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How does prescribed fire shape bird and plant communities in a temperate dry forest ecosystem?

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Abstract

To mitigate the impact of severe wildfire on human society and the environment, prescribed fire is widely used in forest ecosystems to reduce fuel loads and limit fire spread. To avoid detrimental effects on conservation values, it is imperative to understand how prescribed fire affects taxa having a range of different adaptations to disturbance. Such studies will have greatest benefit if they extend beyond short-term impacts of burning. We used a field study to examine the effects of prescribed fire on birds and plants across a 36-year post-fire chronosequence in a temperate dry forest ecosystem in south-eastern Australia, and by making comparison with long-unburnt reference sites (79 years since wildfire). We modelled changes in the relative abundance of 22 bird species and the cover of 39 plant species, and examined how individual species, functional groups, species richness and community composition differed between sites with different fire history. For most individual bird and plant species modelled, relative abundance or cover at sites subject to prescribed fire did not change significantly with time since fire or differ from that of long-unburnt vegetation. When bird species were pooled into functional groups, time since prescribed fire had strong effects on birds that forage in the lower-midstorey, facultative-resprouting shrubs and obligate-seeding shrubs. Species richness for both taxa did not differ between sites subject to prescribed fire and those in long-unburnt vegetation. Bird communities varied significantly between the youngest (0-3 years) and oldest (79 years) post-fire age-classes, driven by species associated with understorey vegetation. Plant community composition showed little evidence of a post-fire successional trajectory. The prevalence of bird species with broad habitat and dietary niches and plant regeneration through resprouting, make bird and plant communities in these forests relatively resilient to small and patchy prescribed fires they have experienced to date. Application of prescribed fire will be most compatible with maintaining biodiversity by taking a landscape approach that: 1) plans for a geographic spread of stands with a range of between-prescribed-fire intervals to ensure provision of suitable habitat for all taxa, and 2) avoids burning in moist gullies to maintain their value as fire refuges.

Keywords:

Community composition, biodiversity, fire management, fire regime, functional traits, planned burn, post-fire succession, time since fire, wildfire.

Introduction

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

A common method used to reduce the risk of large fires to human society and biodiversity values is to reduce fuel loads by using prescribed fire (Price et al. 2015, Stephens et al. 2019, Moreira et al. 2020). In temperate dry forests, prescribed fires generally are less intense and more patchy than wildfires: they consume understorey vegetation and ground-layer fuels, and usually leave the canopy un-scorched (Penman et al. 2008, Fernandes 2018). Empirical data indicate that prescribed fire can reduce the extent of future wildfire in dry forests in south-eastern Australia, but with substantial variation both between and within regions and vegetation communities (Price et al. 2015, Penman et al. 2020). Prescribed fire can also be used more directly to achieve ecological goals, such as to promote plant regeneration and to create particular successional stages as habitats (Ryan et al. 2013).

Prescribed fire has diverse effects on biota, in part depending on the life-history of animal and plant species. For animals, the effect of fire usually is indirect, through changes in the amount of a critical resource. For example, prescribed fire has been reported to increase food availability for some foraging guilds of birds (Pope et al. 2009, Fontaine and Kennedy 2012) and change or remove important structural resources for small mammals (Holland et al. 2017, Flanagan-Moodie et al. 2018). For plants, the effects of fire can differ, depending on the regeneration traits of species and individuals (Penman et al. 2008). Prescribed fire can reduce populations of some plants (Gonzalez-Benecke et al. 2015), but can also stimulate regeneration of certain tree, shrubs and grasses (Hutchinson et al. 2012). There is an urgent need to understand how prescribed fire affects animals and plants in areas likely to be subject to more frequent severe fire.

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

Forest plants, in dry forests have evolved a range of traits (e.g. post-fire resprouting, fire-cued germination) that allow populations to persist in fire-prone environments (Pausas et al. 2004). Classifications based on plant functional traits, such as time to maturity and method of persistence, provide a useful framework to understand and predict species' responses to fire (Bradstock and Kenny 2003, Keith et al. 2007, Shedley et al. 2018). Studies in temperate dry forests have shown that the influence of fire on understorey plant species varies between taxa based on species' life-history traits (Penman et al. 2008, Prior et al. 2016) and within taxa based on vegetation type (Foster et al. 2018). Plant regeneration from seed is often associated with species declining over time following fire and vulnerability to increased fire frequency, while post-fire resprouting is associated with species that increase post-fire (Penman et al. 2009, Enright et al. 2014). There are exceptions, however, and resprouting species may also be vulnerable to increased fire frequency (Fairman et al. 2017).

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

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

We address the general question: how does prescribed fire shape bird and plant communities in temperate dry forests? More specifically, we address questions relating to three levels of biodiversity: how do 1) individual species, 2) functional groups of species, and 3) the composition of communities respond to prescribed fire; and how do these levels of biodiversity differ between sites subjected to prescribed fire and those in long-unburnt vegetation?

Methods

Study location, climate and vegetation

The study took place in temperate dry forests, known as ‘foothill forests’, in Victoria, south-eastern Australia (Fig. 1). The generic term ‘foothill forests’ refers to temperate eucalypt forests that cover ~ 75 000 km^2 in Victoria and occur on the lower- to mid-slopes of the Great Dividing Range. Foothill forests include distinct ecological communities that differ in floristic composition, driven by topographic and climatic variation, ranging from wetter forest types in gullies to drier forests on slopes and ridges. The study area covered ~ 320 km^2 of the Big River State Forest in the Highlands Southern Fall bioregion (-37.516 S, 146.042 E) where the climate is temperate with a mean annual rainfall of ~ 850 mm. The highest monthly rainfall occurs in winter (August) and the hottest month is February (mean daily maximum ~ 29°C) (Lake Eildon, station no. 083023; http://www.bom.gov.au/). The topography is mountainous, often with steep slopes and densely vegetated gullies. Elevation ranges between ~ 450 and 950 m above sea-level.

To avoid topographic differences in vegetation composition and structure (i.e. between gullies and ridges), all sites were located within a single vegetation community, ‘herb-rich foothills forest’ (Victorian Government Department of Sustainability and Environment 2004). The canopy of foothill forests reaches heights of 25 m and is often accompanied by a secondary tree layer of *Acacia* spp. The dominant canopy species were messmate stringybark *Eucalyptus obliqua*, mountain grey-gum *E. cypellocarpa*, broad-leaved peppermint *E. dives* and narrow-leaved peppermint *E. radiata*. All four *Eucalyptus* species resprout epicormically following fire. Smaller trees and shrubs constitute the understorey, including blackwood *Acacia melanoxylon*, silver wattle *A. dealbata*, prickly currant-bush *Coprosma quadrifida*, common cassinia *Cassinia aculeata*, and ferns such as austral bracken *Pteridium esculentum*. The ground layer consists of a rich cover of herbs.

