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Canopy cover mediates the effects of a decadal increase in time since fire on arboreal birds

Michael J.M. Franklin [a,*], Richard E. Major [b], Ross A. Bradstock [a]

[a] Centre for Environmental Risk Management of Bushfires, University of Wollongong, Northfields Avenue, Wollongong 2522, Australia
[b] Australian Museum Research Institute, Australian Museum, 1 William Street, Sydney 2010, Australia

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ABSTRACT

Wildfires impact animal populations directly, and indirectly through alteration of forest habitats. Recovery of populations and habitat structure occurs over time since fire, but knowledge is lacking about the relative importance of these processes as drivers of the occurrence of birds in fire-prone forests. We aimed to determine the extent to which canopy cover mediates the effects of a decadal increase in time since fire on the richness and occurrence of canopy bird species. We established sites at either short (5 years) or mid-range (16 years) time since fire in montane dry sclerophyll forests of south-eastern Australia. Canopy cover estimates were derived from airborne LiDAR data. Birds were surveyed using acoustic recorders, with the resulting data analyzed using Bayesian mediation models to partition direct (population processes) and indirect (canopy cover) effects of time since fire on canopy birds. The predictive accuracy of models representing partial mediation (direct and indirect effects) and complete mediation (indirect effects only) were then compared. The direct effects of wildfire on birds were minimal between five and 16 years since fire. Instead, indirect effects prevailed, with species richness and the occurrence of most canopy species increasing as canopy cover regenerated over time since fire. As these forests transition from short to mid-range time since fire, ongoing increases in canopy cover are of primary importance for birds. We recommend an approach to managing avian diversity that incorporates canopy cover in fire planning to optimize the retention of dwindling amounts of older forest under climate change.

1. Introduction

Time since fire has long been used effectively in fire ecology research (e.g. Specht et al., 1958), as a simple and convenient predictor for a range of ecological processes that occur and interact at variable rates post-fire (Connell et al., 2017). Animal responses to time since fire can vary between habitats (Watson et al., 2012a; Rainsford et al., 2021), over environmental gradients (Kelly et al., 2017), and depending on the state of fire-affected landscapes (Nimmo et al., 2019). Consequently, there is strong potential to increase understanding of animal responses to fire by isolating and separately examining processes that affect animals and their habitat. For example, changes in animal occupancy and diversity over time since fire can be attributed to variable rates of regeneration of vegetation, and/or population recovery (Whelan et al., 2002). To better support management for avian diversity in fire-prone forests, the different effects of time since fire must be disentangled to enable the specific driver/s of avian responses to be identified. The need for such insights is heightened because of increasing wildfire activity in global forested landscapes under climate change (Westerling et al., 2006; Kelly et al., 2020).

Animals are directly impacted by wildfire, and the effects on population processes persist for variable periods following fire, depending on context (Whelan et al., 2002). Animal mortality and emigration can occur during the fire, or at some point in the post-fire period, such as when a temporary refuge from fire proves inadequate for ongoing habitation. Avian population declines following fire can be immediate or delayed, and subsequent increases can be rapid or slow, while the populations of other species may irrupt at some point after fire to peak and then rapidly decline (Whelan et al., 2002). Post-fire recovery of species populations depends on breeding success and/or immigration (Lindenmayer et al., 2016). Altered avian population dynamics are known to persist well into the first (Baker et al., 1997), and second (Benshemesh et al., 2020), decades following fire. Longitudinal research has found that populations of multiple species can continue to decline through time after fire owing to reduced annual productivity, despite ongoing regeneration of vegetation (Brooker, 1998). These population

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* Corresponding author.
E-mail address: mjmf080@uowmail.edu.au (M.J.M. Franklin).

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dynamics arose from greatly reduced breeding activity in the first season after the fire, then sustained higher mortality rates of breeding adults, leading to greater proportions of younger, less-successful breeding birds (Russell and Rowley, 1993; Brooker, 1998). Diminished post-fire bird populations may also be subject to reduced genetic diversity and inbreeding, that potentially contribute to declines in population viability (Brown et al., 2013). The contribution of immigration to bird population re-establishment in burnt areas is influenced by the proximity of source populations in unburnt refugia within or external to the boundary of the wildfire extent, and the dispersal capacity of species (Clarke, 2008). Furthermore, the timing of patch reoccupation is also influenced by the extent to which the burnt landscape matrix is conducive to animal movements that enable recolonization (Nimmo et al., 2019). For example, it can take longer for bird species to reoccupy large areas that were homogeneously burnt at high-severity (Steel et al., 2022), partly because immigration may be delayed if source habitats are distant (Brooker, 1998; Watson et al., 2012b).

