Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests

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Abstract. Fire is a global driver of ecosystem structure, function, and change. Problems common to fire scientists and managers worldwide include a limited knowledge of how multiple taxonomic groups within a given ecosystem respond to recurrent fires, and how interactions between fire regimes and environmental gradients influence biodiversity. We tested six hypotheses relating to fire regimes and environmental gradients in forest ecosystems using data on birds (493 sites), mammals (175 sites), and vascular plants (615 sites) systematically collected in dry eucalypt forests in southeastern Australia. We addressed each of these hypotheses by fitting species distribution models which differed in the environmental variables used, the spatial extent of the data, or the type of response data. We found (1) as predicted, fire interacted with environmental gradients and shaped species distributions, but there was substantial variation between species; (2) multiple characteristics of fire regimes influenced the distribution of forest species; (3) common to vertebrates and plants was a strong influence of temperature and rainfall gradients, but contrary to predictions, inter-fire interval was the most influential component of the fire regime on both taxonomic groups; (4) mixed support for the hypothesis that fire would be a stronger influence on species occurrence at a smaller spatial extent; only for vertebrates did scale have an effect in the direction expected; (5) as predicted, vertebrates closely associated with direct measures of habitat structure were those most strongly influenced by fire regimes; and (6) the modeled fire responses for birds were sensitive to the use of either presence-absence or abundance data. These results underscore the important insights that can be gained by modeling how fire regimes, not just fire events, influence biota in forests. Our work highlights the need for management of fire regimes to be complemented by an understanding of the underlying environmental gradients and key elements of habitat structure that influence resource availability for plants and animals. We have demonstrated that there are general patterns in biotic responses to fire regimes and environmental gradients, but landscape management must continue to carefully consider species, scale, and the quality of biodiversity data to achieve biodiversity conservation in fire-prone forests.

Key words: Australia; biodiversity; birds; boosted regression trees; climate; fire ecology; forest management; mammals; rainfall; sampling design; species distribution models; temperature.

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INTRODUCTION

Fire is a global driver of ecosystem structure, function, and change (Bowman et al. 2009, Archibald et al. 2013) and is used in forest management worldwide (Keeley et al. 2011, Moritz et al. 2014). The increased likelihood of extreme fire weather and the growing use of fire suppression and fuel treatments, such as prescribed burning, create an urgent need to understand plant and animal responses to fire (Gill et al. 2013). Recent advances in understanding of fire regimes have contributed much to the knowledge of forest ecosystems (Bradstock et al. 2012, Fernandes et al. 2013, DellaSala and Hanson 2015), but substantial challenges remain in managing fire for biodiversity conservation. These include limited knowledge of how multiple taxonomic groups within a given ecosystem respond to the spatial and temporal arrangement of fires, how interactions between fire and environmental gradients influence biodiversity, and how the perceived fire responses of species are affected by elements of study design including spatial scale, choice of environmental covariates, and data type.

The complexity of forest ecosystems presents a challenge to understanding and predicting biodiversity responses to fire. Forest landscapes comprise numerous environmental gradients relating to climate, disturbance, topography, and vegetation (Lindenmayer 2009, Romme et al. 2016). Species distribution models (SDMs) that link observations of a species occurrence or abundance with environmental covariates can help to quantify species responses to complex environmental gradients (Elith and Leathwick 2009). Species distribution models are one of the main methods available to predict animal and plant distributions in relation to climate but disturbance variables such as fire are rarely used as predictors (Franklin 2010, Austin and Van Niel 2011). Including fire, together with environmental gradients such as temperature, rainfall, and vegetation, may provide a more complete understanding of species distributions in fire-prone forests. Both theoretical (Austin 2002) and empirical (Tucker et al. 2012) evidence suggest that combining disturbance and environmental variables improves the performance of SDMs. Here, we build on previous work that has largely focused on single species or single taxonomic groups. We use SDMs to model data on birds, small mammals, and plants, systematically collected from a common region, to investigate the relative responses of these multiple taxa to fire. Because disturbance and climate are major drivers of forest ecosystems, we predict that including both fire and environmental gradients in SDMs will improve model fit and performance.

Most studies model the effects of fire on plants and animals by using a single measure of the fire regime such as time since the most recent fire. Although time since fire influences species distributions, there is growing evidence that quantifying the combined effects of recurrent fires and multiple components of fire regimes is needed to better understand plant and animal responses to fire. For example, inter-fire interval (e.g., Morrison et al. 1995, Aponte et al. 2014, Fairman et al. 2016), fire severity (e.g., Nappi and Drapeau 2011, Fontaine and Kennedy 2012), and the spatial patterns of fires (e.g., Sitters et al. 2014a, Sollmann et al. 2016), in addition to time since fire, are known to strongly influence forest plants and animals, but are rarely modeled in combination. Here, we compare sets of SDMs with a single measure of fire (time since fire) to those that include multiple measures of the fire regime. We hypothesize that models that include several fire regime variables will outperform univariate models because biota must contend with and recover from the combined effects of recurrent fires and their characteristics, not just a single fire event.

Fire regimes have been linked to population changes in species of birds, small mammals, and plants in forests worldwide (DellaSala and Hanson 2015). However, the relationship between fire regimes and biodiversity can vary between different species, taxa, and ecosystems (Clarke 2008). For more mobile groups, such as birds and mammals, time since the last fire often strongly influences species distributions (Catling et al. 2001, Lindenmayer et al. 2011). For less mobile
groups, such as plants, inter-fire interval usually is a strong influence (Gill and McCarthy 1998, Enright et al. 2015). We test the hypothesis that the relative influence of fire regime characteristics on forest species will vary between plants and vertebrates. We predict that plants will be more sensitive to inter-fire intervals because they generally need to recover on site from stored seedbanks or vegetative buds. Furthermore, we predict that birds and mammals will be more strongly influenced by measures of the last fire event, including time since fire and fire severity, because they often are forced from burnt sites and are relatively mobile and more likely to find alternative habitat that has recovered sufficiently from the last disturbance.

In addition to taxonomic group and choice of environmental covariates, sampling design influences the inferences drawn from SDMs (Guisan et al. 2007). One important influence is spatial scale (Merow et al. 2014). Changing the spatial extent, for example, can change the environmental gradients sampled and the factors controlling fire regimes (Parisien and Moritz 2009). Consequently, species can respond differently to fire in different geographic locations, particularly where climate interacts with vegetation dynamics (Nimmo et al. 2014). Determining how spatial extent influences model performance is important because it can help forest managers determine which data and models will most effectively inform fire planning. To date, few studies have examined the consistency of plant and animal responses to fire at different spatial extents. In this study, we investigate the effect of sampling design on species–fire relationships at two spatial scales: a large spatial extent encompassing multiple regions and a smaller extent encompassing a single region. We predict that fire will have a stronger influence on species at a smaller spatial extent (a single region) than at a larger spatial extent (multiple regions) where greater variation in environmental gradients and community assembly could mask or change associations with fire regimes.

A second important influence of sampling is the type of data collected. Species distribution modeling studies in forest ecosystems commonly use occurrence data (presence–absence) and derive estimates of probability of occurrence (Swan et al. 2015). This approach is useful because many species occur at low prevalence and, when species occur at few sites, variation in occurrence and abundance data is similar (Cushman and McGarigal 2004). However, different ecological processes can drive occurrence and abundance (Howard et al. 2014). The increasing availability of remotely sensed fire data, and large databases of species occurrence records, means that it is now more important than ever to understand how different data types influence model outcomes. Few empirical tests exist on how the choice of response variable influences modeled species–fire relationships. Here, we compare SDMs built by using occurrence vs. abundance data, for a subset of bird species. We predict that the strength and shape of species responses to fire regimes and environmental gradients will be sensitive to the use of presence–absence data or abundance data. Abundance data contain more information and we expect that it is more closely related to population dynamics than presence–absence data.

