional states while accounting for the influence of environmental gradients and differences in survey effort and described the shape of the response curve following Watson et al. (2012a). For each species, a separate line was fitted for each vegetation type within the two ecosystems (i.e., three curves were fitted for each species). Response shapes were classified as: "bell": initial increase followed by a decrease, "incline" = monotonic increase, "plateau"=initial increase followed by stabilization, "decline" = decrease, "u" = initial decrease followed by an increase, "ns" = not significant (Watson et al. 2012a). A response was considered "not significant" if a horizontal line could fit within the 95% confidence interval of the plotted smooth term for that variable. For each fire regime attribute, we then calculated the percentage of species whose fitted model resembled each response shape and compared these between two common vegetation types representative of each ecosystem—Triodia mallee and Dry foothill forests.

To investigate the influence of species' traits on their relationships with fire regime attributes, we modelled functional group responses to attributes following the same modelling steps outlined for individual species.

In addition, we used descriptive statistics to compare the composition of the bird communities between ecosystems, by contrasting the dominant taxonomic bird families, widespread species, and the percentage of species in broad diet, foraging, and nesting groups.

## Results

## Bird community composition

We collated data on relative abundance for a total of 64 diurnal bird species in mallee woodlands (67% of species occurred in mallee woodlands but not foothill forests) and 97 species in foothill forests (78% occurred in foothill forests but not mallee woodlands). Although the species assemblages differed, the functional composition of the bird communities was similar in both ecosystems, based on species' diet, foraging location, and nest type (Fig. 2A-C). The dominant bird families were also similar in both ecosystem (Fig. 2D,E), these were Meliphagidae (honeyeaters), Artamidae (magpies and butcherbirds), and Acanthizidae (thornbills and scrubwrens). Species that were widespread (>45 sites) and common to both ecosystems were the rufous whistler Pachycephala rufiventris, spotted pardalote Pardalotus punctatus, striated pardalote Pardalotus striatus, and white-eared honeyeater Nesoptilotis leucotis. The most widespread species in mallee woodlands (total sites=555) were the vellow-plumed honeyeater Ptilotula ornatus (54% of sites), spotted pardalote (46%), and white-eared honeyeater (46%). In foothill forests (total sites = 458), the most widespread species were the spotted pardalote (83% of sites), yellow-faced honeyeater Lichenostomus chrysops (83%), crimson rosella Platycercus elegans (80%), and striated thornbill Acanthiza lineata (79%).

## Bird species' responses to fire regimes

We built GAMs for 22 species in mallee woodlands and 33 species in foothill forests that occurred at  $\geq$  45 sites. Models were built for six species that occurred in both ecosystems. Within mallee woodlands and foothill forests, the overall influence of time since fire and the spatial fire regime attributes was similar and consistently modest (median deviance explained ~ 3 – 8%); with responses to time since fire and amount late noticeably weaker in foothill forests than in mallee woodlands (Fig. 3). However, some species showed stronger responses to particular fire regime attributes. Overall, in foothill forests, the explanatory power of models that included both time since fire *and* a spatial fire regime attribute together was substantially greater than that of models that included *only* time since fire (Fig. 3B); but less so for mallee woodlands when assessed across multiple species (Fig. 3A). In foothill forests, this difference was particularly strong for the silvereye *Zosterops lateralis* and rose robin *Petroica rosea* (Fig. 3B). In mallee woodlands, including both time since fire and a spatial attribute together in models resulted in a marked increase in explanatory power for the striated grasswren *Amytornis striatus* (Fig. 3A).

Vegetation type within each ecosystem influenced species' responses to fire regimes (Figs. 4 and 5). Only one species in mallee woodlands, southern scrub-robin Drymodes brunneopygia, showed the same response to a fire regime attribute (time since fire) in all three vegetation types (Additional file 3). In mallee woodlands, more species responded to time since fire in Triodia Mallee than either Chenopod Mallee or Heathy Mallee (Additional file 6) and most species that responded to time since fire showed a peak in mid to late-successional vegetation (i.e., bell, e.g., southern scrub-robin; incline or plateau response, e.g., yellow-plumed honeyeater) (Figs. 4A and 5A). The yellow-plumed honeyeater showed a similar response (incline) to amount late in Chenopod Mallee and Triodia Mallee, whereas the response of the whiteeared honeyeater to amount late varied between Chenopod Mallee (decline) and Triodia Mallee (bell) (Fig. 4B). Fifty percent of species in Triodia mallee responded to the amount of surrounding early-successional vegetation (Fig. 5C). Responses to this attribute were either "bell" (e.g., white-eared honeyeater, Fig. 4C) or "decline" (e.g., yellow-plumed honeyeater, Fig. 4C). Relatively few species in mallee woodlands responded to spatial diversity (Fig. 5D); however, the relative abundance of the yellow-plumed honeyeater decreased, and the relative abundance of the white-eared honeyeater increased with increasing spatial diversity of successional vegetation (Fig. 4D).