Structural attributes of forests regenerate over time since fire (Haslem et al., 2016) and particular bird species respond to the indirect effects of time since fire on habitat structure (Sitters et al., 2014; Kelly et al., 2017). Vegetation structure is associated with a range of resources used by birds, including food (Law and Chidel, 2008), nest hollows (Salmona et al., 2018), and cover for protection from predators (Doherty et al., 2022). The structure of resprouting eucalypt forest canopies regenerate over decadal scales following wildfire (Catling et al., 2001; Haslem et al., 2016; Price and Gordon, 2016), although the post-fire rate of increase in canopy cover is spatially variable, because environmental factors in addition to time since fire influence cover development (Jucker et al., 2018). Habitat structure variables are thus often better predictors than time since fire in models of avian (Sitters et al., 2014) and mammal (Swan et al., 2015) occurrence. Complex canopy structures contribute to increased diversity of canopy animals, because of the greater variety and extent of niche spaces (Ishii et al., 2004). In the present study, we focus on canopy cover as an important component of canopy structure for birds. For example, bird species with frugivorous or generalist foraging traits have been shown to respond positively at the functional group level to canopy cover in dry eucalypt forest (Sitters et al., 2016). Species-level responses to canopy structure have also been recorded (Barton et al., 2014), which can vary widely within bird assemblages according to the particular requirements of constituent species (Knaggs et al., 2020). Avian assemblage composition varied over 30 years following fire in boreal forest, reflecting changes in the occurrence of species with requirements for suitable levels of habitat structure that were only available for particular periods in the regenerating forest (Haney et al., 2008). However, the relationships between time since fire, forest canopy cover and canopy-foraging birds (hereafter, canopy birds) remain poorly understood.

A range of analytical approaches incorporating hypothesized causal relationships in the system under investigation have been applied to study the effects of fire on plants and animals. These approaches have demonstrated capacity to disentangle some of the complex responses inherent to the problem. Relationships among fire, habitat and fauna have also been investigated in causal frameworks using spatial simulation models (Bradstock et al., 2005), moderated-mediation analyses (Lindenmayer et al., 2016), and Bayesian Networks (Hradsky et al., 2017). Structural equation modelling has been used to investigate causal influences of fire history, local conditions, and position in the landscape on alien plant dominance (Keeley et al., 2005) and plant species richness (Grace and Keeley, 2006) in North American shrubland. The form of a structural equation model reflects the causal pathways hypothesized in a corresponding conceptual diagram (Grace et al., 2009). Mediation analysis is a form of structural equation modelling that enables partitioning of the effects of a causal antecedent variable on a consequent variable into direct effects, and indirect effects that influence the response through a third mediating variable (Grace et al., 2009; Hayes, 2018). Bayesian mediation analysis (Yuan and MacKinnon, 2009) can be conducted using a single model with recently developed statistical tools (Bürkner, 2017). Research conducted in dry eucalypt forests of south-eastern Australia found positive relationships between the occurrence of several species and increasing time since fire (Franklin et al., 2022). In this study, we investigate the direct (population processes) and indirect (via canopy cover) effects of time since fire on canopy birds in these assemblages using Bayesian mediation models. This study employs a space-for-time substitution design using two levels of time since fire: five and 16 years since fire.

We address the importance of changes in canopy cover over time since fire for birds by asking: to what extent does canopy cover mediate the effects of a decadal increase in time since fire on the richness and occurrence of canopy bird species, in montane dry sclerophyll forests? We expect some level of positive avian response to increases in canopy cover through time since fire, but know very little about the relative influence or direction of the direct effects of time since fire on population processes. Dry sclerophyll forests with shrubby understories (Keith and Simpson, 2012) are widespread in south-eastern Australia and have evolved with fire (Gill, 1981), however wildfire activity is increasing in these montane and lowland communities (Fairman et al., 2015, Canadell et al., 2021). Many of the dominant eucalypts in these communities can resprout rapidly from epicormic or lignotuber buds following fire (Keith, 2004), but frequent fire can limit these regenerative mechanisms (Fairman et al., 2015). A fire return interval of 7–30 years over at least 50 % of the distribution of this forest type has been recommended for fire management, to enable community persistence given predominant regenerative/reproductive mechanisms and time to maturity of the flora (Bradstock and Kenny, 2003). Over recent decades, the proportion of these forests with a fire-age of ten years or less has increased in high conservation value landscapes of the region (Fig. 1). This represents a potentially extensive reduction in canopy structure and complexity (Haslem et al., 2016), which has implications for birds of the region that occur in this forest strata.