Fires have both direct and indirect effects on plants and animals (Whelan et al. 2002). Fires can directly cause emigration and mortality in animals, and also indirectly influence animal populations by changing habitat resources associated with vegetation structure and floristic composition. For example, Fox et al. (2003) showed that small mammal species entered the post-fire succession only when vegetation structure became suitable. The utility of fire regime variables as predictors of the distribution of animal species depends on how closely vegetation structure and composition are related to fire (Converse et al. 2006, Di Stefano et al. 2011). Recent studies have shown that habitat variables, measured on-site, can provide greater accuracy and predictive power than relying on fire variables alone (Nimmo et al. 2014, Sitters et al. 2014b). Several studies have tested a priori predictions about species responses to fire, based on species traits and descriptions of habitat use, but have found limited support for predicting post-fire responses using qualitative information (Smith et al. 2013). Here, we explore an alternative approach for developing generalizations about which forest species are most affected by fire regimes. We investigate the potential for field-based measures of habitat structure to predict the distribution of forest birds, and directly compare such habitat models with models built using fire regime variables for the same species. We predict that vertebrates with distributions
strongly linked to direct measures of habitat structure will also be those most influenced by fire, particularly when those measures of habitat structure are associated with fire regimes.

In this study, we quantify the relationships between species, fire regimes, and environmental gradients in dry eucalypt forests of southeastern Australia. Fire is a major natural disturbance in “foothill forests” that cover approximately 7.5 million ha in the State of Victoria. Foothill forests are a unique combination of hilly terrain and dense forest, often bordering towns and city edges. They are a priority for fire management in southeastern Australia, containing high levels of biodiversity and posing risks of fires to people and property. We bring together data from six major studies to provide a more complete picture of biodiversity responses to interactions between fire regimes and environmental gradients in foothill forests. We seek to advance this field by quantifying species responses to recurrent fires, by modeling species responses to a greater range of fire and environmental gradients, by comparing species–environment relationships between multiple taxonomic groups in one ecosystem, and by compiling an extensive data set (>600 biodiversity survey sites) that allows greater exploration of the role of sampling design.

We examine the overarching question of how fire and environmental gradients influence species distributions in forest ecosystems, by using data on birds, small mammals, and vascular plants collected for the purpose of understanding fire responses. We test six primary hypotheses relating to the role of fire in determining species distributions (Tables 1 and 2).

(H1) Disturbance hypothesis: the fit and performance of species distribution models will be improved by including predictor variables relating to fire, a major disturbance in eucalypt forests, in addition to variables representing climate and vegetation type.

(H2) Fire regime hypothesis: the fit and performance of species distribution models will be higher when using variables that represent multiple components of fire regimes rather than a single component.

(H3) Taxonomic group hypothesis: the relative influence of fire regime characteristics will vary between plants (less mobile species) and vertebrates (more mobile species).

(H4) Spatial-scale hypothesis: species–fire relationships will be stronger at a smaller spatial extent, for which other environmental gradients are more muted.

(H5) Data-type hypothesis: the magnitude and shape of a species–fire response is sensitive to the use of either presence–absence data or abundance data.

(H6) Habitat hypothesis: vertebrate species with distributions strongly linked to habitat structure will be those most influenced by fire.

Table 1. Hypotheses tested (H1–6), predictions arising from each hypothesis, and corresponding model sets (M1–6) and comparisons.

| Hypothesis | Comparison |
|------------|------------|
| **H1, Disturbance.** If species distributions are strongly influenced by fire, in addition to climate and vegetation variables, M3 should have higher explanatory power and predictive ability than M1. | M1 vs. M3 |
| **H2, Fire regime.** If species distributions are more strongly shaped by multiple components of the fire regime, than by a single measure (time since fire), M3 should have higher explanatory power and predictive ability than M2. | M2 vs. M3 |
| **H3, Taxonomic group.** If the occurrences of vascular plants and vertebrates are determined by different measures of the fire regime, the relative contribution of fire regime variables within M3 should show marked differences when grouped by taxa. | M3 subsets |
| **H4, Spatial scale.** If the processes that shape species distributions are sensitive to the spatial extent of the data set, the relative contributions of fire, climate, and vegetation variables should differ between M3 and M4. | M3 vs. M4 |
| **H5, Data type.** If species responses to environmental variables are sensitive to the type of response data modeled (occurrence vs. abundance), the magnitude and contribution of fire, climate, and vegetation variables should differ between M3 and M5. | M3 vs. M5 |
| **H6, Habitat.** If vertebrate–fire relationships are largely determined by changes in habitat structure, a model that uses direct measures of habitat structure (M6) should have higher explanatory power and predictive ability than a model that uses fire regime variables (M3). There should also be a positive correlation between species influenced by habitat structure and species influenced by fire. | M3 vs. M6 |

Note: Model sets are described in Table 2.
We address each of these hypotheses by fitting SDMs for data sets of birds, mammals, and vascular plants, which differ in the environmental variables used, the spatial extent of the data, or the type of response data (Table 2).

**METHODS**

**Study area and background**

Foothill forests (~75,000 km²) in Victoria, southeastern Australia, contain large tracts of vegetation characterized by rough-barked eucalypts including messmate *Eucalyptus obliqua*, brown stringybark *Eucalyptus baxterii*, narrow-leaved peppermint *Eucalyptus radiata*, and broad-leaved peppermint *Eucalyptus dives* (Figs. 1 and 2a). Foothill forests occur on hilly terrain; slopes and ridges support drier, more open forest, whereas moister gullies support denser vegetation and include smooth-barked trees including mountain gray gum *Eucalyptus cypellocarpa*, blue gum *Eucalyptus globulus*, and manna gum *Eucalyptus viminalis*. Common midstory species include blackwood *Acacia melanoxylon* and silver wattle *Acacia dealbata*. The understory in drier vegetation types largely comprises a mix of sclerophyllous shrubs, perennial grasses (*Poa* spp.), and herbs and ferns including Austral bracken *Pteridium esculentum*. In wetter vegetation types, an understory dominated by rough tree fern *Cyathea australis*, Australian tree fern *Dicksonia antarctica*, and soft bracken *Calochleana dubia* is more common. Importantly, in foothill forests, most individuals of the dominant eucalypt species survive fire events and regenerate from epicormic buds and basal shoots (Gill 2012, see Fig. 1). Fires also trigger recruitment of eucalypt seedlings. Thus, most stands of foothill forest comprise multi-aged cohorts of resprouting eucalypts. Average annual rainfall ranges from 700 to 1600 mm (http://www.bom.gov.au/).

Much of the study area consists of state-owned reserves that are managed for biodiversity conservation, recreation, water, and timber harvesting. Most forest vegetation has experienced either clear-felling or selective logging in the past 150 yr (DELWP 2014). Fire management on public land has dual objectives of protecting human life and property within and adjacent to reserves, and maintaining or improving ecosystem resilience (DELWP 2012). The occurrence of hot summer days (>35°C) and long periods of drought promote large, intense fires. Major wildfires occurred in the study area in 1939, 1962, 1983, 2003, 2006, and 2009 (Teague et al. 2010). Between 2000 and 2013, approximately 42% of foothill forests were burnt, mostly during large wildfires >10,000 ha. Prescribed burning is widespread and undertaken primarily to reduce fuels and, in some cases, to achieve ecological objectives (Gill 2012). Prescribed burns are commonly of lower intensity than wildfires, often being patchy burns that do not reach canopy strata (Cheal 2010).