Fire regime and fire mapping

In foothill forests, wildfires typically occur in summer (Dec – Feb). Large wildfires (> 10 000 ha) have occurred in the wider foothill forests region in 1939, 1962, 1983, 2003, 2005, 2006, 2009, 2014, 2019 and 2020 (Department of Environment, Land, Water and Planning 2015, Nolan et al. 2020). Mapped prescribed fires in the study area date from the 1970s to the year of surveys (Fig. 1). Prescribed fires at the study sites post-1990 were conducted in autumn, but the season of prescribed fires prior to 1990 is not documented. Prescribed fires are ignited from the ground by field officers and generally are smaller than wildfires: the mean fire size at the study sites was 658 ha (range 44 – 1738 ha).

Fire management for biodiversity conservation is guided by plant life-histories, notably the estimated time required for plants to achieve reproductive maturity (minimum tolerable fire interval) and senescence of plants and exhaustion of seedbanks in the inter-fire period (maximum tolerable fire interval). This minimum and maximum ‘tolerable fire interval’ guides the management of the interval between prescribed fires and wildfires (Cheal 2010). The recommended minimum and maximum tolerable fire intervals for this ecosystem are 15 and 150 years, respectively (Cheal 2010); but in practice, fire intervals vary depending on local management objectives and context. In general, prescribed burns in foothill forests are patchy and do not scorch the canopy or kill canopy trees (McCarthy et al. 2017). Even severe wildfires in foothill forests typically are not stand-replacing. The stems of mature eucalypts, including the four species recorded in this study, generally persist through fire and resprout epicormically from buds protected by thick bark (Collins 2020).

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

Study design

We used spatial map layers of vegetation types and fire history to select potential sites in herb-rich foothill forest, stratified in relation to post-fire age following prescribed burns. A total of 29 sites was selected, spanning a chronosequence from 1 - 36 years post-prescribed fire. A further nine sites last burned by wildfire in 1939 were sampled to represent a 'long-unburnt' state (79 years since fire). Sites were selected to ensure even coverage of a range of post-fire 'age-classes': (sometimes called 'growth stages' or 'successional states') used by regional land managers (Table 1, Fig. 2). Although sites were distributed among four age-classes present in the study area (i.e. 0 – 3, 3 – 10, 10 – 40, >40 years post-fire), based on post-fire vegetation growth stages described by Cheal (2010), there was a gap in the chronosequence from 11 – 30 years post-fire. This was a consequence of the fire history of the study area, with no areas available that were last burned by prescribed fire during this period.

Selected sites were checked in the field for suitability. The mapped time since fire was verified by checking for charcoal on stringybark eucalypts, and other signs of past fire. At each site, we established a 250 m transect that ran along the contour of the slope, located at least 50 - 200 m from a road, at least 100 m upslope from a gully (riparian vegetation) and 50 m from the ridge top, and at least 50 m from a different vegetation type or fire boundary. To ensure independence, plots were at least 1 km apart. The start-point of the transect at each site was randomly selected using GIS.

Birds

At each site, a 2-ha plot centered over the 250 m transect was established, and surveyed for diurnal birds by a single experienced observer (FR) a total of six times: three times during the austral autumn/winter and three times during spring/summer, between 2017 and 2018. Surveys were conducted in clear weather within four hours of dawn, except for two winter survey rounds during which sites were each surveyed once in the morning and once in the afternoon. Each survey was for a 20-min period and all individuals either heard or seen were identified to species level and recorded. The perpendicular distance (m) to each detection from the transect line was estimated and used to test for differences in detectability between sites (see Appendix S1). Nocturnal birds, raptors and swifts were recorded but excluded from analyses as these groups are not reliably detected by the survey methods.

Understorey plants

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

<u>Data analyses</u>

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 midstorey vegetation cover (see Appendix S1). For several bird species/groups, there was a weak negative relationship between midstorey vegetation cover and distance to detection (Appendix S1: Fig. S1), suggesting that some individuals of these species may have been undetected at sites with high midstorey vegetation cover. To control for potential errors due to detectability, we used a presence/absence-based index (reporting rate) to compare the relative abundance of species between sites. Because it does not rely on counts of individuals, reporting rate is less prone to biases caused by differences in detectability or flocking behavior. This approach is a robust alternative to model-based approaches (i.e. distance analysis) for which modelling assumptions cannot be met (Hutto 2016). Below we outline the approach used to address the key questions. All analyses were conducted using the R statistical environment (R Development Team 2018).

Individual species

For individual species that occurred at ≥ 25% (8/29) of sites last burnt by prescribed fire, we used generalised additive models (GAMs) (Wood 2017) to predict changes in relative abundance (birds) and relative cover (plants) with time since fire. For bird species we used reporting rate, the number of survey rounds (out of 6) during which a species was detected. Variation in reporting rate of species between sites is often a result of variation in the abundance of individuals and so is a reliable proxy for relative abundance (Royle and Nichols 2003). For plant species, we used the mean projected foliar cover at sites.

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

By visually assessing the fitted model for each species, we described the shape of the species-fire relationship based on pre-defined generalized response curves (after Watson et al. 2012). We then calculated the percentage of species with a significant relationship, that resembled each response shape. Four main response shapes were observed: ‘irruptive’ (abundance highest in the first few years following fire), ‘bell’ (initial increase followed by a decrease with time since fire), ‘incline’ (gradual increase with time since fire), and ‘plateau’ (initial increase followed by stability in later years post-fire). Non-significant relationships were classed as ‘NS’. We also compared the explanatory power (deviance explained) of models between taxonomic groups by using boxplots.

We compared the relative abundance of species at post-prescribed fire sites with that for long-unburnt vegetation by using ‘age-class’ (AC) categories, representing the time since last fire (Table 1). Sites last burnt by a wildfire in 1939 were categorized as ‘long-unburnt’ (LU). For bird species, we used generalized linear models (GLMs), with the categorical variable ‘age-class’ as the explanatory variable, and a Poisson error distribution, to compare relative abundance between age-classes for species that occurred at ≥ 25% (10/38) of sites. For plant species, we carried out a similar approach, but built beta regression models by using the betareg function in the “betareg” R package (Zeileis et al. 2020). Beta regression models are analogous to GLMs but can incorporate proportion data. A Tukey HSD test was used to determine significant differences between age-classes.

Functional groups

We classified species into functional groups based on their life-history traits (see Appendix S2, Appendix S3). For birds, we grouped species based on three functional traits (Table 2):

(1) foraging location (ground, lower-midstorey, upper-midstorey, throughout), (2) nest type (open, hollow, burrow, brood parasite), and (3) diet versatility, the number of food types (fruit, nectar or pollen, seeds, foliage or herbs, corms or tubers, terrestrial invertebrates, terrestrial vertebrates, carrion) that each constitute at least 1% of the total diet (low: 1 food source, intermediate: 2-3 food sources, high: 4-6 food sources). To assign species to groups, we used a combination of expert knowledge and a published database of Australian birds (Garnett et al. 2015).