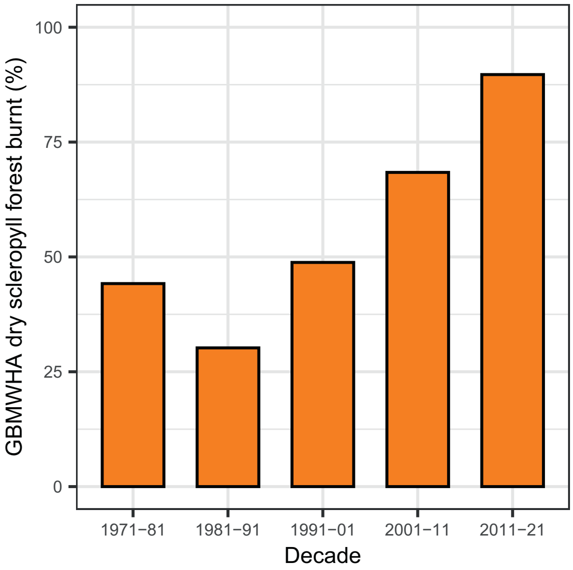

Fig. 1. The percentage of the distribution of dry sclerophyll forest (shrubby sub-formation, Keith and Simpson, 2012) burnt in each decade from 1971 to 2021 (Office of Environment and Heritage NSW, 2017) in the one million-ha Greater Blue Mountains World Heritage Area (GBMWHA), south-eastern Australia. This forest type covers approximately 70 % of the World Heritage Area. Overlaps in the decadal year ranges reflect the start and ends of austral fire seasons, which span from spring at the end of one year into and through the summer of the following year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. Study area

The study was conducted in montane dry sclerophyll forests of the Greater Blue Mountains World Heritage Area. Study sites were located in or adjacent to the Blue Mountains, Gardens of Stone, and Wollemi National Parks. The 46 sites were circular with a radius of 325 m, covering ~33 ha each. These sites were a subset of sites established for a multifaceted study of the fire ecology of birds in the region (Franklin et al., 2021a, Franklin et al., 2022). Sites were located along an 80-km latitudinal gradient from 33°41′S 150°26′E in the south to 32°59′S 150°22′E in the north, at a similar elevation on the highest parts of this section of eastern Australia's Great Dividing Range. A rainfall gradient corresponded to the latitudinal gradient, with annual mean rainfall of up to 1340 mm over sites in the south of the study area, reducing to 62 % of that amount in the north (Xu and Hutchinson, 2011). Bird species distributions can be influenced by rainfall gradients over dry eucalypt forests (Kelly et al., 2017), so we accounted for potential avian responses to rainfall and other environmental change across the study area by including latitude as a covariate in modelling. Furthermore, previous multivariate analysis of bird occurrence in the region showed that bird assemblages were structured strongly by latitude (Franklin et al., 2022). The tree canopies of montane dry sclerophyll forests are dominated by species of *Eucalyptus*, including *E. sclerophylla*, *E. sieberi* and *E. piperita*, which occur with typically diverse understories of shrubs in low-nutrient, sandy soils over sandstone geology. These fire-prone forests are extensive in the region and many of the eucalypts have the capacity to resprout following fire, however the flora have tolerance limits in response to fire frequency, intensity and season, hence fire regimes shape the composition of these plant communities (Keith, 2004).

2.2. Bird surveys

We surveyed birds using acoustic recorders (SM4, Wildlife Acoustics, Maynard, MA, USA) in the late spring/early summer of 2018. Recorders were programmed to record daily for 100 min commencing at dawn, then fastened to a small tree at 2-m above the ground, at the center of the sites. All recorder settings and microphone checks were as per Franklin et al. (2020). The set of eight recorders were collected after at least two clear-weather days had passed, then redeployed, with this process repeated until all sites had been surveyed. Recordings were collected as .wav files and manually processed at the desktop by the first author. This involved listening to calls while viewing them in a spectrogram of frequency/time in Kaleidoscope (Wildlife Acoustics), and recording species detections (Franklin et al., 2020; Franklin et al., 2021b). A site survey involved the processing of a total of 200 min of recordings, which was made up of 100 min of post-dawn recordings on each of two days. This represents a level of sampling effort that is well above average (Watson, 2017). This method has also been shown to be more likely than an established observer-based method to detect many of the same species, given equal sampling time (Franklin et al., 2020). Furthermore, with this method there is no systematic pattern of bias in species detectability that could be attributed to increased bird call attenuation in older, more structurally complex dry sclerophyll forest (Franklin et al., 2022).

2.3. LiDAR-derived canopy cover estimates

Canopy cover estimates for the sites were derived through a process of converting Light Detection and Ranging (LiDAR) point clouds to raster layers of point counts for 0.5 m vertical strata, aggregating these layers vertically to capture the vertical span of canopies, then calculating canopy cover. Source data were multiple 2 × 2-km LiDAR point cloud tiles for the study area produced by the Spatial Services division of the NSW Department of Finance, Services and Innovation, using an airborne scanner, and obtained via the Elvis Elevation and Depth data portal https://elevation.fsdf.org.au/. Data processing was conducted in R (R Core Team, 2022) using the CERMBlidar (Bedward, 2022) and terra (Hijmans, 2022) packages. All LiDAR data used in this study were obtained from flights over the study area in 2017 and 2018. These data were partly processed, including removal of flight line overlap and normalization of point heights, and stored as part of a regional set in a database on a University of Wollongong server as raster layers (10-m cells) of point counts at 0.5-m height intervals. For this study, we aggregated the 10-m cell point counts to 20-m cell counts to match the spatial resolution of fire history data. The 20-m cell counts for 0.5 m strata were then summed over the vertical range in which tree canopies occurred in the sites. To establish the overall vertical range within which tree canopies occurred, maximum canopy heights derived from LiDAR data and a framework for classification of Australian vegetation based on structural form (Specht, 1970) were used. Inspection of distributions of maximum canopy heights across sites revealed that some tree canopies were present between five and 10 m (low forest), most occurred between 10 and 30 m (forest), and some were >30 m above ground (tall forest, Specht, 1970). Consequently, we defined the canopy as all vegetation >5 m above ground (Haslem et al., 2016; Price and Gordon, 2016). Counts of points in the canopy strata were then converted to proportional cover estimates by taking the ratio of the number of canopy points to the total number of points for each 20-m cell. The median value among ~830 20-m cells/site represented the proportion of canopy cover over each site in modelling.