In foothill forests, 36% of species showed a significant response to time since fire (Additional file 6) and only 9% of species responded to this attribute in Dry foothill forest (Fig. 5A). The rose robin and superb lyrebird *Menura novaehollandiae* both showed "incline" responses and the brown-headed honeyeater *Melithreptus brevirostris* showed a "decline" response in Driest foothill forests (Fig. 4E). Several species, such as the rose robin (Fig. 4F), were positively associated with the amount of surrounding late-successional vegetation at sites (Fig. 5B), whereas others, such as the white-eared honeyeater (Fig. 4C), were negatively associated with this attribute. Most species that responded to the amount of surrounding early-successional vegetation at sites in Dry foothill forests showed a "decline" response (Fig. 5C)



**Fig. 2** Functional and taxonomic composition of the bird communities in mallee woodlands (*n* = 64 species) and foothill forests (*n* = 97 species). Bars show the percentage of species in functional groups based on diet (**A**), main foraging stratum (**B**), and nest type (**C**) and in taxonomic families (**D**—mallee woodlands, **E**—foothill forests). Numbers above bars indicate counts of species within groups. Diet groups were based on the main food source following Garnett et al. 2015. If a species uses more than one main food source (e.g., many honeyeaters consume nectar and invertebrates), it was counted in both groups. Foraging location was based on the stratum in which the species forages most of the time. "Open" nests refer to nests constructed outside of hollows or burrows. "Hollow" includes all size classes of hollow



**Fig. 3** The influence of time since fire and spatial measures of fire regimes on the relative abundance of bird species in **A** mallee woodlands (*n* = 22 species) and **B** foothill forests (*n* = 33 species). Points represent the response of single species to each predictor variable. Deviance attributed to a variable (%) represents the influence of each variable from a generalized additive models after accounting for temperature, elevation, vegetation class, and survey effort. Models included either a single attribute of the fire regime or both time since fire plus the best spatial context of fire variable. Notch plots indicate median (line), upper, and lower quartiles (shaded area) and 95% confidence intervals (notches) for each predictor variable. Point labels are abbreviations of species' names: YPHE=yellow-plumed honeyeater, SSR=southern scrub-robin, WEHE=white-eared honeyeater, BHHE = brown-headed honeyeater, SGW = striated grasswren, RORO rose robin, SULB superb lyrebird, SILV=silvereye, SPPA = spotted pardalote, RBTC = red-browed treecreeper

(e.g., silvereye, Fig. 4G). However, the spotted pardalote was positively associated with the amount of surrounding early-successional vegetation in Dry and Mesic foothill forests (Fig. 4G). No species responded significantly to this attribute in Driest foothill forests (Additional file 6). Species showed a range of responses to spatial diversity in foothill forests (Fig. 5D). For example, the silvereye showed a "bell" response, and the spotted pardalote showed an "incline" response (Fig. 4H). Summary data for individual species' models can be found in Additional files 4 and 5 for mallee woodlands and foothill forests, respectively.

### Functional group responses to fire regimes

Categorizing species into functional groups revealed similarities and differences between ecosystems in the influence of the spatial context of fire on birds. In mallee woodlands, canopy/upper-midstorey foragers were most strongly influenced by the presence of late-successional vegetation at a site (Figs. 6A and 7A). Ground foragers, canopy/upper-midstorey foragers, and hollow nesters in mallee woodlands were all positively associated with the amount of surrounding late-successional vegetation (Fig. 7B). The abundance of lower-midstorey foragers was negatively associated with the amount of surrounding late-successional vegetation and showed a "bell-shaped" response to the amount of surrounding early-successional vegetation whereby it increased when surrounding vegetation was < 50% early-successional, but decreased at sites when > 50% of the surrounding vegetation was early successional (Fig. 7C). This group also responded positively to the diversity of successional vegetation (Fig. 7D).

