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Fire and functional traits: Using functional groups of birds and plants to guide management in a fire-prone, heathy woodland ecosystem

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Abstract

Aim: Many dry forests and woodlands worldwide are fire-prone and support bird and plant communities shaped by fire. Changes in fire regimes, including the time between fires, have important implications for population trajectories. We studied the responses of bird and plant communities of heathy woodlands to time since the last fire, a key measure underpinning fire management, to evaluate whether current management strategies will enhance conservation of multiple taxa.

Location: Otway Ranges, south-eastern Australia.

Methods: We surveyed birds and plants at 38 sites, stratified by an 80-year post-fire chronosequence, and modelled the responses of individual species, functional groups and community composition to fire history. Model outputs were used to evaluate the impacts of fire management as guided by (a) domains of tolerable fire intervals, a concept based on plant life history traits, and (b) the spatial arrangement of post-fire age classes, a surrogate for animal habitats.

Results: Bird and plant communities both responded to time since fire. Notable relationships included the following: a high reporting rate of ground-foraging birds and high cover and species richness of shrubs immediately after fire; and a gradual increase up to ~50 years and ~20 years post-fire of birds that forage in the mid-storey and facultative-resprouting plants, respectively. Post-fire age classes had distinct bird and plant assemblages. Tolerable fire intervals currently used by land managers (min 12–max 45 years between fires) encompassed the peak in richness of most plant functional groups but not the preferred habitat of lower-mid-storey foraging birds.

Main conclusions: Fire management based solely on birds or plants risks population declines in other biota. Use of functional groups can help guide strategic planning, such as spatial representation of post-fire age classes across the landscape. Maintaining late-successional vegetation will provide habitat for several groups of birds, while fire is needed at sufficient frequency to prevent loss of plants and ground-foraging birds.

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KEYWORDS

birds, fire interval, fire management, functional traits, habitat, plants, post-fire succession, time since fire

1 | INTRODUCTION

Conservation of biota in fire-prone ecosystems depends on knowing how, and when, populations and communities recover following fire (Turner, 2010; Warchola et al., 2018). There is growing evidence that fire regimes are changing in Mediterranean-type ecosystems—including sclerophyll vegetation of Australia, chaparral in the United States, fynbos in South Africa, and matorral in Chile—with substantial consequences for the biota (González et al., 2018; Keeley & Syphard, 2019; Msweli et al., 2020; Nolan et al., 2020; Vitolo et al., 2019). Shifts in fire regimes can threaten species and ecological communities with risk of local extinction, including by compromising their ability to survive changing conditions (Enright et al., 2015; Giljohann et al., 2015; He et al., 2016; Stephens et al., 2019). There is an urgent need to understand how fire, and fire management practices, affect multiple taxa and biological levels.

For animals, persistence in fire-prone environments is closely linked to habitat structure and depends on their ability to capitalize on food and shelter resources associated with post-fire vegetation changes (Fox, 1982; Sitters et al., 2014; White et al., 2016). For example, the Dartford Warbler (*Sylvia undata*) in southern Europe relies on dense low shrub cover that results from past fires in Mediterranean woodlands (Pons et al., 2012). A focus on post-fire vegetation succession and accompanying changes in habitat structure has translated into management for animals that aims for spatially diverse fire mosaics (Kelly et al., 2018). In south-eastern Australia, for example, post-fire age classes, determined by compositional and structural changes to vegetation, have been defined to represent key “growth stages” in post-fire succession in an ecosystem (e.g., Cheal, 2010). Even though much of the fauna of temperate south-east Australia has not shown strong preferences for particular successional stages (e.g., Rainsford et al., 2021; Swan et al., 2015), the assumption that such categories represent distinct successional communities has rarely been tested for animal taxa.

For plants, persistence in fire-prone landscapes depends on the ability of populations to recover from fire events, either through germination of seeds, resprouting of survivors or a combination of both (Keith et al., 2007; Keeley et al., 2011). As such, the interval between fires is critical for both reproductive and resprouting success, but the required interval depends on species' traits such as time to reproductive maturity and the life span of established plants and seedbanks (Clarke et al., 2015; Enright et al., 2015; Menges, 2007).

An emphasis on the species traits of plants has translated into management that aims for variation in fire intervals over time (Kraaij et al., 2013; Menges, 2007; Noble & Slatyer, 1980;

van Wilgen et al., 2011). An influential approach is the concept of minimum and maximum tolerable fire intervals (TFIs) (closely related to the concepts of “thresholds of particular concern” and “bounded ranges of variation”; Kelly et al., 2018). The minimum tolerable fire interval is based on the number of years required post-fire for key plant species to successfully reproduce and set seed, while the maximum tolerable fire interval represents the age post-fire at which these key species begin to senesce (Bradstock & Kenny, 2003; Kraaij et al., 2013). For example, in Victoria, Australia, fire managers quantify the proportion of the landscape that is either within, or outside, the recommended tolerable fire interval to decide where and when to carry out prescribed burns (York & Friend, 2016). This approach, however, does not explicitly recognize the needs of other taxa, such as animals (Clarke, 2008), although there has been progress in recent years. Diversity metrics based on species' abundances have been used to test the effect of the spatial structure of post-fire age classes on biota (Giljohann et al. 2015; Kelly et al., 2015; Di Stefano et al., 2013). However, a key knowledge gap remains how such practices shape ecological communities.

Recognizing functional groups that share common traits, and doing so for multiple taxonomic groups, has the potential to improve fire management for biodiversity. Recurrent fire has driven the evolution of a variety of traits that enable species to persist in fire-prone landscapes (Pausas & Parr, 2018). For animals, important traits determining post-fire occurrence relate to habitat-use (e.g., foraging behaviour, diet specialization, nest type) (Gosper et al., 2019; Jacquet & Prodon, 2009). Relating these traits to species' fire responses may help to reveal the processes that drive patterns of biodiversity across fire-prone landscapes, which can inform management strategies. Generalizations based on analyses of species' life history traits will build understanding of how ecosystem structure and function change following fire (Gosper et al., 2019; Sitters et al., 2016). This knowledge will help identify those species and ecosystem processes that may be affected by more frequent fires, or benefit from more widespread prescribed burning, and thereby help improve decision making in fire management.

Here, we examine how approaches to fire management may affect bird and plant communities in a heathy woodland ecosystem dominated by epicormic-resprouting *Eucalyptus* trees in south-eastern Australia. Specifically, we aimed to determine how (a) individual species, (b) functional groups of species and (c) the composition of bird and plant communities respond to time since fire. We then discuss these outcomes in the context of the potential impacts of fire management as guided by (a) tolerable fire intervals, based on plant life history traits (e.g., reproductive age), and (b) the spatial arrangement of post-fire age classes (based on vegetation growth stages), on the bird and plant communities of heathy woodlands.