For plants, we used two levels of classification, (1) fire-regeneration trait and (2) growth form. Fire-regeneration traits were used to classify species into four groups following Clarke et al. (2015): facultative-resprouting (capacity to regenerate by resprouting or from seed), obligate-resprouting (regenerates by resprouting but no post-fire seeding), obligate-seeding (no capacity to resprout post-fire, regenerates from a seed bank) and fire-avoider (no post-fire resprouting or seeding). Four growth-form categories were used to group species: herbaceous plants (hemicryptophytes <1 m in Raunkiaer 1934), low shrubs, shrubs and understorey trees (Table 2). Both levels of classification were combined to group species (e.g. obligate-seeding shrubs). To assign species to groups, we used a database of plant vital attributes (Cheal 2011) and the Flora of Victoria online herbarium (Royal Botanic Gardens Victoria, vicflora.rbg.vic.gov.au). If the fire regeneration trait was unknown, data for that species were not included in functional group analyses. A total of 79 species were assigned to functional groups.

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

Species diversity and community composition

To test the influence of prescribed fire on plant and bird communities, we compared (a) species richness and (b) community assemblages between post-prescribed fire age-classes and long-unburned reference vegetation. First, for each taxonomic group at each site, we calculated the total number of species recorded per site. Then, we classified sites into post-fire age classes as above (AC1, AC2, AC3, long-unburnt), and used GLMs to model changes in species richness with time since fire (i.e. between post-fire age-classes).

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

Results

We made a total of 4903 detections of diurnal birds from 43 species (Appendix S2: Table S1). The most speciose bird families were the Meliphagidae (honeyeaters, 5 species), Acanthizidae (thornbills, 4 species) and Petroicidae (Australian robins, 4 species). The number of bird species recorded per site ranged from 13 – 29. The most frequently recorded species were striated thornbill *Acanthiza lineata*, white-throated treecreeper *Cormobates leucophaea*, yellow-faced honeyeater *Lichenostomus chrysops*, and spotted pardalote *Pardalotus punctatus*, which were recorded at all sites.

We recorded a total of 89 species of understorey vascular plants, including three species of understorey tree (mature height > 8 m), 28 shrubs (1 – 8 m), 31 low shrubs (0.1 – 1 m), 26 herbs and one geophyte (shield sundew *Drosera peltata*) (Appendix S3: Table S1). In addition, one non-native species was recorded, but was not included in any analyses. The most speciose families were the Asteraceae (daisies, 13 species) and Fabaceae (peas and wattles, 13 species). The number of plant species recorded per site ranged from 16 – 42. Some of the most widespread plant species were common heath *Epacris impressa*, austral bracken and pink bells *Tetratheca ciliata*. No bird or plant species listed as threatened were recorded.

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

Individual species

We built GAMs for 22 bird species and 39 plant species (9 shrubs, 6 low shrubs, 23 herbs, 1 geophyte) that occurred at ≥25% of sites. Significant responses ($P<0.05$) to time since prescribed fire were obtained for three bird species (14% of modelled species) and eight plant species (21%) (Fig. 3a). For birds, two types of generalized response curve were observed (Fig. 3a): incline (5% of species, e.g. golden whistler *Pachycephala pectoralis*, Fig. 3c) and plateau (10%, e.g. grey fantail *Rhipidura albiscapa*, Fig. 3d). For plants, significant responses to time since prescribed fire included three types of generalized response curve (Fig. 3a): irruptive (8% of species, e.g. moth daisy-bush *Olearia erubescens*, Fig. 3e), bell-shaped (8%) and incline (5%, e.g. pink bells, Fig 3f). Overall, there was no substantial difference in the strength of models (i.e. deviance explained) between bird and plant species (Fig. 3b).

For most species in both taxonomic groups the relationship with time since prescribed fire was not significant (86% of modelled bird species, 79% of modelled plant species), due to high levels of variation in species abundances across the chronosequence. Model outputs for all species are given in Appendices S4 – S5.

We compared the relative abundance/cover of 25 bird and 41 plant species (occurred at ≥25% of sites) between post-prescribed fire age-classes and long-unburnt vegetation. The relative abundance of one bird species (white-browed scrubwren *Sericornis frontalis*, Fig. 4a) 0 – 3 years after prescribed fire (AC1) differed significantly from that of long-unburnt vegetation. For 7% (n = 3 species) of modelled plant species, relative cover differed significantly from long-unburnt vegetation at 3 – 10 years after prescribed fire (e.g. common cassinia, Fig. 4d). For several species, there were non-significant trends of relative abundance differing from long-unburnt vegetation in various age classes (e.g. silvereye *Zosterops lateralis*, Fig. 4b, brown thornbill *Acanthiza pusilla*, Fig. 4c, kurwan *Bursaria spinosa*, Fig. 4e, moth daisy-bush, Fig. 4f). For most bird and plant species, there was little difference with long-burnt vegetation for any post-fire age-class. All species model outputs are provided in Appendix S6 – S7.

Functional groups

The relative abundance or cover of several functional groups, for both birds and plants, was related to time since prescribed fire (Fig. 5). Upper-midstorey foraging birds increased in relative abundance linearly (incline response) with time since fire ($P < 0.05$, deviance explained = 16%, Fig. 5a), lower-midstorey foragers showed a plateau response ($P < 0.001$, deviance explained = 44%, Fig. 5a) and species with low diet versatility ($P < 0.05$, deviance explained = 23%, Fig. 5b) and open-nesting species ($P < 0.05$, deviance explained = 18%, Fig. 5c) both increased linearly (incline response) with time since fire. Facultative-resprouting shrubs ($P < 0.05$, deviance explained = 30%, Fig. 5d) and obligate-seeding shrubs ($P < 0.05$, deviance explained = 25%, Fig. 5f) both showed a bell-shaped response to time since fire.

Relative abundance of one bird functional group, lower-midstorey foragers, differed significantly from that of long-unburnt vegetation in the youngest age class ($P < 0.01$, Fig. 6a). Relative cover of facultative-resprouting shrubs was greater 3 – 10 years after prescribed fire than in the first three years following prescribed fire ($P < 0.001$, Fig 6c) and that of obligate-resprouting shrubs was significantly greater in long-unburnt vegetation than in the first three years following prescribed fire ($P < 0.05$, Fig 6c).

Species richness and community composition

Species richness of both bird and plant species did not differ significantly between sites in post-prescribed fire age-classes and long-unburnt vegetation (Fig. 7).

NMDS ordination analyses showed some evidence of successional trajectories of bird and plant communities after prescribed fire (Fig. 8). This influence was stronger for birds ($P = 0.01$, PerMANOVA) than for plants ($P = 0.081$). Bird community composition showed most dissimilarity between AC1 (0 - 3 years post-fire) and long-unburnt vegetation (Fig. 8a). The main point of differentiation for plant communities was between AC2 (3 - 10 years post-fire) and long-unburnt (LU) vegetation (Fig. 8c).

Vectors of influential bird (Fig. 8b) and plant (Fig. 8d) species showed some clustering of species within the ordinations. A key species cluster in the bird ordination is in the top right corner, in the direction of older age-classes. These species (white-browed scrub-wren, grey fantail, brown thornbill, golden whistler, fan-tailed cuckoo *Cacomantis flabelliformis*) typically are associated with midstorey vegetation structure. A key feature of the plant ordination is the cluster of species to the right-hand side, in line with sites 3 - 10 years post-fire (AC2). These species include the facultative-resprouting and obligate-seeding species from the family Asteraceae, common cassinia (bell-shape response to time since prescribed fire, Appendix S5: Table S1) and common fireweed *Senecio prenanthoides*, respectively.