**Bird, small mammal, and plant data**

We combined biodiversity data from six large-scale studies that systematically surveyed plant

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**Table 2. Model set descriptions (data type and spatial extent in parentheses) with corresponding hypotheses, taxa, and environmental variables.**

| Model sets                                      | Hypotheses | Taxa | Environmental variables† |
|-------------------------------------------------|------------|------|--------------------------|
| M1: climate and vegetation (p/a, all regions)   | H1         | B, M, P | Temperature, Rainfall, Vegetation |
| M2: single measure of fire (p/a, all regions)   | H2         | B, M, P | Temperature, Rainfall, Vegetation |
| M3: multiple measures of fire (p/a, all regions)| H1–H5      | B, M, P | Temperature, Rainfall, Vegetation, Time since fire |
| M4: multiple measures of fire (p/a, Otway Ranges region) | H4 | B, M, P | Temperature, Rainfall, Vegetation, Time since fire, Area burnt, Inter-fire interval, Fire type |
| M5: multiple measures of fire (abundance, all regions) | H5 | B | Temperature, Rainfall, Vegetation, Time since fire, Area burnt, Inter-fire interval, Fire type |
| M6: habitat structure (p/a, Otway Ranges and East Central regions) | H6 | B | Temperature, Rainfall, Vegetation, Litter, Midstory, Upperstory, Tree diameter |

Note: B = Birds; M = Mammals; P = Plants.

† All models for birds and plants also include additional variables to account for spatial and temporal survey effort; all models for mammals include a variable to account for temporal survey effort.
and vertebrate distributions along post-fire gradients: the Faunal Refuges Project; Fire Effects Study Areas; Gippsland Retrospective and HawkEye; the Otways Fire, Landscape Pattern and Biodiversity Project; Otways HawkEye; and Pre- and Post-fire Flora Monitoring (Appendix S1). Different studies were undertaken in different geographic regions across the study area (Fig. 2a). We use data from sites arrayed along a chronosequence of 0–70 yr post-fire. Each study was undertaken within large continuous blocks of forest, and most sites were selected to avoid recent (<30 yr) logging activity.

Data on birds were collected in five of the studies by using either timed point counts or timed area searches (Robinson et al. 2014, Sitters et al. 2014a, b, Lown and McNabb 2015, Muir et al. 2015). Data on small mammals were collected in three of the studies by using aluminum Elliott box traps (e.g., Swan et al. 2015, Chia 2016). The presence of vascular plant species was recorded in five studies via quadrat and transect searches at sites (e.g., Bassett et al. 2015, Cohn et al. 2015). Further information about the number of sample sites from each project, field sampling methods, and the timing of data collection is included in Appendix S1.

In total, the combined data used in the present study consisted of records of 112 bird species from surveys at 493 sites, seven small mammal species from 175 sites, and 233 vascular plant species from 615 sites.

Environmental data

The fire history of sites was obtained from mapping undertaken by the Victorian government land management agency, the Department of Environment, Land, Water and Planning (DELWP). Major fires were mapped from 1903 onward, with the accuracy and resolution of mapping increasing over time with the availability of satellite imagery from the 1970s (DELWP 2014; Fig. 2b). We calculated four fire regime variables for statistical analysis. Time since fire was calculated as the number of years from the most recent fire to the year of the plant or vertebrate survey. The type of the most
Fig. 2. (Top) Extent of foothill forest vegetation in Victoria and (bottom) fire history of foothill forest. Different colors represent foothill vegetation, and surrounding areas, last burnt in each decade since fire mapping started in 1903. Pale gray depicts foothill forests for which no fire has been mapped over this period.
recent fire (wildfire or prescribed burn) was used as a surrogate for fire severity because mapping of fire intensity and severity is not available across the period of fires included in this study. Although they vary in severity (Leonard et al. 2014), wildfires usually are more intense than prescribed fires. Mean inter-fire interval was calculated as the average number of years between successive fires at each site (excluding time since the last fire). For example, the mean inter-fire interval at a site burnt in 2010, 2000, and 1980 would be 15 yr, and the mean inter-fire interval at a site burnt in 2009 and 2008 would be one year. Mean inter-fire interval was highly correlated with minimum inter-fire interval (Pearson’s correlation coefficient = 0.93) and by definition is closely related to fire frequency. To avoid collinearity, we selected only mean inter-fire interval for inclusion in SDMs (hereafter referred to as “inter-fire interval”). Area burnt was calculated as the amount of recently burnt vegetation (<3 yr since the last fire) in a circle with a 1 km radius (314 ha) centered on each site. Time since fire and area burnt were correlated ($r = -0.74$) but we retained both variables in the final model set because we were interested in exploring interactions between the two. Missing fire records were estimated as part of the species distribution modeling procedure described below.

We derived two climatic gradient variables representing the marked variation in temperature and rainfall across the study area (Liu et al. 2013). Mean maximum temperature in January (mid-summer) and mean rainfall in July (mid-winter) were derived from the software package ANUCLIM (Houlder et al. 2003) and applied to a 30-m Shuttle Radar Topography Mission Digital Elevation Model. Temperature and rainfall were represented at a pixel resolution of 75 x 75 m. We classified each site according to local vegetation type by using existing vegetation maps produced by DELWP (2014). Foothill forests comprise local vegetation types that differ in structure and species composition. Here, the broad classification of foothill forest was divided into five categories on the basis of structural similarities and soil type: Foothill Forest, Forby Forest, Grassy/Heathy Forest, Moist Forest, and Tall Mixed Forest (following Cheal 2010).

We also calculated four fine-scale measures of habitat structure representing features we predicted would provide important resources for birds: litter (mean litter depth, mm), midstory (percentage of vegetation cover 1–2 m), upperstory (percentage of vegetation cover ≥4 m), and tree diameter (mean diameter at breast height [cm] of live eucalypts). These habitat variables are empirical data collected at 344 sites, in conjunction with plant and animal surveys. Further details of field measurement methods are provided in Appendix S1. The mean and range for each environmental variable are shown in Appendix S2, and correlations between all environmental variables are shown in Appendix S3.

**Hypothesis testing and model sets**

We built six sets of regression models to address the six hypotheses and their predictions (Table 1). Each hypothesis was tested by comparing models that differed in either the species and taxonomic group included in the analysis (plants or vertebrates), the environmental predictors included (climate/vegetation variables only, climate/vegetation plus time since fire, or climate/vegetation plus multiple measures of the fire regime), the spatial extent of the data (a single region or multiple regions), or the type of response data (presence–absence or abundance) (Table 2).

The first three sets of models were built using presence–absence data for individual plant and vertebrate species. Model Set 1 represented a baseline model of climate and vegetation and included temperature, rainfall, and vegetation type as environmental predictor variables. Model Set 2 included the baseline environmental variables and time since fire, and Model Set 3 included the baseline environmental variables and four fire variables representing the fire regime (area burnt, inter-fire interval, fire type, and time since fire; Tables 1 and 2).

Model Set 4 included the same set of climate and fire regime models as Model Set 3 but used data from only a single focal region: the Otway Ranges. The data from this region span an east–west gradient of ~50 km, compared with a length of ~500 km for multiple regions (Fig. 2). Model Set 5 used the same predictor variables and spatial extent as Model Set 3 but the response variable was the total number of records of each bird species at each site (hereafter “relative abundance”). This allowed comparison with presence–absence models for the same taxa. Model Set 6 included
Species distribution modeling

We used boosted regression trees (BRTs) to determine plant and vertebrate responses to fire regimes and to compare model sets relating to our hypotheses. BRTs provide a flexible framework to model non-linear relationships and to quantify interactions between variables (Elith et al. 2008, Leathwick et al. 2008). Boosted regression trees generally outperform other regression modeling techniques when used to model species distributions (Elith et al. 2006), and have the advantage of imputing missing predictor data as part of the model-fitting procedure (Elith et al. 2008). Data on inter-fire interval were imputed for 126 of 494 bird sites, 180 of 612 plant sites, and 28 of 75 mammal sites using the “surrogate split” method. This method uses information from other predictor variables in the model, such as vegetation type, rainfall, and temperature, to impute missing data (approach summarized in Tiemey et al. 2015). We used imputation, rather than restricting analyses to a smaller data set, to make best use of the information available. Follow-up analysis with only “complete cases” showed that ranking of the importance of the predictor variables was similar to results from imputed data.