2 | METHODS

2.1 | Study area

The study area is part of the Great Otway National Park and Forest Park in the Otway Plains bioregion of southern Victoria, Australia (Figure 1). The climate is temperate with mean annual rainfall ranging from 540 to 895 mm. The highest rainfall occurs in winter (August) and the hottest month is February (mean daily maximum 28°C) (Mount Gellibrand, station no. 090035I, Cape Otway lighthouse,

station no. 090015; <http://www.bom.gov.au/>). The topography is gently undulating with elevation from ~40 to 250 m above sea level.

2.2 | Vegetation

Heathy eucalypt woodlands in south-eastern Australia mostly are confined to coastal areas, with some inland occurrences on nutrient-poor, deep sandy soils. In the study area, the canopy is low (≤ 10 m) and dominated by Brown Stringybark (*Eucalyptus baxteri*) and Western

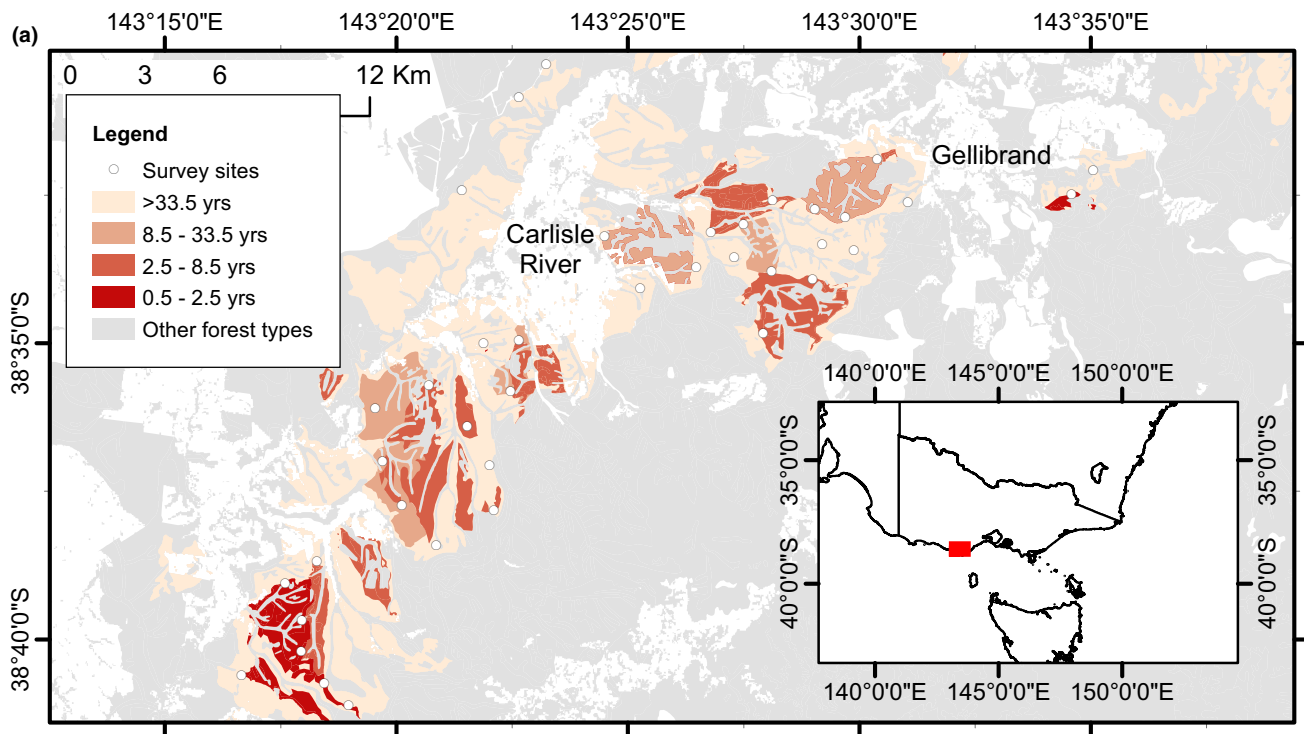


FIGURE 1 Study area and heathy woodland vegetation. (a) Map of the study area showing the extent of heathy woodlands, the location of study sites and distribution of fire age classes (darker tones represent younger age classes). White areas have been cleared or heavily disturbed, including for human settlement and agriculture. Heathy woodland vegetation: (b) ~1 year after prescribed fire, showing a scorched canopy of *Eucalyptus* species resprouting epicormically, Austral Grass-tree resprouting apically; and (c) 51 years after fire with a well-developed mid-storey dominated by *Monotoca glauca* and *Leptospermum* species

Peppermint (*E. fasciata*), both of which can resprout epicormically following fire. The understorey consists of a diverse array of shrubs, including Austral Grass-tree (*Xanthorrhoea australis*), Heath Tea-tree (*Leptospermum myrsinoides*), Prickly Tea-tree (*L. continentale*) and Silver Banksia (*Banksia marginata*) (Victorian Government Department of Sustainability & Environment, 2004). Fire regeneration traits vary between understorey species: for example, Tea-trees resprout from basal lignotubers, Austral Grass-tree resprouts apically and Silver Banksia regenerates from seed. A dense understorey thicket forms over time, following disturbance (Figure 1c) (Rainsford et al., 2020).

2.3 | Fire regime and fire history

In heathy woodlands, wildfires typically occur in summer months while prescribed burning is carried out by government agencies during autumn and early spring. Wildfires occur at ~20- to 100-year intervals (Murphy et al., 2013). In the study area, a wildfire occurred in 1939 and several wildfires also burned patches during the 1960s. Prescribed fire is employed to achieve objectives relating to fuel reduction and, less often, biodiversity conservation. The timing of prescribed burns in Victoria is guided by the designation of minimum and maximum tolerable fire intervals (TFIs) for a particular vegetation type, based on the number of years required for key plant species to set seed (minimum TFI) and begin to senesce (maximum TFI) (Cheal, 2010). Prescribed fires typically burn more patchily than wildfires, but in heathy woodlands both fire types generally scorch the canopy (Figure 1b).

Fire history was determined by using spatial data maps supplied by the Victorian Department of Environment, Land, Water and Planning (DELWP) and analysed using the software ArcMap (ESRI, 2011). Spatial data maps of fire perimeters post-1976 were created by using LANDSAT imagery, and pre-1976 by using historical records.