2.4. Fire history variables

Time since fire for each site was determined using the NSW Fire History spatial data set (Office of Environment and Heritage 2017), and expressed in relation to the year of bird surveys (2018). Sites were located entirely within the boundaries of the footprints of multiple large fires (Wood, 2022) that occurred during either 2002 or 2013, that were spatially interspersed across the study area. Accordingly, time since fire (TSF) was prepared as a binary variable for modelling, with 0 representing 5 years since fire and 1 assigned to 16 years since fire. While not a focus of this study, the severity of the last fire across each site was included as a covariate in modelling because there was potential for it to influence canopy cover (Haslem et al., 2016; Karna et al., 2020) and/or bird occurrence (Robinson et al., 2014). The severity of the last fire (SEV) was expressed as the proportion of each site that had been burnt by high-severity fire, such that the tree canopy had been scorched or incinerated. Gridded fire severity layers for the 2002 and 2013 fires were used to obtain the data required to calculate this proportion (Hammill et al., 2010; Hammill Stone, 2014). These data were based on NDVI (Normalized Difference Vegetation Index) ratios from corresponding pairs of pre- and post-fire Landsat images.

2.5. Data analysis

To establish the extent to which canopy cover mediated the effects of time since fire for each of the ten avian response variables (Table 1), we conducted mediation analyses (Hayes, 2018, Fig. 2) using Bayesian models (Kurz, 2021). Our approach was to run pairs of models representing partial and complete mediation (henceforth partial and complete mediation models, respectively) for each bird response. We then formally compared the estimated out-of-sample (i.e., given new data) predictive accuracy of paired models using leave-one-out cross-validation (LOO, Vehtari et al., 2017). In this context, estimates of predictive accuracy are generated through an iterative process that involves withholding data points from model runs and evaluating model prediction in relation to the left-out data (McElreath, 2020). The relative predictive accuracy of paired models was assessed on the basis of the difference in expected log pointwise predictive density (ELPD) values obtained via LOO (Vehtari et al., 2017). The magnitude of the standard error of the ELPD difference estimate is an important consideration in

Table 1
Comparison of the predictive accuracy of complete and partial mediation models using leave-one-out cross-validation. The model form with zero for the difference in expected log predictive density (ELPD) has the better predictive accuracy. Negative values (and their standard errors) for the ELPD difference are provided under the alternative model. Results for canopy-foraging species recorded in <20 % and >80 % of sites are not shown. See Appendix A for species scientific names, and Appendix B for model coefficients.

Response	ELPD difference	
	Complete mediation model	Partial mediation model
Total no. species	0	−0.8 (0.8)
No. canopy-foraging species	0	−1.2 (0.2)
Brown-headed Honeyeater	−1.1 (1.8)	0
Channel-billed Cuckoo	0	−1.6 (0.3)
Cicadabird	0	−0.8 (0.8)
Gang-gang Cockatoo	0	−0.4 (1.6)
Leaden Flycatcher	0	−1.2 (0.5)
Mistletoebird	0	−1.2 (0.4)
Olive-backed Oriole	0	−0.6 (1.0)
Striated Thornbill	−1.0 (1.7)	0