We modeled the response variable as either the occurrence (binomial distribution) or abundance (Poisson distribution) of a species at a site. The response and environmental variables varied depending on the model set (Table 2). For birds and small mammals, we modeled the response variable as the detected presence–absence (or total number of individuals) of a species at a site, for data pooled over multiple surveys. For plants, we modeled the response variable as the detected presence–absence of a species at a site.

Additional predictor variables relating to survey effort that were specific to each taxonomic group were included in BRTs to account for spatial and temporal variation in sampling (Appendix S2: Tables S1 and S2). For birds, spatial survey effort was modeled as log(area of survey plot) and temporal survey effort was modeled as log(total survey time). For small mammals, temporal survey effort was modeled as log(number of trap nights). For plants, spatial survey effort was modeled as log(area of survey plot) and temporal survey effort was modeled as the total number of site visits. Where fires occurred between successive biodiversity surveys at sites, we selected only one survey period for inclusion in further modeling to ensure that fire history data matched the field survey data.

We modeled bird, small mammal, and plant species that occurred at ≥10% of sites across the study area and, to ensure appropriate spatial coverage, that were present in at least the two geographic regions that encompassed the most survey sites (Otway Ranges and Central Victoria). We assessed the fit of each model by calculating the proportion of deviance explained (% Dev; Zuur et al. 2009). The ability of models to accurately discriminate between a species’ presence and absence was assessed by using the area under the curve (AUC) of a receiver-operating characteristic plot. Models with AUC values of <0.7, 0.7–0.9, and >0.9 were interpreted as offering poor, useful, and very good discrimination, respectively (Pearce and Ferrier 2000). We used 10-fold cross-validation to determine AUC values. We also assessed the correlation coefficient between predicted probabilities and observation of species presence–absence (point-biserial correlation) but the results were similar to AUC and we do not report them here. We assessed the contribution of variables, within each model, by calculating the proportion of deviance explained attributable to each variable (percentage deviance explained/percentage contribution of variable).

Exploration of boosted regression tree model specifications showed that a tree complexity of 3, learning rate of 0.001, and bag fraction of 0.75 achieved minimum predictive error for most species. Learning rate was reduced for some species to achieve model convergence. BRTs were run in R-Studio using R statistical software (http://www.r-project.org/) using the package dismo (Hijmans et al. 2015). To ensure the results were robust to
choice of regression modeling technique, we also ran comparable generalized linear models (GLMs) and generalized additive models (GAMs) for Model Set 3, for all bird species. Visual comparison of species–environment relationships showed that GLM and GAM results were similar to BRTs and we do not report them here.

Analyses were summarized by careful integration of statistical modeling and descriptive statistics. We used box plots and descriptive statistics to summarize how the explanatory power (% Dev), predictive discrimination AUC, and strength of species–environment relationships differed between and within model sets (Appendices S4 and S5). Further insight into the magnitude, direction, shape, and uncertainty of individual species responses to environmental gradients was gained by plotting model predictions and interactions (Appendices S6 and S7).

**RESULTS**

We built SDMs for a total of 77 plant and 35 vertebrate species. Regression modeling showed that the distributions of vascular plants and vertebrates were associated with fire regimes and environmental gradients (Fig. 3a, b). The median explanatory power of binomial models across both taxa, using fire, climate, and vegetation data from multiple regions, was 34% (deviance explained; Appendix S4). Model discrimination between species presence and absence was useful for most species of plants and vertebrates (AUC values ≥ 0.7; Fig. 3c, d).

Species–environment relationships for two exemplar species, characteristic of foothill forests, are shown for binomial models including explanatory variables for fire, climate, and vegetation type (Figs. 4 and 5). Messmate *E. obliqua* was detected at higher probability of occurrence at longer inter-fire intervals (>20 yr) and was associated with lower maximum temperatures in January (20–23°C; Fig. 4). Explanatory power of the model was high (% Dev = 44.5%) and predictive discrimination was useful (AUC = 0.86). Probability of occurrence of the eastern yellow robin *Eopsaltria australis* showed a small increase with time since fire (peaking between 50 and 70 yr) and at longer inter-fire intervals (>15 yr; Fig. 5). Explanatory power of the model was moderate (% Dev = 15.3%) but predictive discrimination was low (AUC = 0.66).

(H1) The Disturbance hypothesis

Prediction: Adding fire to environmental models will improve model fit.—Models including fire variables (M2 and M3 in Table 2) had higher explanatory power (% Dev) than models including only climate and vegetation type (Fig. 3a, b). For plants, median deviance explained increased by 5.5 with the inclusion of fire regime variables (Fig. 3a), a percentage increase of 18.4%. For vertebrates, median deviance explained increased by 2.7 with the inclusion of variables representing fire regimes (Fig. 3b), a percentage increase of 10.7%. Further insight into the relative influence of environmental variables was gained by examining results within the model set that included all fire-, climate-, and vegetation-type predictors (M3). Within this set, the sum of the median model explanatory power attributable to rainfall and temperature gradients for all plant and vertebrate species combined was 13.4%, and the median amounts attributable to fire variables and vegetation type across all species were 9.8% and 3.7%, respectively (Fig. 6; Appendix S5). There was considerable variation between species (Fig. 3a, b; Appendices S4–S6).

Interactions between fire, climate, and vegetation type helped explain the distributions of plants and animals (Table 3). Within M3, the interaction between temperature and rainfall had the highest non-additive influence on species distributions (Table 3). Strong pairwise interactions were also evident between inter-fire interval and rainfall, and time since fire and temperature, for plants and vertebrates (Table 3). Such interactions sometimes resulted in marked variation in the response of species to fire along climatic gradients. For example, the narrow-leaved wattle *Acacia mucronata* showed a pronounced peak of occurrence at sites with lower maximum temperatures in January and longer times since fire (Fig. 7a), and the Australian king-parrot *Alisterus scapularis* showed a clear relationship with time since fire only at sites with lower maximum temperatures in January (Fig. 7b).

Interactions between fire and vegetation were not as pronounced as fire–climate interactions. The responses of messmate and eastern yellow robin to inter-fire interval in different vegetation types highlight a common pattern found for many species: The direction and shape of species responses were relatively consistent in different vegetation
types but with differences in mean probability of occurrence in each vegetation type (Fig. 7c, d).

The increase in model explanatory power with fire variables did not translate into an overall increase in the predictive discrimination of models with fire variables (as measured by AUC). For both plants and vertebrates, predictive discrimination AUC was similar for models including

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**Fig. 3.** Performance of regression models for vascular plants (a, c) and vertebrates (b, d) using occurrence data from all regions. Results are shown for three model sets: climate and vegetation variables only, climate and vegetation plus time since fire, and climate and vegetation plus multiple fire regime variables. Within each model set, points represent deviance explained (%) or area under the curve (AUC) of the model for a single species. Box plots highlight the median, upper quartile, and lower quartile of explanatory or predictive power.
climate and vegetation variables only, compared to models also including fire variables (Fig. 3c, d). However, the addition of fire regime variables did increase predictive discrimination for some individual species when compared with models including only rainfall, temperature, and vegetation type: Models including fire regime variables increased AUC values, by 0.2 or more, for 20 (26.0%) of 77 plants and 14 (40.0%) of 35 vertebrates (Appendix S4).