2.4 | Study design

Potential study sites were selected to meet four main criteria. First, sites were selected to sample a single vegetation type (heathy woodlands Ecological Vegetation Class, Victorian Government Department of Environment & Sustainability, 2004). Second, we used fire history maps (in a GIS) to identify sites spanning a chronosequence from 1- to 79 years post-fire. Sites were selected to evenly cover a range of post-fire “age classes,” successional states based on the vegetation growth stages described by Cheal (2010). These were 0.5 – 2.5 years (AC1, 8 sites), 2.5 – 8.5 years (AC2, 10 sites), 8.5 – 33.5 years (AC3, 8 sites), >33.5 years since fire (AC4, 12 sites). Third, sites were selected to be away from gullies to avoid the influence of inherent differences in productivity and structure of vegetation between gullies and slopes. Last, sites were located at least 1 km apart to enhance sample independence. Potential sites were checked in the field in relation to these criteria. The mapped time since fire was ground-truthed by looking for signs of charring on eucalypt bark, epicormic resprouting and other structural features. In total, 38 sites were selected for study.

2.5 | Data collection

To survey bird and plant communities at each site, we established a 250-m transect, commencing at least 50 – 100 m from a road edge. The start-point of the transect was randomly selected in a desktop GIS.

2.5.1 | Birds

To sample the bird community at each site, a 2-ha plot was centred over the 250-m transect and surveyed by a single experienced observer (FR) a total of six times: three times during the austral autumn/winter and three times during spring/summer, between 2017 and 2018. Surveys were conducted in clear weather within four hours of dawn, except for two winter survey rounds during which sites were each surveyed once in the morning and once in the afternoon. Each survey was undertaken over a 20-min period, and all individuals either heard or seen were identified to species level and recorded. The perpendicular distance (m) to each detection from the transect line was estimated to test for differences in detectability between sites. Nocturnal birds, raptors, and swifts were recorded but excluded from all analyses as these groups of birds are not reliably detected using these surveys methods.

2.5.2 | Understorey plants

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

2.6 | Data analyses

2.6.1 | Individual species

To account for potential issues of detectability of birds, we first used linear regression to test for a relationship between the distance to detection of species (or groups of similar species) and mid-storey vegetation cover (see Appendix S1). For several bird taxa, there was a weak negative relationship between mid-storey

vegetation cover and distance to detection, suggesting some individuals of these species may not have been detected at sites with high mid-storey vegetation cover. To control for potential errors due to detectability, we used a presence/absence-based index (reporting rate) to compare the relative abundance of species between sites. Reporting rate is the number of survey rounds during which a species was detected (here, from 0 to 6). Because it does not rely on counts of individuals, reporting rate is less prone to biases caused by differences in detectability or flocking behaviour. This approach is a robust alternative to model-based approaches (i.e., distance analysis) for which modelling assumptions cannot be met (Hutto, 2016) and is a reliable proxy for relative abundance (Royle & Nichols, 2003).

For individual species of birds and plants that occurred at ≥ 7 sites, we used generalized additive models (GAM) (Wood, 2017) to

predict changes in reporting rate and cover, respectively, with time since fire. Models for species with fewer records failed to converge. For birds, models were fitted using the Poisson error distribution. An observation-level random factor was used in this mixed-model framework if overdispersion of data was detected, following Harrison (2014).

For plants, the mean projected foliar cover was modelled by using the beta error distribution. The beta distribution can overcome inherent problems with proportion data (i.e., bounding at zero and one) that violate the assumptions of other distributions (Douma & Weedon, 2019). For one species, silver banksia, using a beta distribution, was problematic and a better model was fitted by using the Gaussian error distribution. The distribution of data supported this decision. GAMs were built using the *MGCV* package in R (Wood, 2017).

TABLE 1 Functional groups of birds and plants in heathy woodlands

Taxon	Category	Group	Description	Number of species
Birds	Foraging location	Ground	Takes most food from the ground. Includes species that perch in vegetation and pounce to take prey from the ground, and species that forage from the ground	11
		Lower-mid-storey	Mostly forages in vegetation ≤ 3 m above ground	10
		Upper-mid-storey	Mostly forages in vegetation > 3 m above ground. Includes species that forage among the canopy as well as those that fly out from within vegetation to take air-borne prey	17
		Throughout	Forages throughout the range of vertical strata, from ground to the canopy	5
	Nest type	Aerial	Forages on the wing, above the canopy	1
		Brood parasite	Lays eggs in the nests of other species. Does not build a nest (cuckoos)	2
		Burrow	Nests in a tunnel in the ground	1
	Diet versatility ^a	Open	Constructs nest outside of hollows or burrows	34
		Hollow	Nests in a large or small cavity in a tree	7
		Low	Only one food type that constitutes $\geq 1\%$ of the total diet	19
Plants	Regeneration trait	Intermediate	Two-three food types each constitute $\geq 1\%$ of the total diet	20
		High	Four-six food types each constitute $\geq 1\%$ of the total diet	5
		Facultative resprouter	Individuals regenerate either from seed and/or resprouting following fire	43
	Growth form	Obligate resprouter	Resprouts following fire but does not regenerate from seed following fire	4
		Obligate seeder	Individuals have no capacity to resprout following fire. Regeneration occurs via seed stored in the seed bank	11
		Shrub	Phanerophytes. Shrubs 1–8m	22
		Low shrub	Chamaephytes. Shrubs 0.1–1m	22
		Herb	Hemicryptophytes. Persistent buds at soil surface. Includes sedges	21
		Geophyte	Seasonal reduction to belowground storage organ	2

Classification of plant regeneration traits follows Clarke et al. (2015). The classification system for plant growth forms was based on Meers et al. (2010) and Gosper, Yates, et al. (2013). The number of species detected within each group is given. Individual species classifications can be found in Appendices S2 and S3.

^aFood types include fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion (Garnett et al., 2015).

By assessing fitted response curves, species were each assigned to a generalized response curve as described by Watson et al. (2012). We then calculated the percentage of species with a significant relationship with time since fire ($p < .05$) that resembled each response shape. Four response shapes were detected: “irruptive” (abundance highest in the first few years following fire), “bell” (initial increase followed by a decrease with time since fire), “incline” (gradual increase with time since fire) and “plateau” (initial increase followed by stability in later years post-fire). Non-significant relationships were classed as “NS.”