Discussion

Overall, our findings show a high level of resilience to prescribed fire by birds and plants in temperate dry forests. We showed that for most individual bird and plant species modeled, relative abundance or cover was not significantly related to time since prescribed fire. Yet, consideration of whole communities provided important insights. Key functional groups of bird and plant species were related to time since prescribed fire including lower-midstorey foraging birds, facultative-resprouting shrubs and obligate-seeding shrubs. Additionally, variation in the composition of bird and plant communities was greatest between recently burnt and long-unburnt vegetation. Next, we discuss factors contributing to the apparent resilience of temperate dry forest plant and bird communities to prescribed fire, and the implications for fire management in these and other temperate forests.

Bird community response to prescribed fire

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

There also was a significant, but less-strong relationship between the abundance of both upper-midstorey foragers and dietary specialists with time since fire. Both of these guilds include grey fantail and golden whistler, insectivores that showed individual responses to fire which depend on a well-developed midstorey structure. Their responses are consistent with previous studies in wooded ecosystems (e.g. Davis et al. 2016). Diet specialization can influence the response of species to fire (Santos et al. 2014). Species with more versatile diets may be less susceptible to a reduction in the diversity of available food resources after fire, as they can more easily switch between foods in response to prevailing conditions.

Plant community response to prescribed fire

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

Similarly, there was a strong response of facultative-resprouting shrubs to time since fire. Although they have the capacity to resprout, several of these species (e.g. common cassinia, narrow-leaf bitter-pea *Daviesia virgata*, gorse bitter-pea *D. ulicifolia*) also display fire-cued regeneration from seed. This helps explain the similarity between the shapes of the response curves for obligate-seeding and facultative-resprouting shrubs. Plant species that display fire-cued germination may be at risk of senescence or decline in the absence of fire. For such species, introducing fire can potentially stimulate regeneration and local persistence. In contrast to these bell-shaped responses, the cover of obligate-resprouting shrubs was significantly reduced 0 – 3 years post-prescribed fire compared to in long-unburnt vegetation.

A resilient ecosystem?

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

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

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

Variation in fire regeneration traits of plant species influence post-fire ecosystem trajectories (Pausas and Keeley 2014). The prevalence in temperate dry forests of species with a capacity for post-fire resprouting means that many species are still present at sites immediately after fire, leading to rapid recovery of above-ground plant diversity and vegetation structure (Rainsford et al. 2020). In particular, *Eucalyptus* trees are capable of epicormic resprouting along trunks and branches following fire, which enhances the rate of recovery of vegetation structure (Keith 2012, Collins 2020), and provides important resources (e.g. foraging substrates, refuge, nest sites) for birds soon after fire. Thus, the prevalence of regeneration through post-fire resprouting of major trees and shrubs is a key factor in the resilience of this ecosystem to prescribed fire.

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

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

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

Implications for management

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

First, the frequency at which prescribed fire is applied has consequences for at least three main functional groups: understorey-foraging birds, obligate-seeding shrubs and facultative-resprouting shrubs. Ensuring a fire interval of ~15 – 30 years across substantial areas will accommodate the life-cycle of most understorey plant species that we detected and may stimulate regeneration of several shrub species that benefit from recurrent fire. This minimum interval between fire is in line with the recommended minimum tolerable fire interval of 15 years (Cheal 2010) for this ecosystem. Burning below this minimum interval could put some plants at risk of local extinction if they are burnt before reaching reproductive maturity. Nevertheless, there are many different types of fire that could be applied to forest landscapes. There is a growing recognition of the value and need for Indigenous knowledge in fire management (Trauernicht et al. 2015), including cultural burning done at different times and ways, and our recommendations relate to the types of prescribed burning that we measured in the present study.

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

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

Lastly, we identified bird and plant groups that are relatively sensitive to prescribed fire in foothill forests. These groups could be used as indicators of the successional state of plant and bird communities in ecological monitoring programs. These findings could also be extrapolated to other taxa (e.g. other vertebrate groups, invertebrates) that share foraging locations with the groups studied here and used to make testable predictions of the ecosystem response to prescribed fire.

Concluding remarks

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

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Supporting Information

Additional supporting information may be found online at: [link to be added in production]

Data Availability

Data are available in the Dryad Digital Repository (Rainsford 2020): https://doi.org/10.5061/dryad.fttdz08rd

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Tables

Table 1. The distribution of sites among post-fire age-classes

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

Table 2. Functional groups of bird and plant species used in analyses of the response of taxa to time since prescribed fire.

Taxon	Variable	Level	Description	Number of species
Birds	Foraging location	Ground	Mostly forages or takes prey from the ground.	12
		Lower-midstorey	Forages mostly in vegetation < 3 m height.	5
		Upper-midstorey	Forages mostly in vegetation > 3 m height (including canopy vegetation).	20
		Throughout	Forages throughout the vertical strata, from the ground to the canopy.	6
	Diet versatility †	Low	Species with high level of dietary specialization. Only one food type that contributes ≥ 1% of total diet.	23
		Intermediate	Two – three food types each contribute ≥ 1% of total diet.	16
		High	Four – six food types each constitute at ≥ 1% of total diet.	4
	Nest type	Burrow	Nests in a burrow in the ground.	1
		Hollow	Nest in a cavity in a tree branch or trunk. Includes obligate and facultative cavity nesters.	9
		Open	Constructs a nest in the 'open', not in a cavity or burrow. Includes species that construct bowl, dome or saucer nests.	32

		Brood parasite	Lays eggs in the nest of other species (cuckoos).	1
Plants	Fire regeneration trait	Obligate seeder	Adult plants are killed by fire. Regeneration from seed.	17
		Obligate-resprouting	Adults capable of surviving fire and resprouting. Includes basal, epicormic and rhizomal resprouting. Does not regenerate from seed.	14
		Facultative resprouter	Adults capable of surviving fire and resprouting, but regeneration also occurs from seed.	48
	Growth form	Herb	Herbaceous plants	26
		Low shrub	Shrubs, 0.1 – 1 m height	31
		Shrub	Shrubs, 1 – 8 m height	28
		Understorey tree	Small trees, > 8 m height	3

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

Figure captions

Figure 1. Distribution of foothill forests (shaded area in main panel) and locations of study area (star in main panel) in Victoria, Australia. Top left panel: shades of blue represent post-prescribed fire age classes: 0-3 years, 3-10 years, 10-40 years since prescribed fire. Simple hatch represents long-unburnt vegetation (79 years since wildfire). Yellow circles represent study sites.

Figure 2. Foothill forests vegetation in four post-fire age-classes (AC). (a) long-unburnt: 79 years after wildfire. (b) AC1: 0-3 years after prescribed fire. (c) AC2: 3-10 years after prescribed fire. (d) AC3: 10-40 years after prescribed fire.