In foothill forests, ground foragers showed a "u-shaped" response to time since fire in Driest foothills vegetation and declined in response to this attribute in Mesic vegetation (Fig. 7E). For lower-midstorey foragers in foothill forests, the negative influence of the amount of surrounding early-successional vegetation was stronger than the positive influence of the amount of surrounding late-successional vegetation (Figs. 6G,H and 7F,G). Hollow nesters in foothill forests showed a decline response to the amount of surrounding early-successional vegetation



Fig. 4 Responses to fire regime attributes in mallee woodlands (A–D) and foothill forests (E–H) for selected bird species to illustrate the strongest and key types of responses observed in each ecosystem. Lines are fitted generalized additive models. Line color indicates vegetation types within each ecosystem. In mallee woodlands: yellow lines=Triodia mallee, red lines=chenopod mallee. In foothill forests: turquoise lines=driest, blue lines=dry, purple lines=mesic. Shaded areas indicate 95% confidence intervals. YPHE=yellow-plumed honeyeater, SSR=southern scrub-robin, WEHE=white-eared honeyeater, BHHE=brown-headed honeyeater, RORO=rose robin, SULB=superb lyrebird, SILV=silvereye, SPPA=spotted pardalote

in Mesic vegetation (Fig. 7G). Canopy/upper-midstorey foragers did not show a significant response to any of the fire regime attributes and no functional groups in foothill forests showed a significant response to spatial diversity; however, ground foragers showed a non-significant incline trend in response to this variable (Fig. 7H).

## Discussion

The spatial context of fire can influence resource distribution and, consequently, bird abundances in forests and woodlands. This study advances understanding of the relative importance of site and neighborhood attributes of fire regimes on species and functional groups by showing that (a) model explanatory power was greatest when time since fire and spatial context were included together in foothill forests but less so in mallee woodlands; (b) the availability of late-successional vegetation, both at and surrounding a site, is important for many birds, particularly canopy/upper-midstorey foragers in mallee woodlands; (c) lower-midstorey foragers show opposing responses to surrounding late-successional vegetation in mallee woodlands (decline) and foothill forests (incline), but in both ecosystems decrease in abundance when the amount of surrounding early-successional vegetation is high (>50% of total vegetation). This variation in bird-fire relationships among species and functional groups, both within and between ecosystems, underscores the need for nuance in understanding and managing biodiversity in fire-prone regions.

## Between-ecosystem differences in bird responses to fire regimes—plant traits are important

Fire affects faunal species directly, through mortality and emigration, and indirectly through changes in vegetation (habitat) structure (Fox 1982; Sitters et al. 2014b; Stillman et al. 2019). Given the similarity in dominant taxonomic and functional groups of birds between the two ecosystems, we suggest differences in their responses to fire regime attributes are driven by interactions between bird traits and post-fire resilience of stand structure and climate, rather than fundamental differences in the functional composition of bird communities. We note two key points. First, in mallee woodlands, above-ground vegetation of canopy trees typically is consumed by fire and trees recover by basal resprouting (Haslem et al. 2011). In contrast, in foothill forests, canopy trees resprout from epicormic buds along the trunk and branches, such that the structure of the tree layer largely persists through fire and canopy recovery is much more rapid (Haslem et al. 2016; Rainsford et al. 2020). Second, climatic conditions



**Fig. 5** Responses of bird species to **A** time since fire, **B** amount late, **C** amount early, and **D** spatial diversity of fire in Triodia mallee (n=22 species) and Dry foothill forests (n=33). Bars represent the percentage of species modelled in each vegetation type whose fitted response curve resembled each of six response shapes (brown = bell, light blue = incline, peach = plateau, dark blue = decline, purple ="u-shape", gray = not significant [horizontal line can fit within the 95% confidence interval of the predicted response curve]) following Watson et al. 2012a. Numbers within bars indicate counts of species within groups

affect plant growth rates and hence vegetation structural recovery (Puig-Gironès et al. 2022). The more-arid conditions in mallee woodlands make post-fire recovery slow (Haslem et al. 2016; Kenny et al. 2018), with structural resources, such as large trees with cavities and dense canopy foliage, taking many decades to develop following fire (Haslem et al. 2011). This in turn affects the trajectory of bird species that use these resources (e.g., canopy/upper-midstorey foragers). Indeed, many species in mallee woodlands are associated with late-successional vegetation at a site (see also Watson et al. 2012a and Connell et al. 2017).