2.6.2 | Community composition

To test the influence of time since fire on the composition of bird and plant communities, we used the four post-fire age classes (AC1 to AC4, see above) based on vegetation growth stages (Cheal, 2010). AC4 included two growth stages, “waning” and “senescence,” because there were fewer sites in these categories and their vegetation structure is similar. We then used reporting rate (for birds) and relative cover (for plants) matrices and non-metric multidimensional scaling (NMDS) ordination analysis. NMDS represents ecological communities in lower-dimensional space, based on their dissimilarity (Legendre & Legendre, 1998). We used the Bray–Curtis index to calculate dissimilarities as it is less sensitive to rare species than other techniques such as Euclidian distance. The NMDS was undertaken using the metaMDS function in the “vegan” package (Oksanen et al., 2019) and ordination plots. Nonparametric permutation tests (PerMANOVA, ADONIS in the “vegan” package) were used to test for significant ($p < .05$) effects of age class on community composition. Species detected at a single site only were removed from the analysis to reduce the leverage of rare or vagrant species. We used the “betadisper” function in the vegan package to test for the potential influence of location and within-group dispersion on the community analyses.

2.6.3 | Functional groups

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

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

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

3 | RESULTS

We made 3,975 detections of 44 species of diurnal bird (Table S2). The dominant bird families were the Meliphagidae (honeyeaters, $n = 9$ species), Acanthizidae (thornbills, $n = 4$), Artamidae (butcherbirds, $n = 4$) and Pachycephalidae (whistlers, $n = 4$). Widespread bird species included the Yellow-faced Honeyeater (*Lichenostomus chrysops*) (38/38 sites), Brown Thornbill (*Acanthiza pusilla*) (38/38 sites), Grey Fantail (*Rhipidura albiscapa*) (37/38 sites) and Crescent Honeyeater (*Phylidonyris pyrrhopterus*) (36/38 sites).

We detected 67 species of vascular plants (Table S4). The most species rich plant families were the Fabaceae (peas and wattles, $n = 8$ species), Cyperaceae (sedges, $n = 7$), Ericaceae (heaths, $n = 6$), Proteaceae ($n = 4$), Asteraceae (daisies, $n = 4$) and Dilleniaceae ($n = 4$). Most species were capable of resprouting post-fire: 43 species were facultative resprouters and four species were obligate resprouters. Eleven species were obligate seeders. Five of the obligate seeders were from the Fabaceae and three from the Asteraceae. Widespread species included the shrubs: Prickly Tea-tree (*Leptospermum continentale*) (38/38 sites), Heath Tea-tree (*L. myrsinoides*) (38/38 sites), Austral Grass-tree (*Xanthorrhoea australis*) (37/38 sites) and Silver Banksia (*Banksia marginata*) (37/38 sites) and the low shrubs: Smooth Parrot-pea (*Dillwynia glaberrima*) (38/38 sites) and Erect Guinea-flower (*Hibbertia riparia*) (38/38 sites).

We built models (GAMs) for 25 bird and 39 plant species that occurred at ≥ 7 sites. Five bird and 12 plant species were significantly related to time since fire (Figure 2). We detected four types of generalized response curves: irruptive (five plants, one bird), bell (three plants, one bird), incline (one plant, one bird) and plateau (three plants, two birds). Outputs for all models are provided in Appendices S4 and S5.

Non-metric multidimensional scaling analyses and PerMANOVA showed there was a significant relationship ($p < .01$) between post-fire age classes and the composition of the bird and plant communities (Figure 3). Clustering of age classes in the ordination plots was more distinct when based on the bird community (Figure 3a) than the plant community (Figure 3c). Vectors of influential species revealed