Fig. 4. Response of messmate *Eucalyptus obliqua* to predictor variables using occurrence data from all regions. Solid black lines are predictions of the probability of occurrence from a boosted regression tree model. Solid gray lines are bootstrapped 95% confidence intervals. The distribution of study sites across each continuous variable is shown on the x-axis in deciles.
**H2** The Fire regime hypothesis

**Prediction:** Multiple fire regime variables will outperform a single measure of fire.—Models including multiple measures of the fire regime (area burnt, fire type, inter-fire interval, and time since fire) had marginally higher explanatory power than models including time since fire (Fig. 3a, b). For plants, median deviance explained increased by 2.7 with the inclusion of multiple fire regime variables, a percentage increase of 8.4% (Fig. 3a). For vertebrates, median deviance explained increased by 1.1 with the inclusion of several...
Fig. 6. Influence of predictor variables on vascular plants (a) and vertebrates (b) from a model including climate, vegetation, and fire regime variables and using occurrence data from all regions. Within each predictor variable, points represent the response of a single species to a predictor variable. Deviance explained attributable to each variable (%) represents the influence of each variable from a boosted regression tree model including all variables. A higher amount represents a stronger effect of that variable. Box plots highlight the median, upper quartile, and lower quartile of species responses to each predictor variable.

Table 3. The five pairwise interactions between environmental variables with the highest median contributions to boosted regression tree models relating the distributions of vascular plants and vertebrates to fire, climate, and vegetation type.

| Vascular plants                  | Value | Vertebrates                  | Value |
|----------------------------------|-------|------------------------------|-------|
| Rainfall & temperature           | 6.04  | Rainfall & temperature       | 2.18  |
| Temperature & vegetation         | 4.76  | Inter-fire interval & rainfall| 0.92  |
| Rainfall & vegetation            | 2.89  | Inter-fire interval & temperature| 0.85  |
| Inter-fire interval & rainfall   | 1.43  | Temperature & time since fire| 0.66  |
| Temperature & time since fire    | 1.28  | Temperature & vegetation     | 0.54  |

Note: Each value is the median across all species in each taxonomic group and indicates the relative degree of departure from a purely additive effect, with a value of zero indicating that no interaction is present.
variables representing fire regimes, a percentage increase of 4.1% (Fig. 3b).

The direction, shape, and strength of fire responses varied markedly between species. For example, birds including eastern yellow robin, rose robin Petroica rosea, silvereye Zosterops lateralis, superb fairy-wren Malurus cyaneus, and white-browed scrubwren Sericornis frontalis showed higher probabilities of occurrence at longer inter-fire intervals or time since fire (Appendix S6), whereas the occurrence of the buff-rumped thornbill Acanthiza reguloides and flame robin Petroica phoenicea was associated with shorter fire intervals or recently burnt vegetation (Appendix S6). Plants including messmate and prickly currant bush Coprosma quadrida were associated with longer fire intervals. Hare's tail Echinopogon ovatus and small St. John's wort Hypericum gramineum were associated with shorter intervals (Appendices S5 and S6). The probability of occurrence of mammals

Fig. 7. Influence of interactions between environmental variables on species distributions. The interactions between a categorical variable, vegetation type, and a continuous variable, inter-fire interval, for (a) messmate Eucalyptus obliqua and (b) eastern yellow robin Eopsaltria australis. The interactions between two continuous variables, mean maximum temperature in January and time since fire, for (c) narrow-leaved wattle Acacia mucronata and (d) Australian king-parrot Alisterus scapularis. Lines are predictions of the probability of occurrence from a boosted regression tree model.
showed a more muted relationship with fire variables (Appendices S5 and S6). The bush rat *Rattus fuscipes* was the only mammal species that was correlated with fire, occurring slightly more frequently in areas with longer inter-fire intervals (Appendices S5 and S6).

The increase in model explanatory power with addition of multiple fire variables did not translate into an increase in median model predictive ability when compared with models including a single fire predictor (M2 vs. M3), when the data were summarized by taxonomic group (Fig. 3c, d). Models including fire regime variables (cf single fire predictor) increased AUC by small amounts (0.01–0.02) for 21 (27.3%) of 77 plant species and 15 (42.9%) of 35 vertebrates (Appendix S4).

(H3) The Taxonomic group hypothesis

*Prediction: Vertebrates and plants will respond differently to fire and environmental gradients.*—The strongest influences on the occurrence of both plants and vertebrates were rainfall and temperature gradients (Fig. 6). Of variables representing fire regimes, inter-fire interval was the strongest influence on species occurrence for plants and vertebrates, with time since fire also an important driver of some species (Fig. 6). Area burnt had a greater influence on the distribution of plants than vertebrates but graphical exploration of species responses to this measure indicated that, on its own, this variable had little influence on changes in probability of occurrence of plants or vertebrates (Appendix S6). Fire type (wildfire vs. prescribed fire) had a negligible effect on the distribution of plants and vertebrates (Fig. 6). The explanatory power of regression models was generally higher for plants (median deviance explained = 35.2%) than for vertebrates (28.0%; Fig. 3a, b).

Many species were closely associated with high rainfall, including silver wattle *A. dealbata*, common woodruff *Aspercula conferta*, Tasman flax lily *Dianella tasmanica*, blue gum *E. globulus*, flax-leaved rice flower *Pimelea linifolia*; and the birds, striated pardalote *Pardalotus striatus* and yellow-faced honeyeater *Lichenostomus chrysops*. Species more common in lower rainfall areas included small grass tree *Xanthorrhoea australis*, blue bottle daisy *Lagenophora stipitata*, and the birds superb fairy-wren *Malurus cyaneus* and white-eared honeyeater *Lichenostomus leucotis* (Appendices S5 and S6). Species associated with lower maximum temperature in January included mountain gray gum *E. cypellocarpa*, prickly currant bush, toothed clematis *Clematis aristata*, and the birds crescent honeyeater *Phylidonyris pyrrhopterus* and striated pardalote. Species more common in areas with higher maximum temperature included Australian blue-bell *Wahlenbergia stricta*, wattle mat rush *Lomandra filiformis*, common hovea *Hovea heterophylla*, and the birds rufous whistler *Pachycephala rufiventris* and spotted pardalote *Pardalotus punctatus*.

(H4) The Spatial-scale hypothesis

*Prediction: Fire will be a stronger influence at a smaller spatial extent.*—Fire regime variables improved model fit for plants and vertebrates, both across multiple regions and within a single focal region (the Otway Ranges; Figs. 3 and 8). For vertebrates, fire was a stronger relative influence within a focal region than at a spatial extent spanning multiple regions. Median deviance explained increased by 7.2 with the inclusion of variables representing fire regimes within the focal region (Fig. 8b), compared to an increase of 2.7 for the same measure across all regions (Fig. 3b). The relative influence of fire variables was similar at both spatial extents for vertebrates; inter-fire interval was influential, with some explanatory power attributable to time since fire and area burnt (compare explanatory power in Figs. 6 and 9).

For plants, the relative influence of inter-fire interval, compared to climatic gradients, was higher within the single focal region compared to the larger extent (compare Figs. 6a and 9a). However, this did not translate into an overall stronger influence of fire on plants at the smaller spatial extent. Median deviance explained increased by 3.2 with the addition of fire regime variables (to environmental variables) in the focal region, but there was a larger increase across multiple regions (5.5; Figs. 3a and 8a). This can be explained by a decline in the relative influence of other fire variables (time since fire, area burnt) within the focal region (Fig. 9).

In summary, fire correlated more strongly with vertebrates at the smaller spatial extent (Fig. 3b vs. Fig. 8b). For plants, there was a stronger relative influence of fire interval at smaller spatial extents, but fire did not have a greater effect on plants in the focal region than across multiple regions (Fig. 3a vs. Fig. 8a). For both taxonomic
groups, there was considerable variation between species in the spatial extent that produced the strongest responses to fire (Appendix S4: Tables S1–S4).