Figure 3. Responses bird and plant species to time since prescribed fire in foothill forests. (a) Percentage of plant and bird species for which the modelled response to time since prescribed fire resembled different types of generalized response-curves (after Watson et al. 2012). 'NS' refers to non-significant relationships. (b) Explanatory power of generalized additive models of the relative abundance of bird (n = 22) and relative cover of plant (n = 39 species) species as a function of time since prescribed fire. Points represent the deviance explained (%) of models. Notch plots indicate the median, upper and lower quartiles and 95% confidence intervals for each taxonomic group. (c - f) Models of selected bird (orange lines) and plant (green lines) species to time since prescribed fire. Lines are fitted models. Shaded areas are 95% confidence intervals. P = *P*-value, D = deviance explained.

Figure 4. Relative abundance of selected bird (top panels) and relative cover of plant (bottom panels) species in post-fire age-classes (AC) in foothill forests. Points represent mean values. Vertical lines represent 95% confidence intervals. AC1 = 0-3, AC2 = 3-10, AC3 = 10-40 years since prescribed fire, LU = 79 years since wildfire. Generalized linear models with Poisson error distribution were used to model bird responses. Beta regression was used to model plant species responses to age classes. Letters above points indicate significant differences ($P < 0.05$) determined by Tukey HSD.

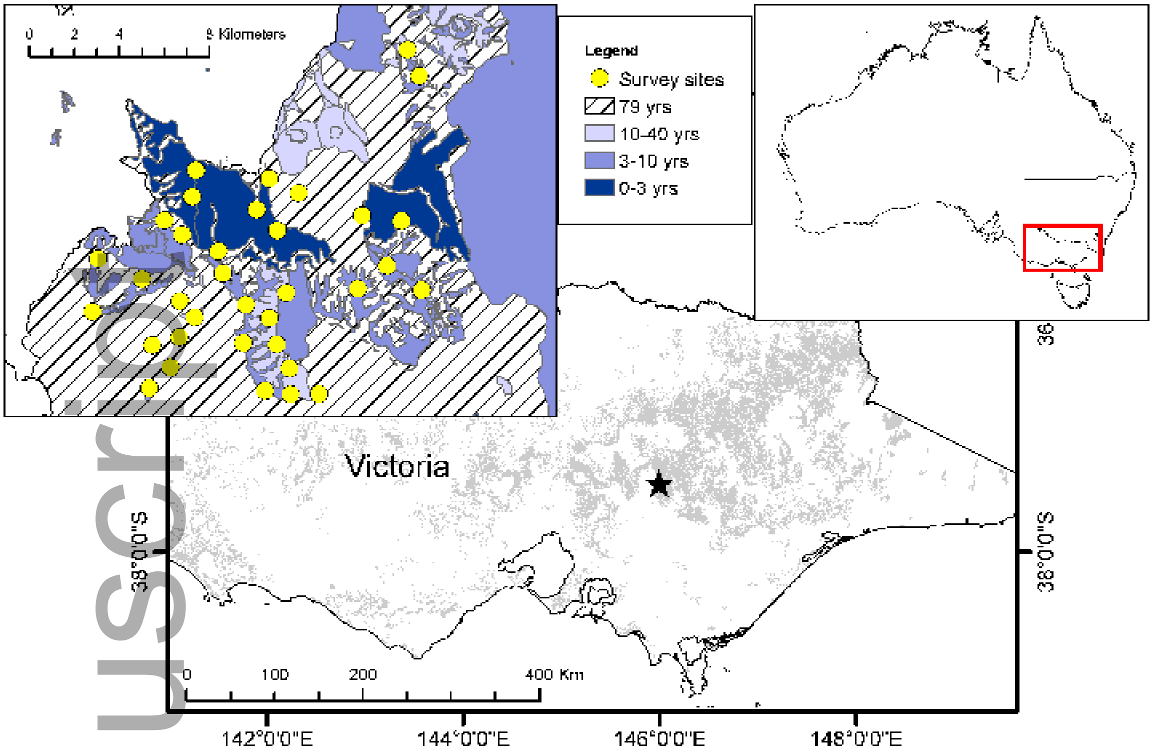
Figure 5. Response of functional groups of bird and (a – c) plant (d – f) species to time since prescribed fire in foothill forests. Birds were grouped according to (a) foraging location (upper-midstorey: n = 20 species, lower-midstorey: n = 5, throughout: n = 6), (b) diet versatility (low: n = 23, intermediate: n = 16, high: n = 4) and (c) nest type (open: n = 32, hollow: n = 9). Plants were grouped according to fire regeneration traits and growth form: (d) facultative-resprouting shrubs (n = 11 species) and low shrubs (n = 18); (e) obligate-

resprouting shrubs (n = 9) and low shrubs (n = 3); (f) obligate-seeding shrubs (n = 6) and low shrubs (n = 6). Lines are fitted responses from generalized additive models of the total relative abundance/cover of species in each group. Shaded areas are 95% confidence intervals. Lines without shaded areas indicate non-significant relationships.

Figure 6. Response of selected bird (a – c) and plant (d – f) functional groups to post-fire age-classes (AC) in foothill forests. Points indicate mean relative abundance of (a) lower-midstorey foraging birds, (b) birds with low dietary versatility, (c) open nest bird species, and mean relative cover of (d) facultative-resprouting shrubs, (e) obligate-resprouting shrubs and (f) obligate-seeding shrubs in post-fire age-classes. Vertical lines represent 95% confidence intervals. Letters indicate significantly different means ($P < 0.05$) determined by Tukey HSD. AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since prescribed fire, LU: long-unburnt (79 years since wildfire).

Figure 7. Response of bird and plant species richness to post-fire age-classes (AC) in foothill forests. Points indicate mean (a) bird and (b) plant species richness. Vertical lines represent 95% confidence intervals. Letters indicate significantly different means ($P < 0.05$) determined by Tukey HSD. AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since prescribed fire, LU: long-unburnt (79 years since wildfire).

Figure 8. Non-metric multidimensional scaling (NMDS) ordinations showing similarity in bird (a – b) and plant (c – d) community composition between post-fire age classes in foothill forests. Colours and symbols represent time-since-fire age-classes: AC1 = 0-3, AC2 = 3-10, AC3 = 10-40 years since prescribed fire, 'LU' = 79 years since wildfire. (a) Bird community composition. (b) Bird community composition with arrows to represent vectors of influential species. (c) Plant community composition. (d) Plant community composition with arrows to represent vectors of influential species. PerMANOVA showed significant effects of post-fire age class on bird ($P = 0.01$) but not plant ($P = 0.081$) community composition. Species names are represented by capitalized generic name followed by the first four letters of the specific name (e.g. S.fron = *Sericornis frontalis*). Species lists are provided in Appendices S2-S3.