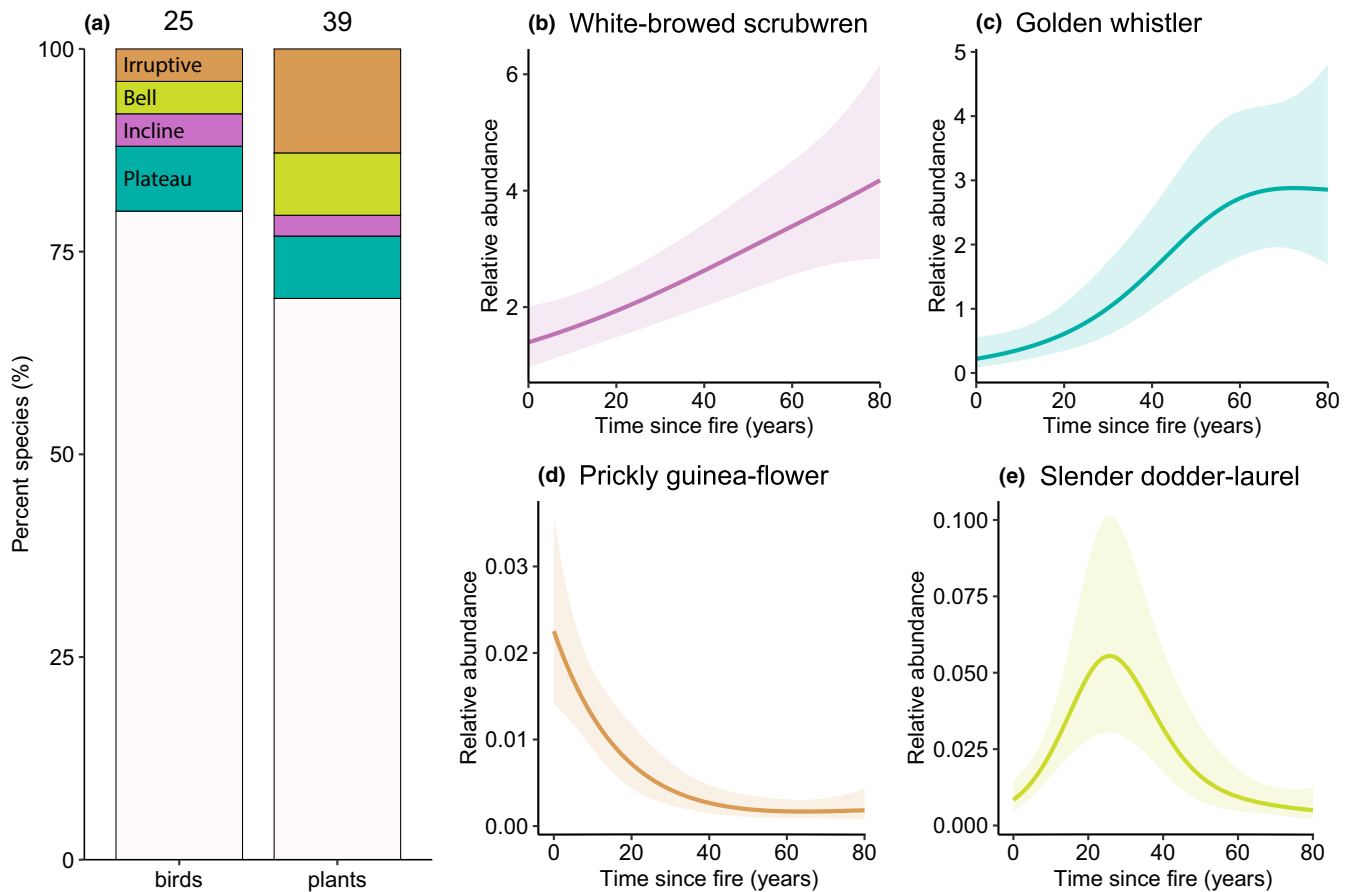


FIGURE 2 Generalized response curves from generalized additive models of the relationship between bird and plant species and time since fire in heathy woodlands. (a) The percentage of species modelled in each taxonomic group for which the response to time since fire resembled four generalized response curves (after Watson et al., 2012): “irruptive” (brown), “bell” (green), “incline” (purple) or “plateau” (blue). Off-white bars represent non-significant responses. Numbers above bars indicate the number of species modelled in each taxonomic group. (b–e) Examples of each response shape from bird (top) and plant (bottom) species: (b) incline, (c) plateau, (d) irruptive, (e) bell. Lines are fitted from models, and shaded ribbons indicate 95% confidence intervals

a strong influence of species traits on the composition of the bird communities (Figure 3b). There were two notable features in the ordination: (a) the association of lower-mid-storey foraging bird species [e.g., Brown Thornbill, New Holland Honeyeater, White-browed Scrubwren (*Sericornis frontalis*), Silvereye (*Zosterops lateralis*)] and upper-mid-storey foraging species [Golden Whistler (*Pachycephala pectoralis*), Grey Fantail (*Rhipidura albiscapa*)] with the oldest age class (AC4, >33 years) and (b) the association of ground-foraging species [Grey Shrike-thrush (*Colluricincla harmonica*), Laughing Kookaburra (*Dacelo novaeguineae*), Superb Fairy-wren (*Malurus cyaneus*), Scarlet Robin (*Petroica boodang*), Common Bronzewing (*Phaps chalcoptera*)] with recently burned vegetation (i.e., AC1, <2.5 years).

Variation in plant community composition was greater between the oldest and youngest age classes compared to the two intermediate age classes (Figure 3c). There was greater variation within age classes in the plant community compared to bird community composition. Key influential plant species (Figure 4d) included *Monotoca glauca*, which was associated with the oldest age class (AC4); *Hibbertia fasciculata* and Austral Grass-tree, which were associated with intermediate age classes (AC2,3); and Tree Everlasting

(*Ozothamnus ferrugineus*) and Austral Bracken (*Pteridium esculentum*) which were associated with the youngest age class (AC1).

We did not detect a significant effect of location or within-group dispersion on the differences between post-fire age classes in either bird ($p = .968$) or plant ($p = .418$) community composition (Appendix S8).

Functional group analyses revealed a strong influence of life history traits on bird species' relationships with time since fire, in some cases (Figure 4). The summed reporting rate of ground-foraging species was greatest in recently burnt vegetation, then declined rapidly in the first 20 years after fire ($p < .01$, deviance = 35% Figure 4a). The reporting rate of birds that forage in lower-mid-storey vegetation increased with time since fire and plateaued at ~50 years post-fire ($p < .001$, deviance = 57%, Figure 4b). For birds that forage in the upper-mid-storey, reporting rate increased linearly with time since fire ($p < .05$, deviance = 13%, Figure 4b) and species that forage throughout the vertical strata did not respond to time since fire. The reporting rate of open-nest species increased with time since fire ($p < .01$, deviance = 22%, Figure 4c). Hollow-nesting species were not strongly associated with time since fire. Reporting rate of birds

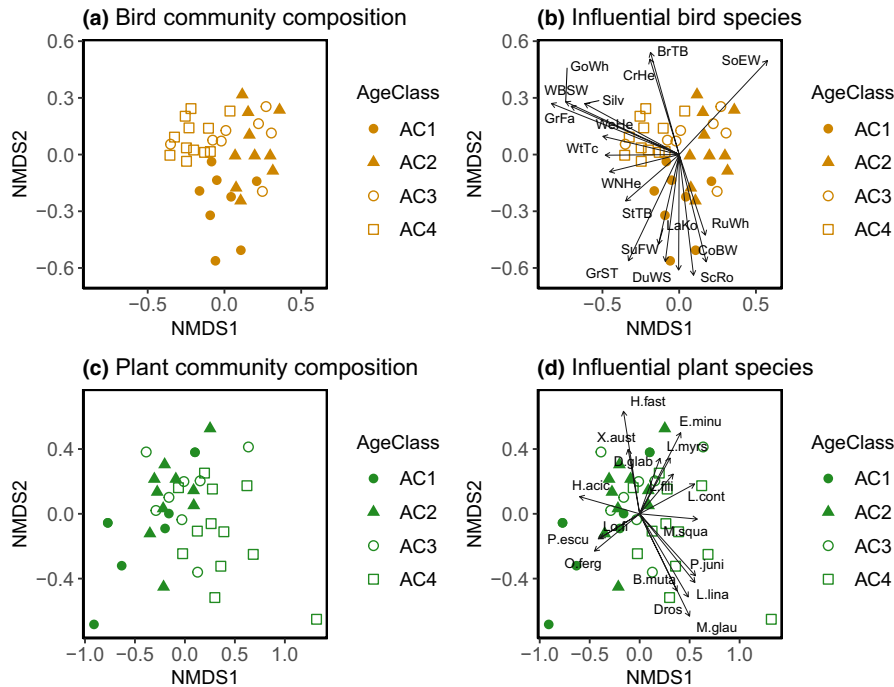


FIGURE 3 The influence of time since fire on the composition of bird (a, b) and plant (c, d) communities in heathy woodlands. Ordinations represent NMDS analyses on species reporting rate/cover matrices. Points represent sites. Symbols represent post-fire age classes. The distance between sites represents the degree of dissimilarity between the composition of bird ($n = 40$ species) and plant ($n = 56$ species) communities. Arrows (b, d) represent vectors of influential species. The length of the vector represents the strength of the relationship. Species codes indicate the common name for birds (e.g., BrTB, Brown Thornbill) and the genus (capital letter) and the first four letters of the species name for plants (e.g., H.fast = *Hypolaena fastigiata*). PerMANOVA showed a significant effect of post-fire growth stage on the composition of both the bird ($p < .001$) and plant ($p < .001$) communities. Species that occurred at a single site only were removed from the analyses

with an intermediate level of dietary versatility increased linearly with time since fire ($p < .001$, deviance = 42%, Figure 4c). Models of the number (richness) of species within each functional group generally were similar in shape to those based on the summed reporting rate of species.