(H5) The Data-type hypothesis

Prediction: Fire responses will be sensitive to presence–absence data vs. abundance data.—We compared regression models using presence–absence...
data (M3, binomial models) or abundance data (M5, Poisson models) for 32 bird species (Fig. 10). Fire was a moderate driver of both bird occurrence and abundance; however, data type influenced the strength and shape of species–fire relationships (Fig. 10; Appendices S6 and S7). Time since fire was a stronger influence on bird species abundance than occurrence, while fire interval was a relatively stronger driver on bird species occurrence (Fig. 10). Several species that did not show a clear response to measures of the fire regime when presence–absence data were modeled showed a response to fire when abundance data were modeled: These included fan-tailed cuckoo *Cacomantis flabelliformis*, golden whistler *Pachycephala pectoralis*, black-faced cuckoo-shrike *Coracina novaehollandiae*, yellow-faced honeyeater, and white-naped honeyeater *Melithreptus lunatus*. Two species showed a clear response to fire only when using presence–absence data: buff-rumped thornbill and superb fairy-wren (Appendices S6 and S7).

Further exploration of models for individual bird species indicated that differences between data types could be explained, in part, by differences in species prevalence. For species occurring at relatively few sites (10–20% of sites), modeling the data as either presence–absence or abundance yielded similar species–environment relationships (Appendices S5–S7). For example, the distribution of the flame robin (present at 14% of sites) was associated with recently burnt vegetation in models using presence–absence and...
abundance data (Fig. 11a, b). For several species occurring at a large number of sites (>70% of sites), abundance data yielded stronger species–environment relationships. For example, the abundance of the yellow-faced honeyeater (present at 81% of sites) was higher with increasing time since fire, but probability of occurrence remained high across all time since fire ages (Fig. 11c, d).

(H6) The Habitat hypothesis
Prediction: Response to habitat structure will be correlated with response to fire.—We compared presence–absence models for 32 bird species that included either four predictor variables representing fire attributes or four predictor variables representing habitat structure (M3 vs. M6, with M3 re-modeled using data from only the two regions with field-measured habitat data). Models including habitat structure had a moderately higher model fit, and a small increase in predictive ability, than those using fire regime variables (Fig. 12). Tree diameter and leaf litter were stronger drivers of the occurrence of birds than other local habitat variables (Fig. 13). We used linear regression to quantify the relationship between deviance explained attributable to fire variables \( (y) \) and deviance explained attributable to habitat structure \( (x) \). There was a positive correlation between the effect of fire regime variables and the effect of habitat structure variables on birds \( (y = 0.56x + 9.12, R^2 = 15\% ; \) Fig. 14).
DISCUSSION

This study provides new insights into plant and animal distributions in fire-prone forests and how to model them. We have shown that interacting fire regimes and environmental gradients influence the distribution of birds, small mammals, and plants; multiple components of the fire regime drive the distributions of plants and vertebrates; inter-fire interval is a strong influence on both taxa in the forests of southeastern Australia (but with substantial variation between species); the spatial extent and type of response data influence the detection and strength of species–environment relationships in fire-prone forests; and vertebrate species with distributions closely linked to habitat structure are those most likely to show strong responses to fire regimes. We discuss these findings below in relation to the six major hypotheses tested.

Fig. 11. Responses of flame robin *Petroica phoenicea* (a, b) and yellow-faced honeyeater *Lichenostomus chrysops* (c, d) to time since fire using occurrence data or abundance from multiple regions (M4 and M5). Solid black lines are predictions of the probability of occurrence from a boosted regression tree model. Solid gray lines are bootstrapped 95% confidence intervals. The distribution of study sites across each continuous variable is shown on the x-axis in deciles.
Environmental gradients and fire regimes interact and drive species distributions

Foothill forests in southeastern Australia encompass broad-scale gradients of temperature, rainfall, and vegetation type. Along these gradients, fires create mosaics of vegetation with different disturbance histories relating to time since fire, inter-fire interval, fire type, and spatial pattern in the landscape. Our analysis supported the disturbance hypothesis: Models that included fire variables, in combination with other predictors, generally had higher explanatory power than models including only temperature, rainfall, and vegetation type. For example, models of the occurrence of messmate and eastern yellow robin were a better fit to empirical data when measures of fire regimes were included. Fires influence biota directly through mortality and emigration, and indirectly by changing resource availability and by biotic interactions. Immediate resource changes following fires in foothill forests that are likely to influence biota include an increase in open ground and reductions in leaf litter depth, coarse woody debris and, depending on flame height, percentage canopy cover (Aponte et al. 2014, Haslem et al. 2016), followed by a rapid increase in shrub cover and reduced open ground in subsequent years (Loyn 1997, 2012).

An increase in the explanatory power of models when including fire regime variables was also reported by Tucker et al. (2012): Fire variables, in addition to climate and soil variables, improved the fit of SDMs for Proteaceae species in the Cape Floristic Region of South Africa. Other work has shown that SDMs can capture the responses of birds and small mammals to fire regimes (Kelly et al. 2011, Regos et al. 2015), and recent work in our study area has demonstrated that fire influences the occurrence of birds (Robinson et al. 2014, Sitters et al. 2014a, Loyn and McNabb 2015) and, to a lesser extent, mammals (Chia et al. 2015, Swan et al. 2015) and plants (Cohn et al. 2015). However, predictive discrimination between a species’ presence and absence remains difficult

Fig. 12. Performance of regression models for birds using occurrence data from the Otway Ranges and Central Victoria (M6). Results are shown for two model sets: climate and vegetation plus fire regime variables and climate and vegetation plus habitat variables. Within each model set, points represent deviance explained (%) (a) or area under the curve (AUC) (b) of the model for a single species. Box plots highlight the median, upper quartile, and lower quartile of explanatory or predictive power.
In this study, improvements in model fit did not necessarily lead to better model predictive performance. Options for improving the predictive accuracy of models are discussed in more detail below (see What next for understanding and predicting species distributions in fire-prone forests?).

Although fire regimes influenced a suite of species, environmental gradients were a stronger influence for most birds, mammals, and plants.

Our data set encompassed wide gradients in mean maximum temperature in mid-summer (20–30°C) and mean rainfall in mid-winter (40–220 mm). Environmental gradients are important in dry eucalypt forests: Cork and Catling (1996) showed that broad-scale gradients in nutrients, associated with vegetation type, influenced mammal distributions, and in our study area, smaller-scale gradients in rainfall influence species richness of birds and plants (Sitters et al. 2014a, Cohn et al. 2015). Here, we built on previous work by showing that interactions between fire, climate, and vegetation type influence the distributions of plants and animals: Species can have different responses to fire along broad rainfall and temperature gradients (e.g., narrow-leaved wattle and Australian king-parrot).

Environmental gradients are important drivers in other forest ecosystems. Temperature and rainfall gradients affect plants and vertebrates directly by influencing growth, reproduction, and mortality (Austin 2002). In subalpine forests in the USA, Romme et al. (2016) found that gradients of substrate, temperature, and rainfall were consistently important drivers of plant distributions. Two
mechanisms could explain why species respond differentially to fire along such environmental gradients. As the composition of plant and animal communities changes along environmental gradients, so too will biotic interactions (e.g., competition, facilitation, predation). This can lead to differential post-fire vegetation dynamics, which in turn influence critical resources and the strength, direction, and shape of biotic responses to fire. Additionally, different environmental conditions along gradients of climate and geology will shape fuel moisture, flammability, and local fire regimes, with fires occurring at different intervals and spatial configurations across the gradient, thereby influencing plant and animal occurrence. Keeley et al. (2011) argued that plant and animal distributions in Mediterranean forests worldwide cannot be understood without considering an environmental template comprising climate, fire, and geology.

**Multiple characteristics of fire regimes influence the distribution of forest species**

Most studies model the effects of fire on plants and animals by using time since the most recent fire. There is growing evidence that to understand plant and animal distributions, the combined effects of multiple fires need to be quantified (Bradstock et al. 2005). Our results provide moderate support for the fire regime hypothesis: Models representing fire regimes generally fitted empirical data better than models using a single measure of fire, but there was substantial variation between species.