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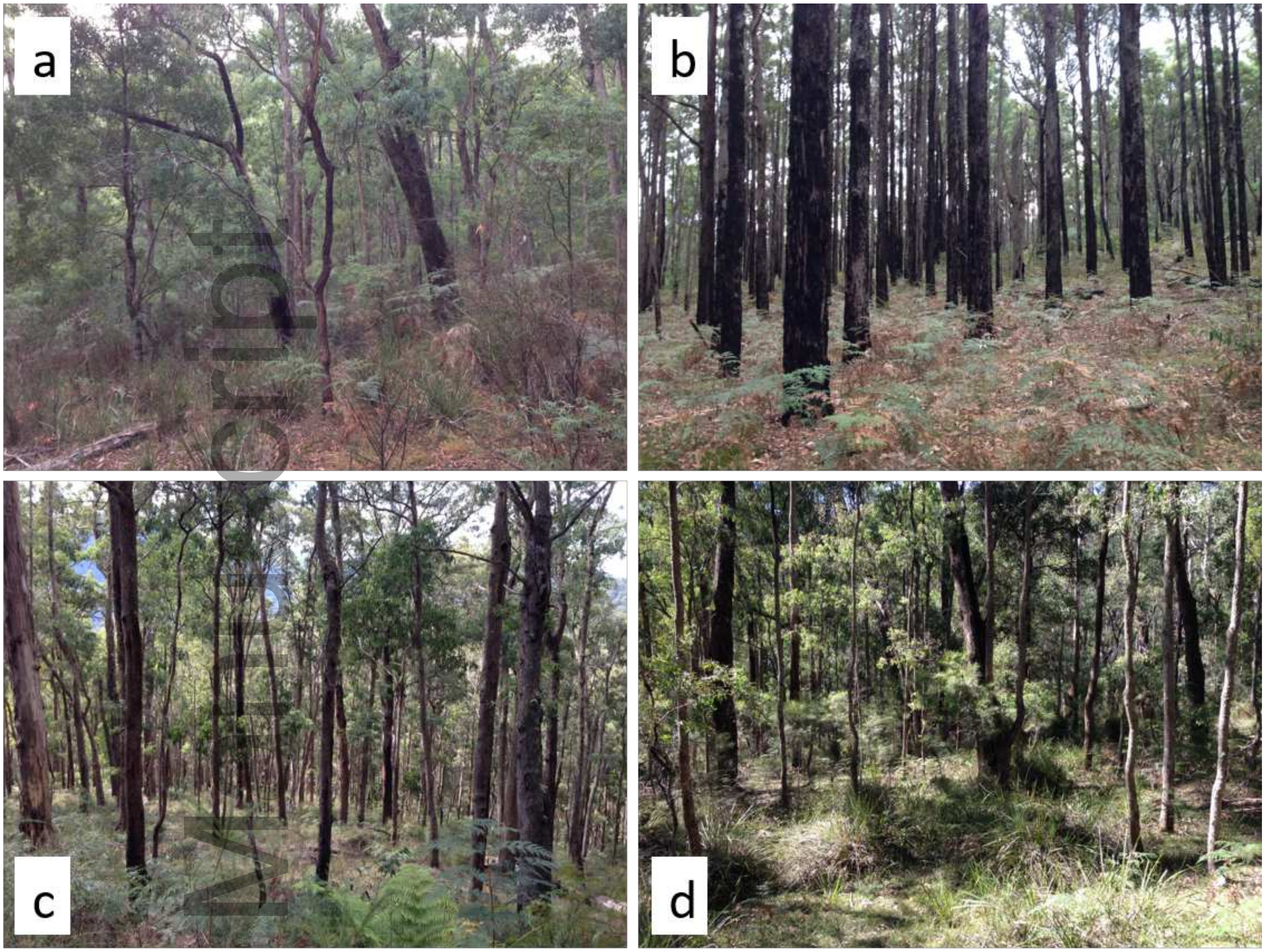

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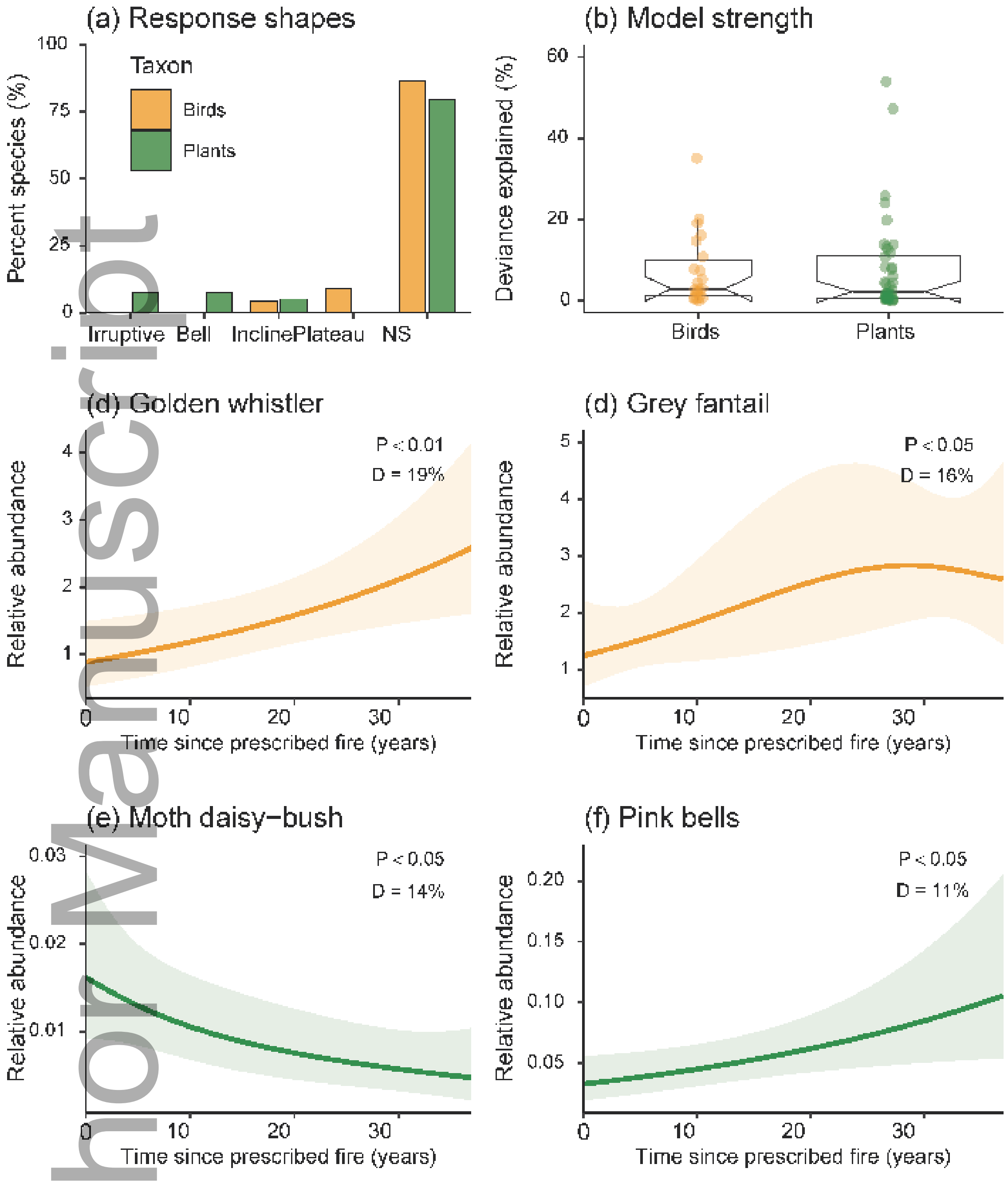