In foothill forests, several structural components of the habitat (e.g., leaf litter depth, understorey vegetation) also develop with time since fire (Haslem et al. 2016; Rainsford et al. 2020). This helps to explain the contrasting responses of lower-midstorey foraging birds in each ecosystem—in early-successional mallee vegetation, the lower-midstorey is the dominant stratum, whereas in foothill forests, the understorey vegetation takes years to develop (Rainsford et al. 2020) and the abundance of birds that rely on this stratum changes accordingly. The abundance of ground-foraging birds in foothill forests decreased as time since fore increased, likely because the development of dense understorey vegetation impedes foraging for this functional group. However, overall, we found relatively fewer bird species are associated with specific post-fire successional states in foothill forests compared with mallee woodlands. We attribute this more muted response to the greater structural resilience of foothill forest vegetation to fire (Collins 2019).

## Within-ecosystem variation in bird responses to fire regimes

All but one species, the southern scrub-robin in mallee woodlands, showed different responses to fire regime



**Fig. 6** The influence of temporal and spatial attributes of fire regimes on the relative abundance of functional groups of birds in mallee woodlands (**A–E**, orange points) and foothill forests (**F–J**, green points). Points represent the deviance explained attributed to time since fire (**A**, **F**), amount late (**B**, **G**), amount early (**C**, **H**), spatial diversity (**D**, **I**), and time since fire + spatial attribute (**E**, **J**) from generalized additive models after accounting for the influence of environmental gradients (temperature, elevation, vegetation class) and survey effort. Note the different *x*-axis for mallee woodlands (**A–E**) and foothill forests (**F–J**)

attributes across vegetation types within an ecosystem. Three potential, inter-related explanations for these differences relate to (a) differences in fire behavior between vegetation types within ecosystems, (b) differences in post-fire vegetation recovery, and (c) bird preferences for vegetation types.

Variation in species' responses to fire regimes across vegetation types has been explored previously in mallee woodlands: differences between Triodia Mallee and Chenopod Mallee are attributed to the greater capacity for hummock grasses in Triodia Mallee to carry fire, leading to distinct changes in understorey structure with time since fire (see Haslem et al. 2011; Watson et al. 2012a). Here we showed that bird functional group responses to fire regimes, in addition to individual species, are also related to vegetation structural patterns. For example, canopy/upper-midstorey foragers increased in abundance with time since fire in all three mallee vegetation types, whereas lower-midstorey foragers showed a response to time since fire (decline) only in Triodia Mallee. Species' prevalence also helps explain within-ecosystem variation: the yellow-plumed honeyeater showed strong responses in Chenopod Mallee and Triodia Mallee but not Heathy Mallee, because this species was recorded at only a few sites in Heathy Mallee compared to many sites in Chenopod Mallee and Triodia Mallee (Additional file 7).

In foothill forests, the main difference between the vegetation types recognized here is moisture availability, which influences vegetation composition and structure and, potentially, fire behavior and post-fire vegetation recovery. This likely affects species responses to fire regimes in foothill forests. However, further research is needed to better understand the mechanisms driving within-ecosystem variation in species' fire responses.

## Spatial patterns of fire influence bird species distributions—foraging traits matter

Both mallee woodlands and foothill forests encompass broad climatic and environmental gradients that interact with fire regimes to shape the distribution of biota (Clarke et al. 2021; Kelly et al. 2017b). Here, we show that the effect of the spatial context of fire on bird abundances is influenced by the environmental conditions in which those spatial attributes occur. This has broad implications when considering the findings in relation to the spatial attributes of fire regimes. The spatial extent and configuration of fire surrounding a site influence a species' capacity to recolonize and persist in the post-fire landscape (Watson et al. 2012b; Lindenmayer et al. 2014;



Fig. 7 Responses of functional groups of birds to fire regime attributes in mallee woodlands (A–D) and foothill forests (E–H). Significant responses are displayed to illustrate the key responses observed in each ecosystem. Lines are fitted generalized additive models. Line color indicates vegetation types within each ecosystem. In mallee woodlands: red = chenopod mallee, brown-green lines = Heathy mallee, yellow lines = Triodia mallee. In foothill forests: turquoise lines = Driest, blue lines = Dry, purple lines = Mesic. Shaded areas indicate 95% confidence intervals and lines with no shaded area are not significant. "Can/up" = canopy/upper-midstorey foragers, "Low-mid" = lower-midstorey foragers, "Ground" = ground foragers, "Hollow" = hollow nesters