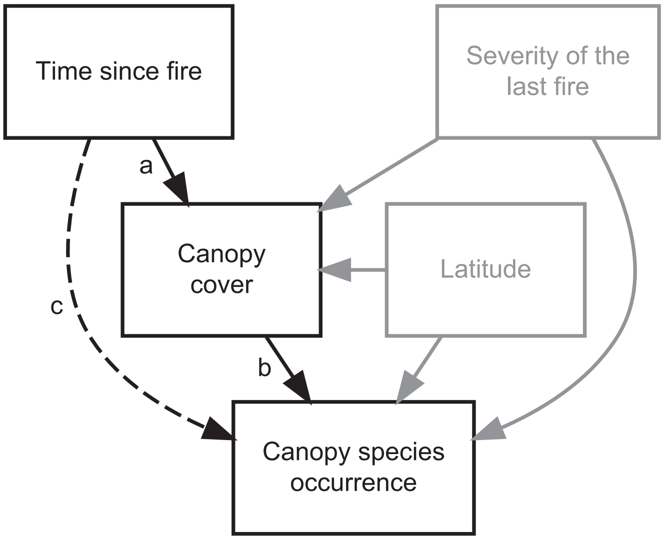

Fig. 2. Graphical model of hypothesized causal relationships among fire history, site attributes and canopy birds in montane dry sclerophyll forest. Two statistical models were built and compared to investigate the extent to which canopy cover mediated the effect of time since fire on canopy birds. The partial mediation model partitioned the indirect effect of time since fire that passes through canopy cover (path ab), and the direct effect (path c), within the total effect (path ab + path c). The complete mediation model did not include the c pathway, with all of the effect of time since fire on canopy birds mediated by canopy cover. The severity of the last fire and latitude had the potential to influence canopy cover and/or canopy birds, so they were included in both models as background covariates.

model comparison, although ELDP differences less than four are small (Vehtari et al., 2017, Sivula et al., 2020, Thompson et al., 2022). Absolute values for difference estimates that are less than their corresponding standard errors indicate no clear difference in predictive accuracy (Sebald et al., 2019; Cheng et al., 2022).

Predictions were then obtained from the model form with the best predictive performance. If predictive accuracy did not differ, predictions were taken from the more parsimonious complete mediation model (Choi et al., 2020). Paired complete and partial mediation models differed in one way only: the addition of time since fire as a direct predictor of the bird response in the partial mediation model (Fig. 2). Comparison of the relative influence of indirect and direct effects of time since fire using the partial mediation model (path ab vs path c in Fig. 2) was planned for cases where the partial model had better predictive accuracy than the corresponding complete model.

All forms of mediation model (Eqs. (1)–(4)) consisted of two submodels that were fitted as bivariate models using the brms package (Bürkner, 2017) in R (R Core Team, 2022). Canopy cover was the mediator in all mediation models, and the submodel predicting canopy cover did not vary among mediation model forms. However the distributions of bird response variables differed between counts of species (Eqs. (1)–(2)) and individual species occurrence (Eqs. (3)–(4)).

Complete mediation models for the total number of species and the number of canopy-foraging species were of the form:

$$\begin{aligned}&\mathrm{logit(CPY)} = \beta_1 + \beta_2\mathrm{LAT} + \beta_3\mathrm{SEV} + \beta_4\mathrm{TSF},\\ &log(\text{Number of sp.}) = \beta_5 + \beta_6\mathrm{LAT} + \beta_7\mathrm{SEV} + \beta_8\mathrm{CPY}\end{aligned} \tag{1}$$

where CPY, the proportion of canopy cover over the site, was treated as being drawn from a Beta distribution (Douma and Weedon, 2019) with a mean value related to an intercept, latitude (LAT), severity of the last fire (SEV) and time since fire (TSF) via a logit link function. The total number of species and the number of canopy species were count variables that were modelled using the Conway-Maxwell Poisson distribution, since exploratory analyses indicated that the count values were under-dispersed (Guikema and Goffelt, 2008; Lynch et al., 2014). The number of total/canopy species was related to an intercept, latitude, severity of the last fire and canopy cover via a log link function.

Partial mediation models for the total number of species and the number of canopy foraging species were the same as their corresponding complete mediation model, except for the addition of time since fire (TSF) as a predictor for the number of species (Eq. (2)).

$$\begin{aligned}&\mathrm{logit(CPY)} = \beta_1 + \beta_2\mathrm{LAT} + \beta_3\mathrm{SEV} + \beta_4\mathrm{TSF},\\ &log(\text{Number of sp.}) = \beta_5 + \beta_6\mathrm{LAT} + \beta_7\mathrm{SEV} + \beta_8\mathrm{CPY} + \beta_9\mathrm{TSF}\end{aligned} \tag{2}$$

Complete mediation models for the occurrence of eight canopy species were structured similarly to complete mediation models for the number of species (Eq. (1)), except that species occurrence was modelled using a Bernoulli distribution with a logit link:

$$\begin{aligned}&\mathrm{logit(CPY)} = \beta_1 + \beta_2\mathrm{LAT} + \beta_3\mathrm{SEV} + \beta_4\mathrm{TSF},\\ &\mathrm{logit(Sp.occurrence)} = \beta_5 + \beta_6\mathrm{LAT} + \beta_7\mathrm{SEV} + \beta_8\mathrm{CPY}\end{aligned} \tag{3}$$

Partial mediation models for individual canopy species had the same structure as their complete mediation model counterpart (Eq. (3)), but included time since fire (TSF) as an additional predictor of species occurrence (Eq. (4)).

$$\begin{aligned}&\mathrm{logit(CPY)} = \beta_1 + \beta_2\mathrm{LAT} + \beta_3\mathrm{SEV} + \beta_4\mathrm{TSF},\\ &\mathrm{logit(Sp.occurrence)} = \beta_5 + \beta_6\mathrm{LAT} + \beta_7\mathrm{SEV} + \beta_8\mathrm{CPY} + \beta_9\mathrm{TSF}\end{aligned} \tag{4}$$