Inter-fire interval was the most important fire variable for plants and animals when data were pooled across each taxonomic group. Mean inter-fire intervals in our data set ranged from 1 to 72 yr. For plants, the occurrence of species such as messmate and prickly currant bush was associated with longer fire intervals. The interval between fires can influence plant populations in a variety of ways, such as by influencing the likelihood of mortality of standing plants and seeds; influencing seed production, seed release, germination, and establishment; and interrupting plant growth (Keith 1996). Fire intervals that are too short (fires occur before individual plants reach reproductive maturity) and too long (individual plants and their seeds reach senescence) will have a particularly strong influence on site occupancy (Morrison et al. 1995). The occurrence of some bird species, including eastern yellow robin, silvereye, and white-browed scrubwren, also increased with longer fire intervals. In *Eucalyptus* forests, recurrent fires influence important habitat elements for birds including the quantity of coarse woody debris (Aponte et al. 2014, Bassett et al. 2015), the density of live stems (Prior et al. 2016), and hollow-bearing stems (Lindenmayer et al. 2011).

Time since fire influenced vertebrates, particularly bird abundance, more than plants. Of species that responded to time since fire, most were associated with older fire ages (e.g., rose robin, golden whistler, yellow-faced honeyeater). The flame robin was one of few vertebrate species that peaked in probability of occurrence in early-successional vegetation. It has previously been reported at higher frequencies following several large fires in southeastern Australia (Loy, Lindenmayer et al. 2014, Loy and McNabb 2015). In foothill eucalypt forests, time since fire influences ground strata and canopy vegetation (Haslem et al. 2016) and thereby habitat resources for vertebrates. Although time since fire was important for a suite of species, most species showed either a muted or null response to this measure on its own (see also Sitters et al. 2014b, Chia et al. 2015, Swan et al. 2015). For plant species, graphical exploration showed that the probability of occurrence of few species was associated with time since fire when this variable was considered on its own. Time since fire had a stronger influence on plants via interactions with temperature and rainfall gradients.

The role of the amount of recently burnt vegetation was difficult to disentangle from that of time since fire because recently burnt sites often were associated with larger amounts of recently burnt vegetation in the surrounding landscape (within a 1 km radius). Graphical exploration of species responses to amount of recently burnt vegetation in the landscape, and interactions between this and other fire variables, showed no clear influence of area recently burnt on plants and vertebrates when multiple fire variables were included in the same model. Additional exploration of the data showed that this result was robust to the measurement of area burnt at smaller (500 m) and larger (2 km) radii.

Fire type, a surrogate for fire severity, had a relatively minor influence at the long temporal...
scales and large spatial scales of this study. An important feature of foothill forests is the ability of individuals of the dominant *Eucalyptus* species to survive fire events and regenerate from epi-cormic buds and basal shoots (Gill 2012). Rapid recovery of vegetation after both prescribed fire and wildfire is one reason that fire severity may not have affected plants, birds, and mammals in the present study (i.e., the influence of severity quickly dissipates). By contrast, in forests that recover more slowly from fire, or are dominated by obligate seeders, fire severity is often a more important influence on plants and animals (Smucker et al. 2005, Nappi and Drapeau 2011, Fontaine and Kennedy 2012, Bowman et al. 2014).

Although our surrogate for fire severity (wildfire vs. prescribed fire) was coarse, recent work in the study area using the same measure showed that wildfires affected canopy cover more severely than prescribed fires (Haslem et al. 2016). Previous work in this system showed an influence of fire severity on bird community composition in early post-fire succession (<3 yr) when finer-scale measurements of severity were used (Robinson et al. 2014). Severe fire (crown burns) had a stronger effect on bird communities than other fire severity classes (unburnt, crown scorch and ground burnt; Robinson et al. 2014). Better classification of sites in the future will provide further insight into the role of fire severity at large spatial extents.

**Relative influence of fire variables and environmental gradients is similar for plants and vertebrates, but species matter**

We found consistency in the relative importance of fire variables, and climate gradients, when summarized by taxa. Rainfall and temperature gradients were the most important influences on both taxonomic groups. Among fire variables, inter-fire interval was the strongest influence on plants and animals. We correctly predicted that plants would be sensitive to inter-fire intervals because they generally need to recover on site from stored seed-banks or vegetative buds. However, the greater influence of inter-fire interval vs. time since fire on the occurrence of birds was surprising. Although the most recent fire is a strong influence on habitat structure in foothill forests (Haslem et al. 2016), the importance of inter-fire interval suggests that recurrent fires produce some different ecological conditions, such as altered species composition and vegetation structure, rather than simply resetting the successional clock. This is also the case in other forest ecosystems. For example, Fontaine et al. (2009) showed that the response of birds to repeat fires was different to their response to single fires in conifer-dominated forests in the USA. Overall, however, results suggest the species we examined generally are relatively resilient to the effects of fire regimes within the range of variation encompassed by the data.

For each taxonomic group, there was considerable variation between species, in the variables to which they responded, and the direction and shape of those responses. For example, a suite of species was closely associated with high rainfall (e.g., silver wattle, Tasman flax lily, yellow-faced honeyeater), whereas others were associated with low rainfall (e.g., small grass tree, white-eared honeyeater). We expect that species traits and life history characteristics will be associated with climate and fire gradients (Guisan et al. 2007, Kley et al. 2011). In turn, these traits can influence fire regimes across large areas (Rogers et al. 2015). A productive area for future research would be to compare species–fire responses among species that represent different growth strategies (e.g., resprouters vs. obligate seeders) and feeding guilds (e.g., nectarivores vs. insectivores).

**Sampling design influences the detection and strength of species–fire relationships**

Sampling design influences the inferences drawn from SDMs (Guisan et al. 2007, Merow et al. 2014). One important influence is spatial scale. We predicted a stronger influence of fire on species distributions at a smaller spatial extent, encompassing a single region, than at a larger spatial extent that encompasses more marked gradients in temperature and rainfall. There was mixed support for this hypothesis. Spatial extent modified the influence of fire and climate gradients for both plants and vertebrates, but only for vertebrates was it in the direction expected.

For vertebrates, fire was a stronger relative influence within a focal region than at a spatial extent spanning multiple regions. The relative influence of the different fire variables was similar at both spatial extents; inter-fire interval and time since fire were influential for vertebrates. For plants, there was a stronger relative influence of
inter-fire interval at a smaller spatial extent, but overall, fire variables did not have a greater effect on plants in the focal region than across multiple regions. For both taxonomic groups, there was considerable variation between species in the spatial extent that resulted in the strongest responses to fire. Our comparison of two spatial extents for plants and vertebrates suggests that responses to scale are species and data specific. We recommend that fire scientists ask two key questions when modeling fire history data: (1) “Does the spatial extent of the data encompass the range of fire regimes and environmental variables of interest?” and (2) “Is the spatial extent of the observed data appropriate for the species and management decisions that the data will inform?” An important topic for future work is how spatial grain, the spatial properties of the data such as plot or grid cell size (Elith and Leathwick 2009), influences models of species–fire relationships.

To test the data-type hypothesis, we compared SDMs built using either occurrence or abundance data for a subset of bird species. The relative influence of fire regime and climate gradients was sensitive to data type, but there was consistency in responses across data types where species’ occurrence and abundance data were correlated (for species at low prevalence). The additional information associated with abundance data can lead to new insights, including identifying fire responses that would not be possible if presence–absence data were examined in isolation. For example, it was only by modeling abundance data that fire responses of fan-tailed cuckoo, golden whistler, black-faced cuckoo-shrike, yellow-faced honeyeater, and white-naped honeyeater were observed. Nonetheless, two species showed a clear response to fires only when using presence–absence data: buff-rumped thornbill and superb fairy-wren. Thus, although occurrence data are useful for environmental decision making (Guisan et al. 2013), it can be insensitive to demographic changes in plant and animal populations (Bradstock et al. 1997, Thuiller et al. 2014). Effective detection of species responses to fire is critical for managing fire. Forest scientists and managers faced with the task of deciding which data to use will need to assess the trade-offs of different types of data (see Joseph et al. 2006). Abundance data contain more information but presence–absence data are easier to collect.