Nimmo et al. 2019). The spatial diversity of fire history, affects the ability of birds to use the nearby resources in different successional states (Berry et al. 2015; Stillman et al. 2019). Spatial heterogeneity of fire history can positively influence species for which recently burnt vegetation is unsuitable, by facilitating recolonisation or in situ survival (Berry et al. 2015; Burgess and Maron 2016). It can also benefit species for which multiple successional states are required to meet their resource needs (Nappi and Drapeau 2011; Nimmo et al. 2019; Stillman et al. 2019): for example, animals that exploit foraging opportunities in recently burnt vegetation and use the denser cover of older vegetation for refuge or nesting (Lundie-Jenkins et al. 1993, Bliege Bird et al. 2013).

We found that interactions between species' foraging traits and spatial attributes of fire regimes influenced responses of birds to fire. For some species, early-successional vegetation is an important source of resources; whereas for many other species, it has limited value. However, in ecosystems where fire is critical for maintaining species' composition (i.e., where the vegetation will transition into an alternative stable state in the absence of fire), early-successional states are a necessary stage in the subsequent supply of mid- and late-successional vegetation over time. Lower-midstorey foragers in mallee woodlands were positively associated with spatially diverse fire histories and were most abundant at sites in early-to-mid successional vegetation (i.e., <25 years post-fire), suggesting potential resource partitioning between different post-fire successional states. This response may be due to a preference for the foraging conditions associated with early-successional vegetation (e.g., exposed invertebrates) but also the use of resources found in late-successional vegetation (e.g., sheltered roosting sites). Further, this group decreased in abundance when the amount of surrounding earlysuccessional vegetation (i.e., 0-10 years post-fire) was greater than 50%, pointing to potential negative impacts of large fires that burn large expanses of reserves. Such responses highlight the challenge faced by land managers when aiming to limit the extent of large fires and generate an ecologically desirable mix of successional states (Giljohann et al. 2018). Yet, they also highlight the potential opportunity for tailoring actions to promote two objectives, such as where land managers aim for a mix of successional states as a means to reduce the likelihood of large fires. Our findings suggest that too much early-successional vegetation, which would result from large fires, may be detrimental to many bird species. These findings would be even more pronounced if a more conservative

definition of "arly-successional" vegetation were used, for example 0–2 years post-fire (when vegetation is most open).

There was variation among species in the influence of the spatial diversity of fire. Some species likely respond negatively because they benefit from large intact areas of a particular successional state, such as the yellow-plumed honeyeater in mallee woodlands. Other species, however, responded positively to the spatial diversity of successional states; for example, the white-eared honeyeater in mallee woodlands and rufous whistler in foothill forests (Additional files 4 and 5), perhaps because they access and use resources associated with vegetation in different successional states. It will be useful for conservation planning in these two ecosystems to understand how birds use spatially heterogeneous landscapes at finer scales.

When considered as a functional group, hollow-nesting birds in both ecosystems were not strongly related to the fire regimes attributes measured (except for a negative relationship with the amount of early-successional vegetation in foothill forests). We suggest two potential, non-exclusive, explanations: first, that foraging behavior rather than nesting behavior is the main behavioral trait influencing bird species' relationships with fire regimes, as measured in this study; and second, that other aspects of the fire regime, such as fire severity or inter-fire interval, might have greater influence on the availability of tree hollows than time since fire or the amount of surrounding successional vegetation. The negative relationship of hollow-nesting birds with amount of early-successional vegetation in foothill forests suggests a potential negative impact of large fires on this group.

### **Further research**

This study has revealed several knowledge gaps that future research could address. We were able to build models only for the most common species, and therefore omitted several threatened species (Connell et al. 2017; Giljohann et al. 2018). In particular, knowledge of cryptic species such as owls is lacking. A second area for further research could use recent advances in the resolution of fire mapping (Collins et al. 2018; Gibson et al. 2020) to build on current understanding of the role of spatial diversity, configuration, and severity of fire in shaping species' distributions. The resolution of current fire mapping does not always discern unburnt patches within fire boundaries that may act as refuges for birds. For example, unburnt gullies in foothill forests can act as refuges for birds, likely influencing post-fire recolonisation of adjacent burnt areas (Robinson et al. 2014). If unburnt patches were present within a fire boundary, the importance of spatial diversity or the amount of surrounding late-successional vegetation may have been underestimated for some species.