For plants, the relationship with time since fire for functional groups varied depending on the data used in the models (i.e., summed relative cover versus species richness) (Figure 5). The main effect of time since fire on facultative resprouters was a plateau in relative cover after ~20 years post-fire ($p = .012$, deviance = 24%, Figure 5a). Species richness of this group declined with time since fire, but uncertainty around the estimated relationship was high ($p > .05$) (Figure 5e). Cover of obligate resprouters increased with time since fire (Figure 5b), although this estimate also had high uncertainty ($p > .05$), and the number of obligate-resprouting species showed no clear trend (Figure 5f). For obligate-seeding species, the main effect of time since fire was a linear decrease in the number of species per site ($p < .001$, deviance = 32%, Figure 5g). Cover of obligate seeders showed a (non-significant) bell-shaped response to time since fire, peaking at ~20 years post-fire (Figure 5c). The relative cover of shrubs showed a plateau response ($p < .01$, deviance = 36%, Figure 5d) and low shrub and herb cover were not significantly associated with time since fire. The number of species of shrubs ($p < .01$, deviance = 26%, Figure 5d) and low shrubs

($p < .01$, deviance = 28%, Figure 5d) showed irruptive responses to time since fire. Outputs of all functional group models are provided in Appendices S6 and S7.

4 | DISCUSSION

In this study, we examined how communities of birds and plants change over time following fire in a heathy woodland ecosystem by using three approaches: models of change in individual species over time, models of change in functional groups based on life history traits and comparison of community composition between post-fire successional stages. Species' life history traits gave key insights into the mechanisms driving post-fire community change. Notable fire effects included (a) a peak in recently burnt vegetation of ground-foraging birds, (b) a plateau response ~50 years post-fire of birds that forage in lower-mid-storey vegetation, (c) a plateau response ~20 years post-fire of the cover of facultative-resprouting plants and (d) an initial peak soon after fire followed by a decline in the above-ground richness of obligate seeding, shrub and low shrub species. Post-fire age classes represented distinct assemblages, both for bird and for plant communities. Variation in community composition between post-fire age classes can be attributed to species' life history traits and successional changes in habitat conditions. These results

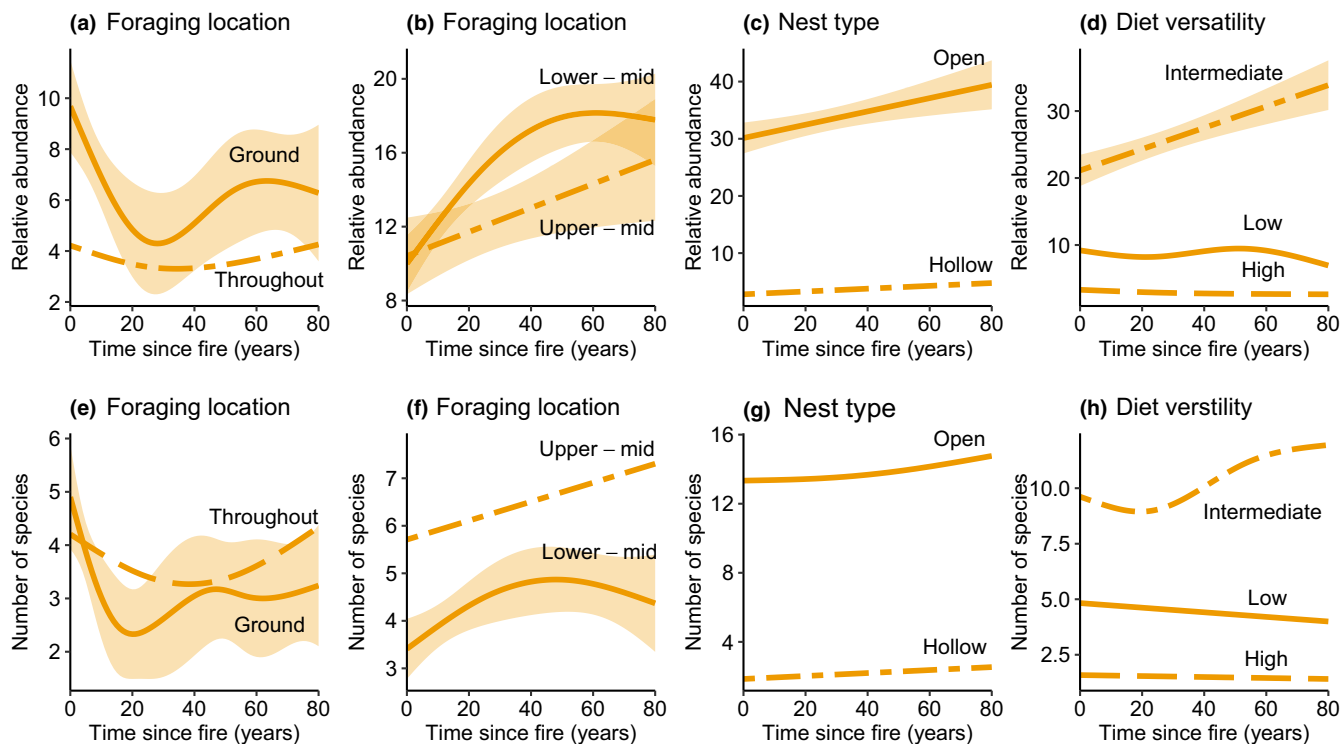


FIGURE 4 The influence of time since fire on the distribution of bird functional groups in heathy woodlands. Lines are fitted from generalized additive models of the summed reporting rate (a–d) and the number of species per site (e–h) within each functional group as a function of time since fire. Shaded areas represent 95% confidence intervals. Lines without shaded areas indicate non-significant relationships

can help guide fire management practices to ensure they are compatible with biodiversity conservation.

4.1 | How do bird and plant communities change with time since fire?