Results for individual canopy species are presented if they were detected in >20 % and <80 % of sites (Sitters et al., 2014). The lower limit was chosen to ensure that there were adequate detections to support inferences given the species occurrence submodel structures, while the upper limit was applied to allow for sufficient contrast in species habitat preferences. The increased model complexity that would have arisen through modelling species detectability was not warranted, because earlier work using this bird data found considerable uncertainty around detection probability estimates, and there were no systematic patterns of detection bias associated with fire history (Franklin et al., 2022). With this approach, there is some potential that unmeasured bias could influence results. Therefore, we frame our inferences around avian responses to the direct and indirect effects of time since fire in terms of species detected by recorders using a robust effort protocol.

In all models, we used Normal (0,10) priors for the intercept, background covariates and predictor variables of interest. The brms default gamma(0.01, 0.01) priors were used for phi, the precision parameter of the beta distribution used to model the proportion of canopy cover over each site. This gamma prior was also used for the shape parameter of the

Conway-Maxwell Poisson distribution used to model under-dispersed counts of total and canopy-foraging species. Models were fitted using Markov Chain Monte Carlo (MCMC) in Stan (Stan Development Team, 2022) through the brms package (Bürkner, 2017) in R (R Core Team, 2022). For all models, four MCMC chains were run to obtain 1000 samples per chain, having discarded 1000 warmup samples and thinned at a rate of 10. The samples from each chain were then consolidated into a single matrix of 4000 samples, from which predictions were generated. Model convergence was evaluated and confirmed using the Gelman-Rubin statistic (Gelman and Rubin, 1992), and by checking the number of effective samples for all parameters. Pairs of complete and partial mediation models for each bird response were compared using leave-one-out cross-validation (LOO) with the loo package (Vehtari et al., 2022) implemented via brms (Bürkner, 2017) in R (R Core Team, 2022). In cases where Pareto k values exceeded 0.7 in the initial comparison, we applied moment matching (Paananen et al., 2021) and repeated the comparison. Model-based Bayesian R^2 estimates were generated using brms (Bürkner, 2017) to provide indications of the proportion of variance explained with new data, rather than for the purposes of comparing paired complete and partial mediation models (Gelman et al., 2019).

3. Results

A total of 74 diurnal bird species were detected in the study, including 17 that forage primarily in the canopy, 23 that forage in the understorey or on the ground, one species that forages in the air and on the ground, and 33 species that forage throughout the forest strata (Appendix A). Paired complete and partial mediation models were fitted and formally compared for the total number of species, the number of canopy species and the eight individual canopy species that were recorded in >20 % and <80 % of sites (Table 1).

The complete mediation model (time since fire affects birds exclusively through canopy cover) was estimated to have slightly better predictive accuracy than the partial mediation model (as per complete model plus direct effects of time since fire on birds) for most avian responses. These included the number of species, number of canopy-foraging species, and the occurrence of six of the eight focal canopy-foraging species (Table 1). However, for several of the comparisons, standard errors of the differences were large relative to the estimates, suggesting that differences in the predictive performance between those particular model pairs may have been slight, or potentially non-existent (Sivula et al., 2020).

Partial mediation models for the Brown-headed Honeyeater (*Melithreptus brevirostris*) and Straited Thornbill (*Acanthiza lineata*) were estimated to have slightly better predictive accuracy than their corresponding complete mediation models. However, in both cases, the standard error was much greater than the estimate of the difference in predictive accuracy between model forms (Table 1). Because prediction of bird species numbers or occurrence was not clearly improved by fitting time since fire as a direct predictor of bird responses in partial mediation models, we generated predictions from the more parsimonious, complete mediation models (Figs. 3-4). Across all mediation models, canopy cover submodels were estimated to have capacity to account for a mean of 57 % of variation given new data, with variable R^2 estimates that were mostly in the moderate to low ranges evident among bird responses (Fig. 3).

Canopy cover increased from a median of 31 % at five years since fire to 46 % at 16 years since fire (Fig. 4a). There were strong positive relationships between canopy cover and the total number of detected species (Fig. 4b), and the number of canopy-foraging species (Fig. 4c). Over the range of median canopy cover values among the sites, the total number of species increased from 23.1 to 35.0 species on average, and the number of canopy foraging species doubled: increasing from 4.6 to 9.2 species (Fig. 4b-c).