## Conclusions

Fire regimes play an important role in the distribution of many birds in fire-prone landscapes, but the influence of fire regime attributes varies among species within sites, across landscapes and among ecosystems. This underscores the need for a nuanced approach to fire management. Here, we demonstrated that (i) fire responses of birds must be understood in ecological context; (ii) the spatial context of fire is critical; and (iii) species foraging traits influence relationships with fire regime attributes differently depending on vegetation regeneration patterns and help to understand the myriad of relationships. These findings shed light on the complex interplay between birds and fire regimes. This more comprehensive understanding will be valuable for informing fire management strategies to better support bird conservation objectives.

## Supplementary Information

The online version contains supplementary material available at https://doi. org/10.1186/s42408-023-00221-3.

Additional file 1. Bird surveys methods. Table 1. Survey methods for birds in projects contributing data on the avifauna of mallee woodlands and foothill forests. Total survey time is the summed time of all surveys across multiple survey rounds.

Additional file 2. Species recorded in mallee woodlands. Table S2. Bird species recorded, and the number of sites at which they were recorded, in mallee woodlands. Behavioral traits plausibly related to species' fire responses include: the main foraging stratum (ground, lower-midstorey, canopy/upper-mid/, throughout, above canopy), diet (invertebrates, fruit, nectar, seeds, vertebrates, omnivorous) and nest type (bowl, burrow, cup, dome, ground, hollow, hollow in termite nest, parasite) are given. Classifications are based on Garnett et al. (2015), BirdLife Australia species profiles (www.birdlife.org) and expert knowledge of the authors. Taxonomy for bird names follows: BirdLife Australia (2019). The BirdLife Australia Working List of Australian Birds; Version 3.

Additional file 3. Species recorded in foothill forests. Table S3. Bird species recorded, and the number of sites at which they were recorded, in foothill forests. Behavioral traits plausibly related to species' fire responses include: the main foraging stratum (ground, understorey, canopy/uppermidstorey, throughout, above canopy), diet (invertebrates, fruit, nectar, seeds, vertebrates, omnivorous), nest type (bowl, burrow, cup, dome, ground, hollow, hollow in termite nest, parasite) are given. Classifications are based on Garnett et al. (2015), BirdLife Australia species profiles (www. birdlife.org) and expert knowledge of the authors. Taxonomy for bird names follows: BirdLife Australia (2019). The BirdLife Australia Working List of Australian Birds; Version 3.

Additional file 4. Individual species model outputs – mallee woodlands. Table S4. Generalized additive model outputs for birds in mallee woodlands (n = 22 species). Models were built for each species in which the fire regime variables differed (time since fire, amount of late-successional vegetation, amount of early-successional vegetation or spatial diversity of fire ages, time since fire + spatial context, no fire variable). Models were built for species that occurred at  $\geq$  45 sites. All fire models included an interaction between the fire regime variable and vegetation type as well as variables to represent gradients of temperature and elevation. The deviance explained attributed to each fire variable was calculated by subtracting the deviance explained of the 'no fire variable' model (model 6) from the total deviance explained of each of the 'fire' models (i.e., models 1 - 5). The shape of response curves was determined by plotting fitted models to fire variables – a separate line was fitted for each vegetation type. Response shapes were described following Watson et al. (2012a, b). A response was considered not significant (ns) if a horizontal line could fit within the 95% confidence intervals of the fitted model.

Additional file 5. Individual species model outputs - foothill forests. Table S5. Generalized additive model outputs for birds in foothill forests (n = 33 species). Models were built for each species in which the fire regime variables differed (time since fire, amount of late-successional vegetation, amount of early-successional vegetation or spatial diversity of fire ages, time since fire + spatial context, no fire variable). Models were built for species that occurred at ≥45 sites. All fire models included an interaction between the fire regime variable and vegetation type as well as variables to represent gradients of temperature, elevation and survey effort. The deviance explained attributed to each fire variable was calculated by subtracting the deviance explained of the 'no fire variable' model from the total deviance explained of each of the 'fire' models (i.e., models 1 - 5). The shape of response curves was determined by plotting fitted models to fire variables - a separate line was fitted for each vegetation type. Response shapes were described following Watson et al. (2012a, b). A response was considered not significant (ns) if a horizontal line could fit within the 95% confidence intervals of the fitted model.