The main effects of time since fire on the bird community were likely driven by the post-fire development of understory vegetation structure. Species that forage in the lower-mid-storey were more abundant in late-successional vegetation when the cover of the shrub layer has been restored, whereas those that forage on the ground were more abundant in the first few years after fire, when the ground-layer habitat is open. Species that forage in the upper-mid-storey (including canopy) were not strongly associated with time since fire, although there was a positive trend with considerable uncertainty. Epicormic resprouting of *Eucalyptus* trees enables rapid regeneration of the upper-mid-storey and canopy vegetation (Pausas & Keeley, 2017), buffering the effect of time since fire on birds that forage in this stratum. This buffering effect of epicormic-resprouting trees means that the post-fire composition of the bird community was shaped primarily by the dynamics of the understory vegetation structure.

Neither the richness nor abundance of hollow-nesting birds was related to time since fire in this study. This result contrasts with a study in a semi-arid *Eucalyptus* woodland dominated by

obligate-seeding trees (Gosper et al., 2019) that showed a strong influence of time since fire on the abundance of hollow-nesting birds. Tree hollows are a limiting resource for many Australian faunal species because they take decades to develop (Gibbons et al., 2000) and may be destroyed by fire (Haslem et al., 2012). There are two plausible hypotheses to explain this contrast (a) because the stems of canopy trees in heathy woodlands are not killed by fire (c.f., the obligate-seeding trees), the presence of tree hollows in this ecosystem is not strongly associated with time since fire and so this nesting resource is not a limiting factor post-fire; and (b) hollow-nesting birds may forage within heathy woodlands but nest in adjacent vegetation types (e.g., wet forest, foothill forest). Further studies to determine the nesting behaviour of birds in heathy woodlands and the surrounding landscape would benefit fire management.

For plants, key changes in community structure over time since fire are attributed to (a) increasing cover of facultative-resprouting and shrub species and (b) declining species richness of obligate-seeding, low shrub and shrub species. A decline in plant diversity over time following fire has been observed in several ecosystems (e.g., Fournier et al., 2020; Gosper et al., 2012, 2013; Keeley et al., 2005; Penman et al., 2009). When fire consumes aboveground biomass, light, nutrients and space become more accessible, facilitating germination of seeds and/or growth from resprouting buds, depending on species (Safford & Harrison, 2004). Consequently, aboveground species richness often is high soon after fire. Then, over time, some species become dominant (e.g., Austral Grass-tree,

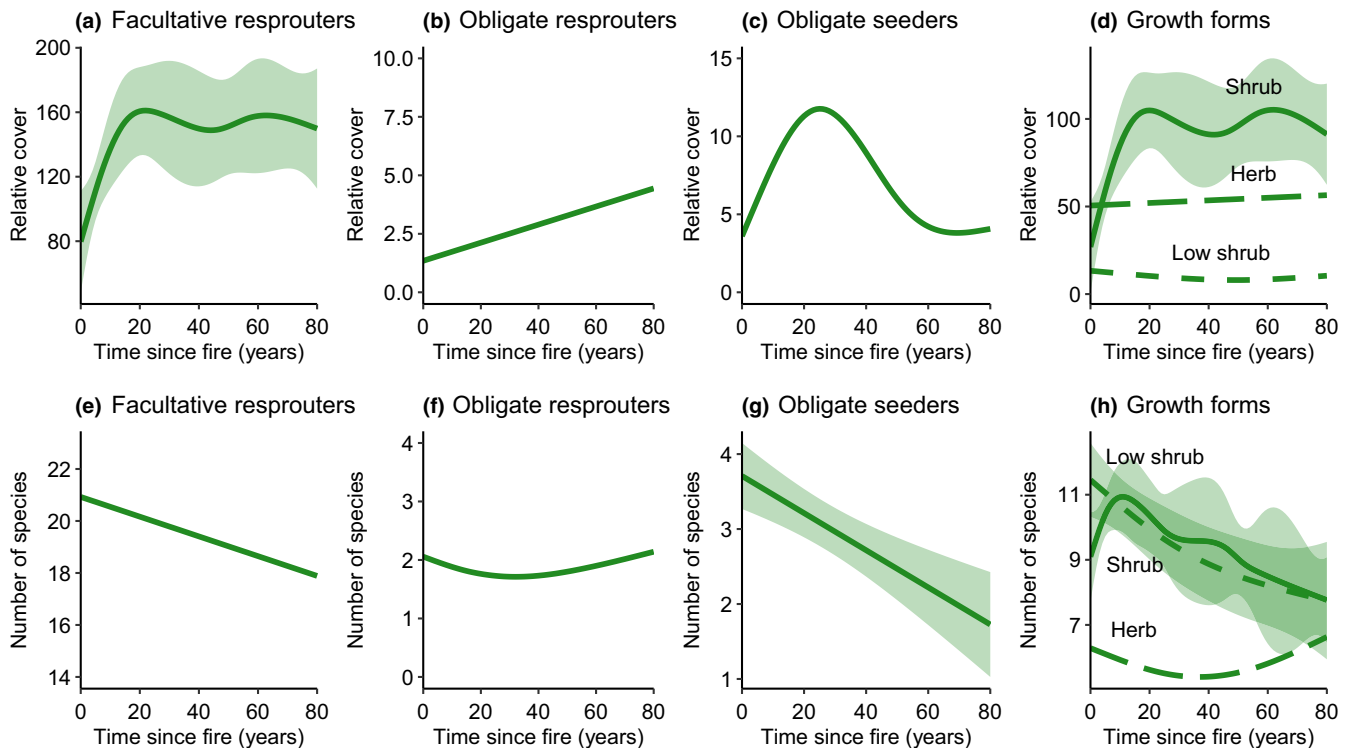


FIGURE 5 The influence of time since fire on the distribution of plant functional groups based on regeneration traits (a, b, c, e, f, g) and growth form (d, h) in heathy woodlands. Lines are fitted from generalized additive models based on the summed cover (a–d) and the number of species per site (e–h) of plants within each group as a function of time since fire. Shaded areas represent 95% confidence intervals. Lines without shaded areas indicate non-significant relationships

Leptospermum species) and potentially exclude poorer competitors, driving down species richness.

Although there was evidence of directional change in the composition of the plant community with time post-fire in heathy woodlands, variation within each post-fire age class indicates that factors additional to time since fire also influence plant community composition. Multiple factors influence the temporal and spatial variation in plant communities in fire-prone landscapes, including primary productivity (Safford & Harrison, 2004), climate and weather (Burrows et al., 2019; Parra & Moreno, 2018), and other attributes of the fire regime (Keeley et al., 2005; Kelly et al., 2017). In this study, it is likely that between-site differences in productivity influenced variation within age classes, due to differences in topography (e.g., position on slope) and soils (e.g., depth of sand).