The probability of occurrence of most of the individual canopy-foraging species detected in >20 % and <80 % of sites increased with

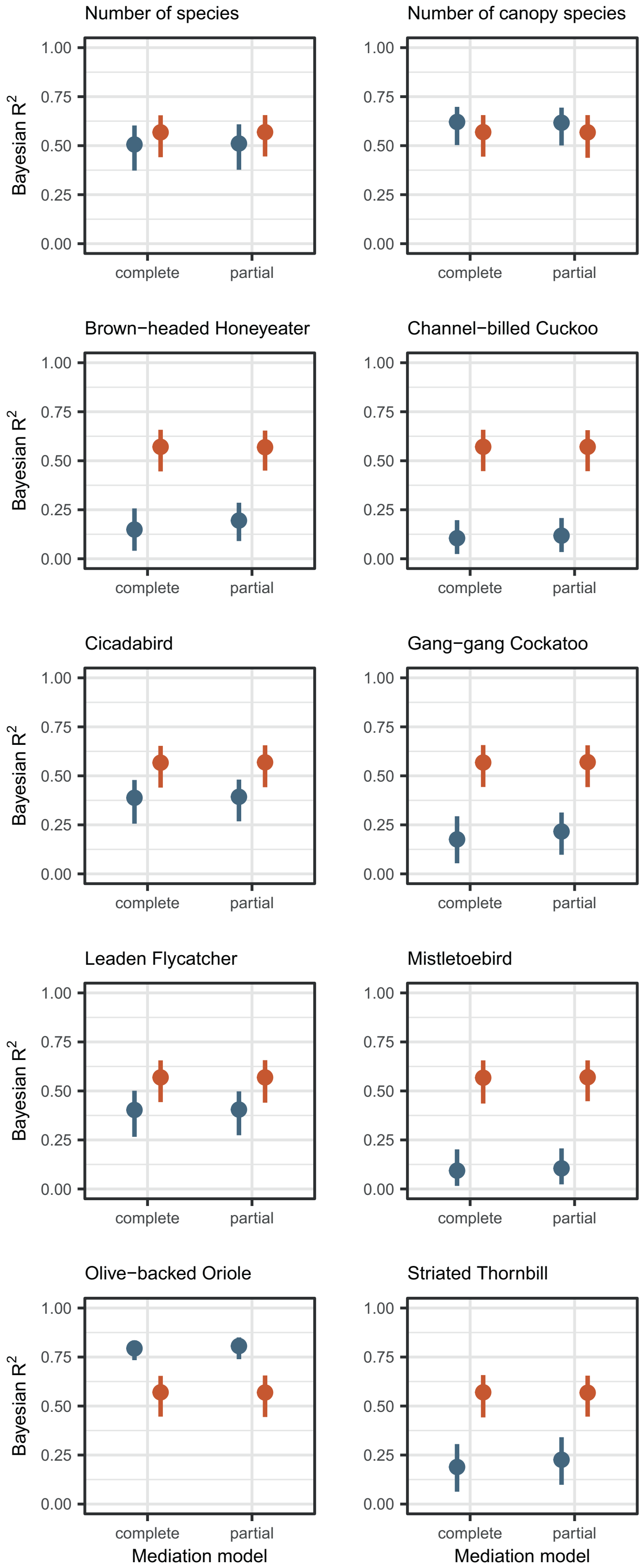

Fig. 3. Means and central 90 % of distributions of Bayesian R^2 estimates for complete and partial mediation models for each bird response. Bar colors indicate R^2 values for the bird response submodel (charcoal) and the canopy cover response submodel (copper) within each mediation model (Eqs. (1)–(4)).

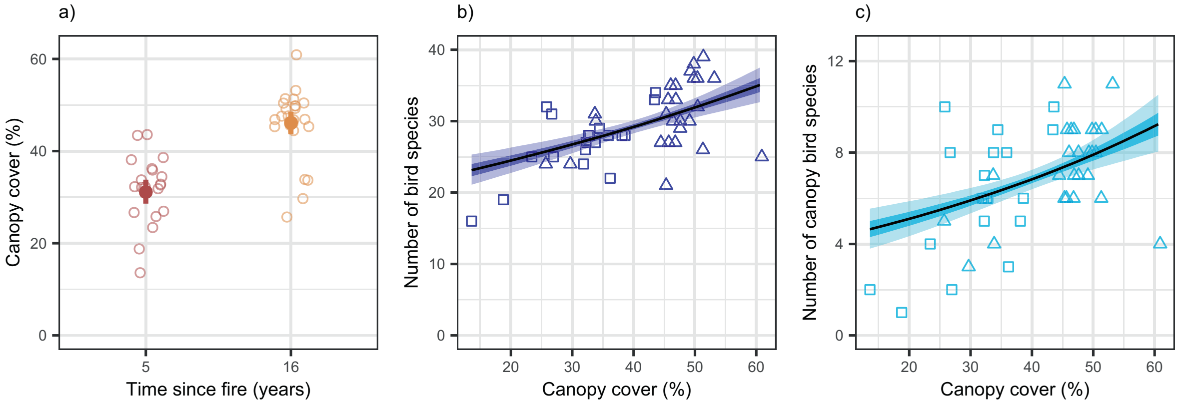

Fig. 4. Predicted and observed (open shapes) relationships between a) canopy cover and time since fire, b) the total number of detected bird species and canopy cover, and c) the number of canopy-foraging bird species and canopy cover. In a), bars around medians (solid circles) represent the central 90 % of distributions of Bayesian complete mediation model predictions. In b) and c), open squares and triangles indicate sites at five and 16 years since fire respectively, and lines are medians with bands representing the central 50 % and 90 % of distributions of Bayesian complete mediation model predictions.