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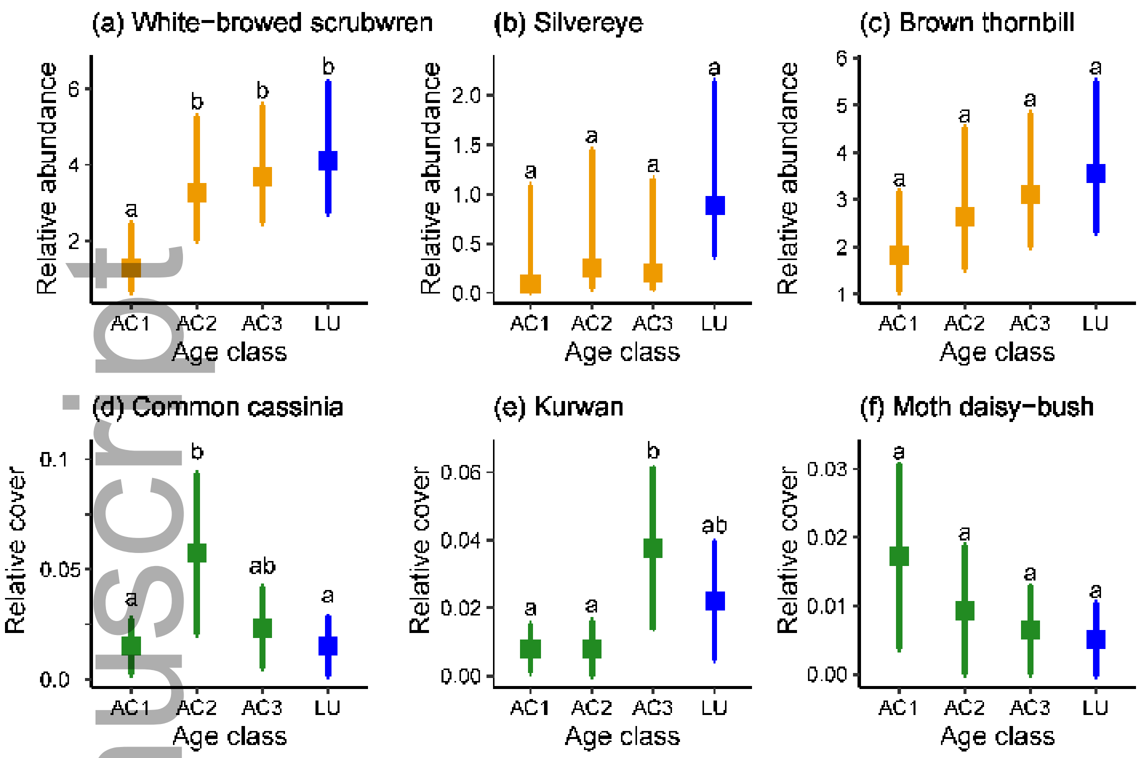

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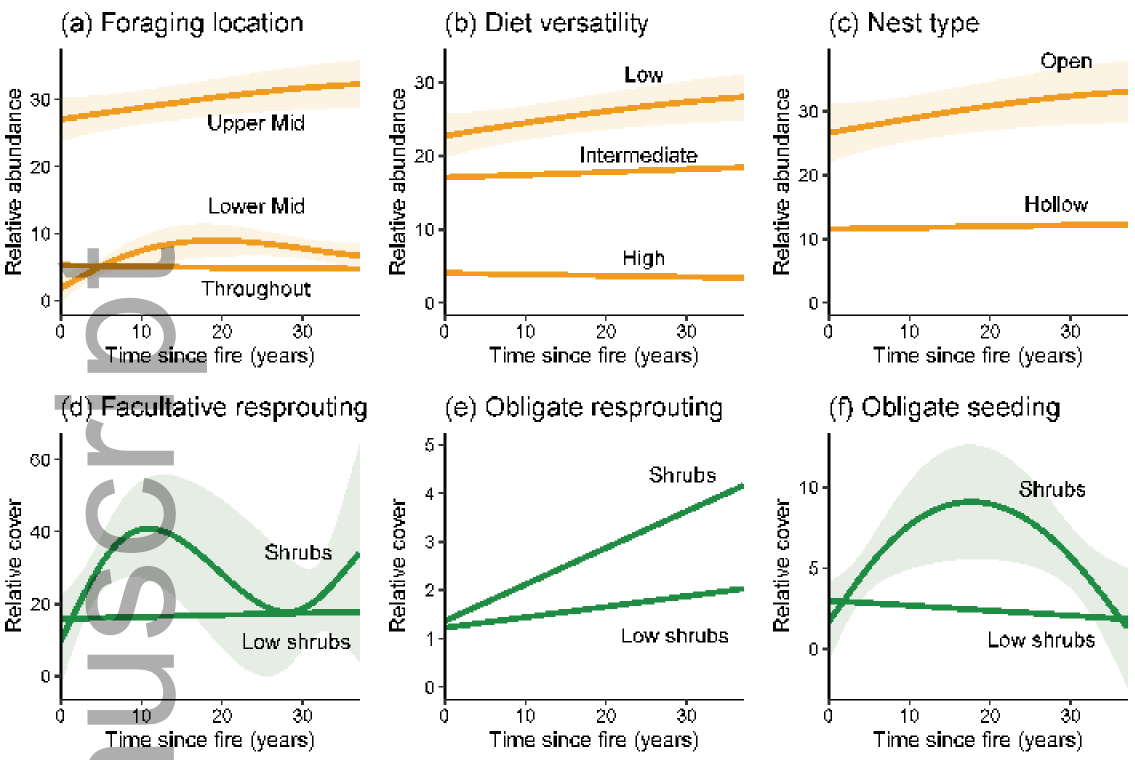