Species closely associated with habitat structure are those mostly likely to be influenced by fires

The habitat hypothesis predicted that vertebrate species with distributions strongly linked to direct measures of habitat structure will also be those most influenced by fire. We identified a positive correlation between the effect of habitat structure and the effect of fire regimes on birds.

Models including habitat structure had a moderately higher model fit and predictive ability than those using fire regime variables. Tree diameter and leaf litter were particularly strong drivers of the occurrence of birds when data were assessed across 32 species. For example, rose robin was more likely to occur at sites with larger trees and greater canopy cover (Appendix S5: Table S6). It is likely that these habitat changes, along with associated resources provided by large eucalypts and Acacia spp., drive this species’ positive association with time since fire. This general result is consistent with recent studies showing that habitat variables, especially when measured on-site, can provide greater accuracy and predictive power than relying only on proximate fire variables (Di Stefano et al. 2011, Nimmo et al. 2014, Sitters et al. 2014b, Swan et al. 2015). It is also consistent with forest studies that have interpreted species–fire responses in relation to changes in habitat structure. For example, in both spruce- and mixed conifer-dominated forests, black-backed woodpeckers Picoides arcticus are associated with recently burnt vegetation because they forage on deadwood in these landscapes (Nappi and Drapeau 2011, Hutto et al. 2016). Our results extend previous work by directly modeling the association between species responses to multiple aspects of the fire regime and to multiple habitat elements. Our work suggests that modeled habitat associations will better predict vertebrate responses to fire than qualitative measures (e.g., descriptions of species’ habitat requirements from field guides).

What next for understanding and predicting species distributions in fire-prone forests?

There are several ways in which our modeling approach of incorporating fire regime variables together with environmental variables in SDMs could be extended. Continued improvement in mapping fire intensity and fire severity (Leonard et al. 2014) means that as new fires are mapped,
more detailed information on these and other measures will be gained. This new information, coupled with targeted biodiversity surveys, could then be incorporated into SDMs. We focused here on four measures of fire regimes that we hypothesized would have the strongest influence on plants and vertebrates. Other aspects of the fire regime may also be modeled, including fire season and additional measures of spatial configuration. Another improvement would be to incorporate into SDMs predictor variables that represent additional ecological processes. This could include measures of dynamic processes, linked to the timing of biodiversity surveys, such as antecedent rainfall, predation, and competition. Finer-scale mapping of key habitat features, such as large trees, is also likely to improve predictive accuracy of models for vertebrates.

Our approach has several caveats. We modeled the distributions of 112 species but modeling of additional rare species was restricted by low numbers of records. Combining this approach with alternative SDM techniques that use presence-only data, such as maximum entropy models (MaxEnt: Merow et al. 2013), will allow more species to be modeled in the future. We expect that stronger responses to fire regimes may be detected for rarer species with potentially narrower tolerances of fire regime attributes and smaller range sizes (e.g., serotinous obligate seeders). We employed correlative species distribution modeling because it is one of the most useful methods of estimating plant and animal responses to environmental gradients (Elith and Leathwick 2009, Guisan et al. 2013). An important caveat of this correlative approach is that modeled distributions do not necessarily reflect responses to fire, per se, but to environmental factors that correlate with fire occurrence (and mean inter-fire interval, for example). A useful next step would be to directly measure and model species’ population dynamics. This could include detailed field studies of species’ population dynamics and reproductive success (e.g., Wiebe 2014), and building process-based models for selected species. Population dynamics could be modeled for a large number of plant and vertebrate species by coupling SDMs with stochastic population models that incorporate information on species’ vital rates (Keith et al. 2008).

New insights for biodiversity conservation in forest landscapes

Managing fire for biodiversity conservation is becoming increasingly important in forests worldwide (Gill et al. 2013, Moritz 2014, Hessburg et al. 2016). Problems that are common to fire ecologists and forest managers include a limited knowledge of how multiple taxonomic groups within a given ecosystem respond to fire regimes, how interactions between fire and environmental gradients influence biodiversity, and how conclusions about fire responses are affected by sampling design. Our results from the foothill forest ecosystem in southeastern Australia usefully illustrate how to address such knowledge gaps: These extensive forests have high biodiversity, flammable vegetation, and are experiencing growing use of prescribed burning.

First, our results show that understanding fire regimes, not just fire events, is important for managing plants and vertebrates in forests. The particular components of the regime that will be most important will vary among ecosystems and among taxa (Keeley et al. 2009). In the foothill forest ecosystem, the interval between recurrent fires was an important influence on biodiversity, with long-unburnt areas being particularly important for birds (some of which reached higher probabilities of occurrence or abundance when fire intervals were long). Nevertheless, not all species respond in this way and several species of birds were more likely to occur in recently burnt vegetation and at sites with short fire intervals. We recommend that forest managers go beyond simple measures of fire events and set biodiversity objectives for plants and animals based on fire regimes. This concept is starting to be accepted by fire scientists and managers, but to achieve such sophisticated management requires a commitment to systematic recording and mapping of fire attributes over time (including historical reconstruction) so that the regime arising from multiple fires can be reliably quantified across space.

Second, although common patterns can be recognized, differences between species in response to fire regimes are important. For example, fire regimes that benefit species that are common after short fire intervals will need to be balanced with the requirements of species more likely to occur following longer fire intervals. Fire intervals that
occur within the primarily juvenile period of plants can threaten some species, particularly obligate seeders (Bowman et al. 2014, Fairman et al. 2016). Foothill forests are dominated by trees that rapidly recover from wildfires and, on the whole, our results show that common plant species in foothill forests are likely to be tolerant of wide variation in fire regimes. However, although many plants and animals in these forests are resilient to variation in current fire regimes, the potential for large wildfires at shorter intervals, associated with a warmer and more extreme climate, warrants attention from both scientists and land managers (Mok et al. 2012, Enright et al. 2015).

Third, fire regimes in forests need to be understood and managed in the context of environmental gradients, even within a single forest type. Fire, climate, and geology form the environmental template that drives plant and animal distributions. Variation along environmental gradients (e.g., vegetation) influences management options and the effectiveness of fire suppression and prescribed burning (Price et al. 2015). Species distribution models could be used to map the occurrence and abundance of species along environmental gradients, as well as the factors that control fire regimes (Parisien and Moritz 2009), and these outputs used to inform when and where to conduct planned burning and fire suppression in forest landscapes.

Fourth, it is necessary to complement management of fire regimes with understanding of the key elements of habitat structure that influence resource availability for plants and animals. Species relationships with fire regimes may be easier to translate into management plans, but this approach risks missing key habitat components on which taxa depend. Knowledge of species’ relationships with structural habitat components, and of how fire affects those components (e.g., Haslem et al. 2011), will ensure a more nuanced approach to fire management, particularly to the use of prescribed burning to achieve ecological outcomes.

Finally, our results suggest the need to carefully assess the type of biodiversity data used to determine conservation objectives. Models of species occurrence will be sufficient in some cases, but some fire management decisions will require more detailed data on population abundance, demographics, and persistence. In particular, there is a need for data and analytical approaches that can provide guidance on the fire responses of rarer or more cryptic species, often those of greatest conservation concern. Most studies, including this one, draw conclusions based on the responses of relatively common species, and may overlook rare species that may be vulnerable to fire.

In conclusion, we have demonstrated that there are general patterns in biotic responses to fire and environmental gradients, but landscape management must continue to carefully consider species, scale, and the quality of biodiversity data to achieve biodiversity conservation in fire-prone forests.

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