Additional file 6. Responses of bird species to temporal and spatial attributes of fire regimes in mallee woodlands (A, D, G, J, n = 22 species) and foothill forests (B, E, H, K, n = 33) by vegetation type (x-axis, CM = chenopod mallee, HM = heathy mallee, TM = Triodia mallee). In the left and middle columns bars represent the percentage of species modelled in each ecosystem whose fitted response curve to time since fire (A-B), amount late (D-E), amount early (G-H) and spatial diversity (J-K) resembled each of six response shapes (brown bars = bell, light blue = incline, red = plateau, dark blue = decline, purple ='u-shape', gray = not significant [horizontal line can fit within the 95% confidence interval of the predicted response curve]) following Watson et al. 2012a, b. In the right-hand column, bars represent the percentage of species in mallee woodlands (MW) and foothill forests (FF) that showed a significant response to time since fire (C), amount late (F), amount early (I) and spatial diversity of successional vegetation (L), irrespective of vegetation type. Numbers above and within bars indicate counts of species within groups.

Additional file 7. Counts of modelled bird species at sites in mallee woodlands by vegetation type. CM= chenopod mallee, HM= heathy mallee, TM=Triodia mallee. Letters above plots are represent species' common names. ARPA = Australian ringneck parrot, BHHE brown-headed honeyeater, CBB = chestnut-browed babbler, CQT = chestnut quail-thrush, CRT = chestnut-rumped thornbill, GBB = gray butcherbird, GST gray shrike-thrush, ITB = inland thornbill, JW = jacky winter, RWH = rufous whistler, SCHE = spiny-cheeked honeyeater, SGW = southern grasswren, SHW = shy heathwren, SPPA = spotted pardalote, SSR = southern scrub-robin, STPA = striated pardalote, WBB = white-browed babbler, WBL = weebill, WEHE = white-erared honeyeater, WFHE = white-fronted honeyeater, WWTA = willie wagtail, YPHE = yellow-plumed honeyeater.

Additional file 8. Counts of modelled bird species at sites in foothill forests by vegetation type. Letters above plots are represent species' common names. Akpa = Australian king parrot, bfcs = black-faced cuckoo-shrike, bftb = buff-rumper thornbill, bhhe = brown-headed honeyeater, brtb = brown thornbill, crhe = crescent honeyeater, crro = crimson rosella, easp = eastern spinebill, eyro = eastern yellow robin, flro = flame robin, ftcu = fan-tailed cuckoo, ggco = gang gang cockatoo, gowh = golden whistler, grft = gray fantail, grst = gray shrike-thrush, lako = laughing kookaburra, picu = pied currawong, rbtc = red-browed treecreeper, rewb = red wattlebird, roro = rose robin, ruwh = rufous whistler, sbcu = shining bronze cuckoo, silv = silvereye, spa = spotted pardalote, stpa = striated pardalote, sttb = striated thornbill, sufw = superb fairywren, sulb = superb lyrebird, whsw = white-browed scrubwren, wehe = white-eared honeyeater, whnhe = white-naped honeyeater.

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### Authors' contributions

FR lead the analysis and writing. FR, LK, KG, and KS worked collaboratively on the analyses and interpretation. LK, KG, AB and MC were involved in designing the study. LK, SW, HS and JM were involved in data collection and collation. All authors contributed critically to drafts.

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#### Availability of data and materials

Data will be made available on request.

## Declarations

## Ethics approval and consent to participate

Not applicable.

**Consent for publication** Not applicable.

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## Competing interests

The authors declare that they have no competing interests.

### Author details

<sup>1</sup> Department of Environment and Genetics, La Trobe University, Bundoora, VIC 3086, Australia. <sup>2</sup>Research Centre for Future Landscapes, La Trobe University, Bundoora, VIC 3086, Australia. <sup>3</sup>School of BioSciences, University of Melbourne, Parkville, VIC 3052, Australia. <sup>4</sup>CSIRO Environment, Clayton, VIC 3168, Australia. <sup>5</sup>Department of Energy, Environment, and Climate Action, Arthur Rylah Institute for Environmental Research, 123 Brown Street, Heidelberg, VIC 3084, Australia. <sup>6</sup>School of Agriculture, Food and Ecosystem Sciences, University of Melbourne, Parkville, VIC 3052, Australia. <sup>7</sup>Victorian Government Department of Energy, Environment and Climate Action, East Melbourne, Victoria, Australia.

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