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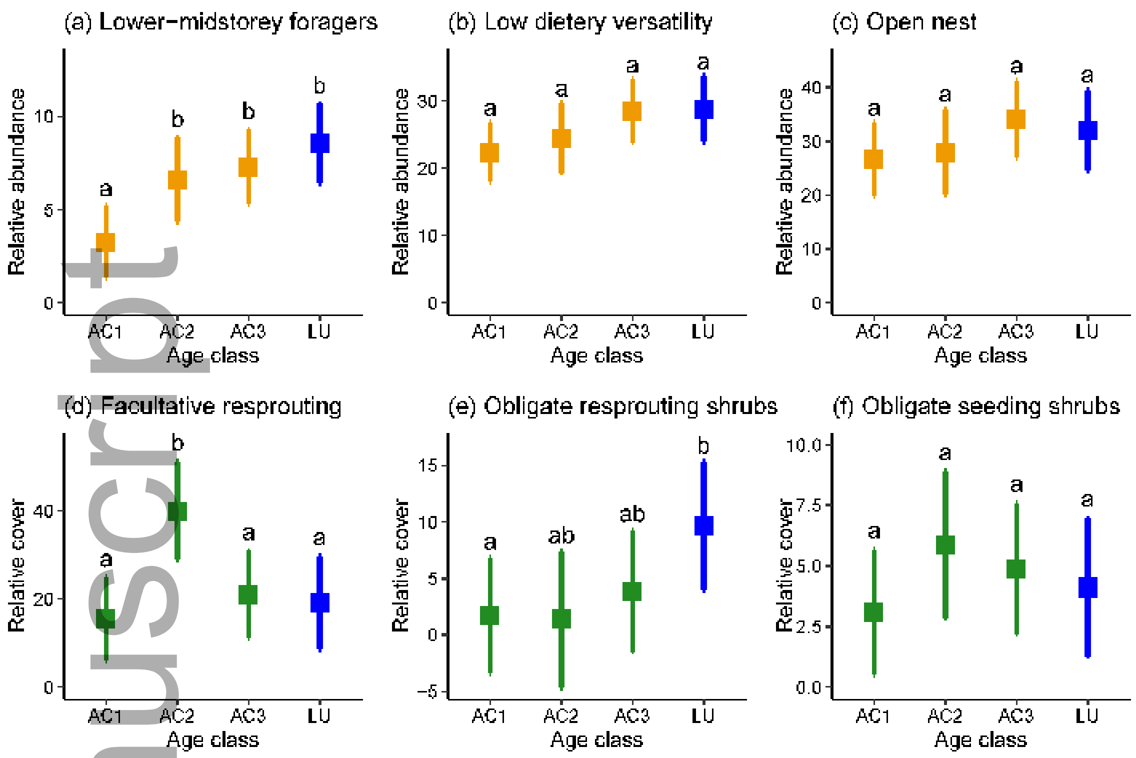

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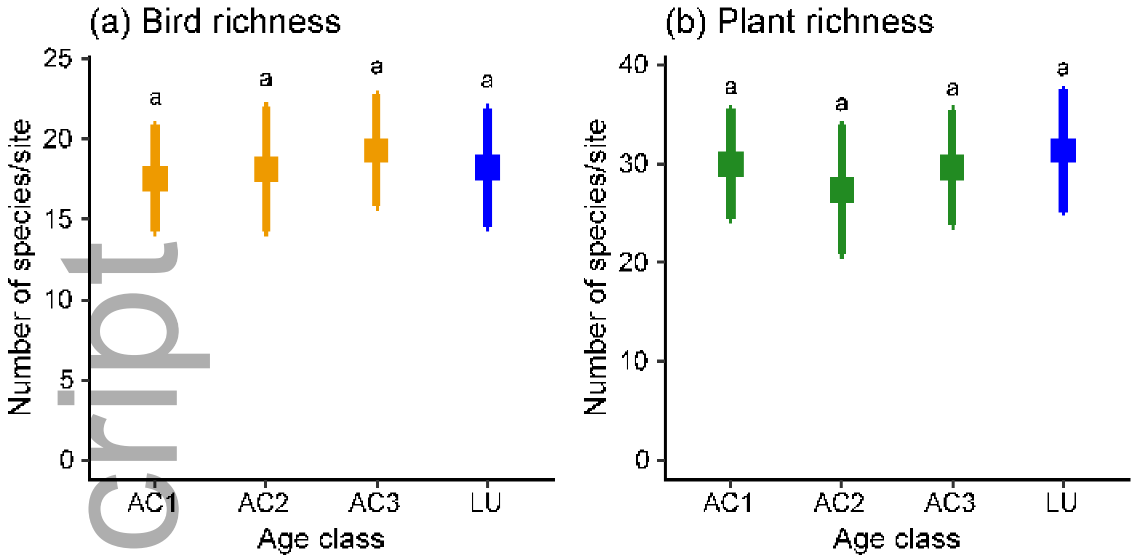

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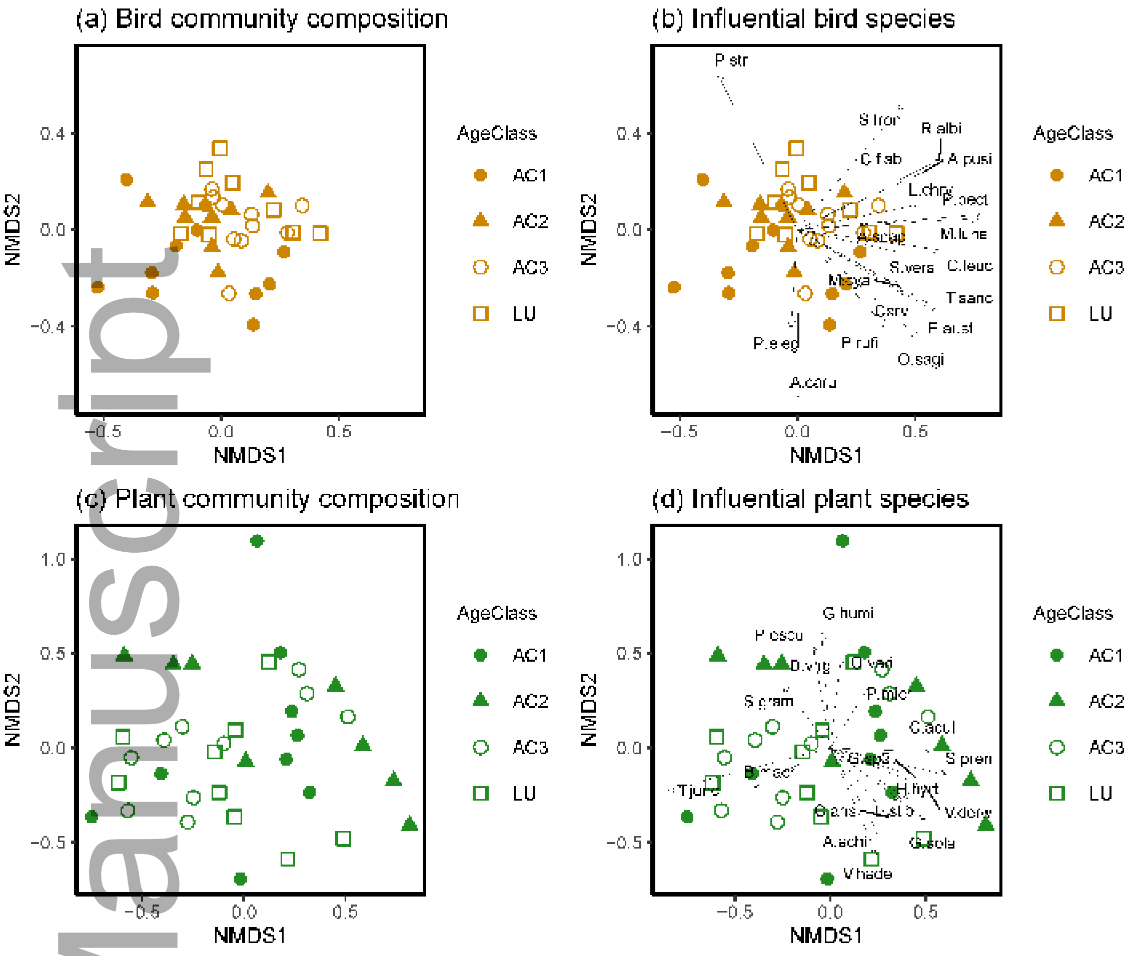

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