A key difference between the responses of bird and plant communities was the decline in aboveground species richness of most plant functional groups with time since fire versus the increase and plateau response of lower-mid-storey foraging birds. This presents a challenge for conservation management in heathy woodland ecosystems, due to a risk of (a) potential loss of floristic diversity in the absence of fire, and (b) reduction in bird species abundances if fire is too frequent. We note that patterns of seedbank diversity of plants in heathy woodlands may show alternative patterns to that of aboveground mature plants (Chick et al., 2019). Knowledge of the length of seed viability for obligate-seeding plants, and other

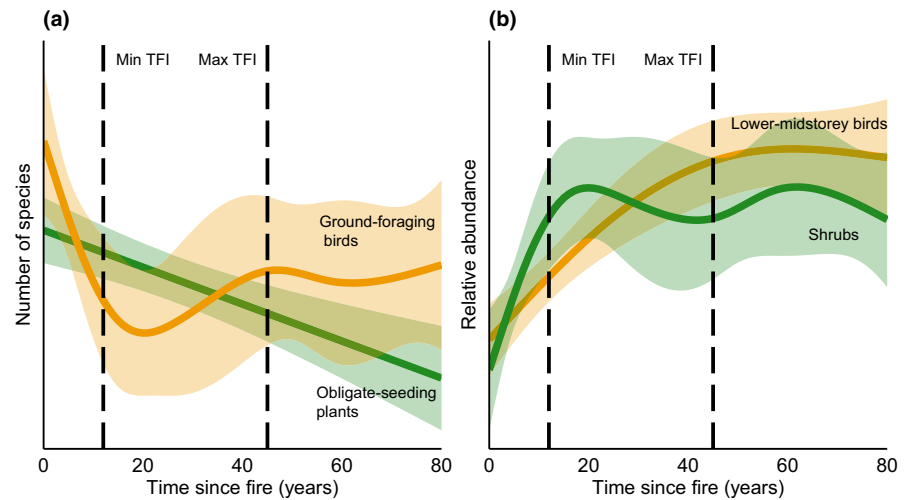
groups, is useful for determining the maximum fire intervals tolerated before significant loss of species occurs. Nevertheless, there will likely be loss of adult obligate-seeding plants in the complete absence of fire.

4.2 | Implications for fire management

Fire management strategies, including the timing and placement of prescribed burns, will have greatest benefit if they incorporate biodiversity responses to fire along with reduction of risk to human life and property from wildfire (Driscoll et al., 2010). Our results have implications for two approaches to fire management that largely are based on plant responses to fire.

First, this study highlights a particular challenge to the timing of prescribed fire based on tolerable fire intervals (TFIs) because these differentially affect taxa. The peak in species richness of obligate seeders, shrubs and low shrubs and the cover of facultative resprouters and shrubs, coincides with the minimum tolerable fire interval for heathy woodlands (i.e., 12 years; Cheal, 2010), whereas the peak in abundance of lower-mid-storey foraging birds was later than the maximum TFI (i.e., 45 years) (Figure 6). Other work on plant responses to fire in heathy woodland vegetation (Chick et al., 2019; Duff et al., 2013) also suggests that introducing more fire into the landscape would benefit plant diversity. This could be

FIGURE 6 The response of bird and plant functional groups to time since fire and tolerable fire intervals (TFI) in heathy woodlands. (a) The number of species of ground-foraging birds and obligate seeder plants. (b) The reporting rate of lower-mid-storey-foraging birds and the relative cover of shrubs. Lines are fitted generalized additive models. Shaded areas represent 95% confidence intervals. Values on the y-axis are relative to each taxon



achieved by burning patches of vegetation towards the minimum tolerable fire interval (TFI) (e.g., at a frequency of ~12 to 20 years). However, by reducing the cover of understorey shrubs, this strategy will disadvantage substantial components of the bird community and other faunal groups (Di Stefano et al., 2013). If tolerable fire intervals are to be used as a guide for fire management, then maintaining stands of vegetation across the landscape at *both* the upper and lower TFIs is necessary to promote landscape biodiversity in heathy woodlands.

Second, maintaining proportions of the landscape at different post-fire ages (i.e., vegetation growth stages) to meet the needs of diverse taxonomic groups often is a goal of fire management (Menges et al., 2017; York & Friend, 2016). Diversity metrics can be used to optimize the spatial distribution of age classes, based on species' abundances (Giljohann et al. 2015; Kelly et al., 2015; Di Stefano et al., 2013). However, the assumption that such age classes represent distinct successional communities has rarely been tested for animal taxa. Here, we showed that post-fire age classes (based on vegetation growth stages) in heathy woodlands do represent distinct bird and plant communities. This can be attributed to responses associated with species' life history traits (foraging behaviour in birds, fire regeneration and life-form in plants). This new knowledge will help inform fire management planning to conserve bird and plant diversity in heathy woodlands, especially when species-level data are lacking.

It is important to note that several components of bird and plant communities were not related to time since fire (e.g., birds that forage throughout the strata, hollow-nesting birds, herb and low shrub species). The distribution of these groups is likely influenced by landscape heterogeneity not related to fire (e.g., topographic variation), other components of the fire regime (e.g., between-fire interval, spatial configuration) or their generalist traits. Incorporating further complexity, in addition to time since fire (e.g., Swan et al., 2018, Hutto et al., 2020), into a landscape mosaic approach to fire management will further benefit bird and plant diversity.

5 | CONCLUDING REMARKS

By identifying mechanisms that shape bird and plant communities post-fire, a deeper understanding is gained of how manipulating fire regimes influences components of biodiversity. Fire management guided by measures based solely on plant functional traits (e.g., TFI) can disadvantage faunal communities. Rather, incorporating the responses of both plant and animal communities to fire by spatial representation of post-fire age classes of greatest value to different plant and animal groups (Kelly et al., 2015; Di Stefano et al., 2013) will help conserve multiple taxa in fire-prone landscapes. However, incorporating further complexity in landscape planning in addition to time since fire is needed to represent those components of ecosystems not strongly related to time since fire. This includes explicitly incorporating environmental gradients and topographic variation, as well as considering other temporal attributes of the fire regime (e.g., between-fire interval), the spatial context of fire (e.g., amount or diversity of fire) and landscape context (e.g., surrounding vegetation types, connectivity). Finally, incorporating species' functional traits into fire management frameworks can also help guide management actions to achieve explicit conservation targets, based on how ecosystems change over time following fire. This may be especially useful in instances where data and knowledge of particular species are lacking.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Depository: (Rainsford et al. 2021; DOI <https://doi.org/10.5061/dryad.qfttdz0gj>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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BIOSKETCH

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