greater canopy cover (Fig. 5). The strongest positive response among these eight species was shown by the Striated Thornbill, which increased in probability of occurrence by ~63 % over the range of canopy cover. No canopy species exhibited a clear negative response to canopy cover (Fig. 5). Of these species, only the Striated Thornbill was exclusively sedentary, while the remainder were relatively mobile, undertaking nomadic and/or migratory movements at the individual or species levels (Garnett et al., 2015).

4. Discussion

The effects of a decadal increase in time since fire were strongly mediated through canopy cover for the total number of species, number of canopy species, and occurrence of individual canopy species. The responses of canopy species to canopy cover were mostly positive, and there were no negative responses to increased cover. The inclusion of time since fire as a direct predictor of any of the bird responses did not increase the predictive accuracy of mediation models. These results suggest that the direct effects of an increase in time since fire from five to 16 years on these species were slight or negligible. Most of the canopy species investigated were nomads and/or migrants, which are relatively mobile in fire-prone landscapes of the region (Franklin et al., 2021a). As such, these species may have had the capacity to avoid substantial direct population disturbance through emigration to refugia, and to recolonize burnt habitat fairly rapidly once in a suitable state. Furthermore, as canopy species, some of these species may have avoided direct mortality by moving to canopies where fire was only burning, or had recently burnt, the understory, thereby obtaining vertical refuge in forest burnt at low severity (Robinson et al., 2014).

4.1. Time since fire and canopy cover

In the montane dry sclerophyll forests of the region, canopy cover increased substantially from five to 16 years after fire. Similar positive trends have been recorded for the total canopy (Haslem et al., 2016) or mid-canopy (Sitters et al., 2014) in other eucalypt forests of south-

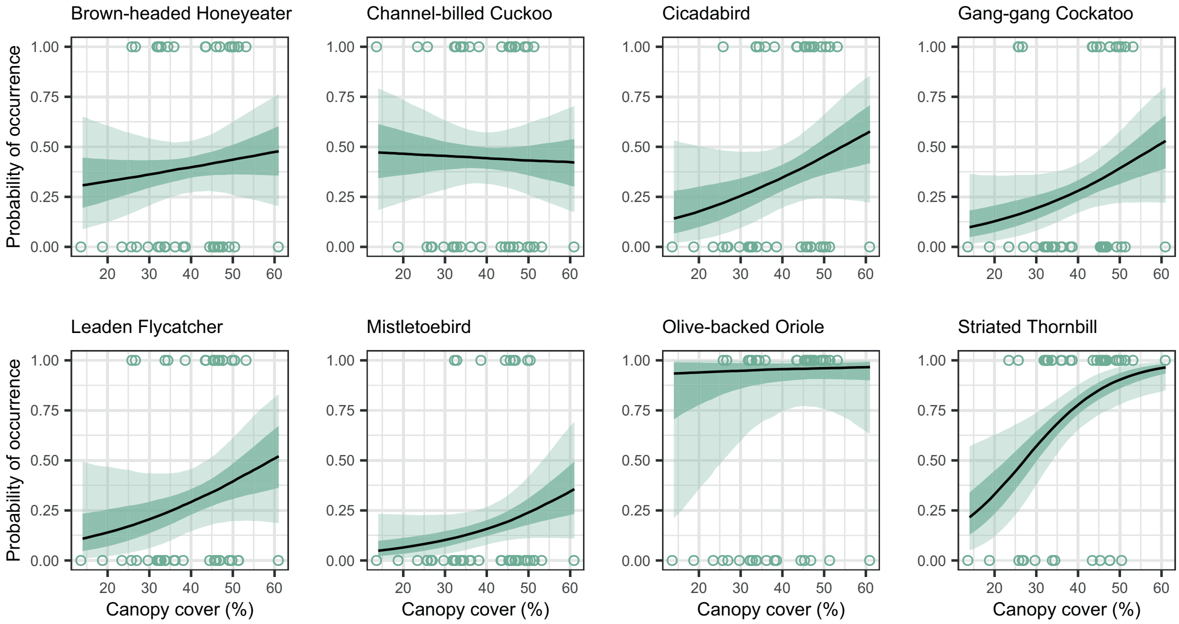

Fig. 5. The probability of occurrence of canopy-foraging species in relation to canopy cover in montane dry sclerophyll forest. Open circles indicate the observed presence/absence (1/0) of species in sites. Lines are medians with bands representing the central 50 % and 90 % of distributions of Bayesian complete mediation model predictions. Results for canopy-foraging species recorded in <20 % and >80 % of sites are not shown. See Appendix A for species scientific names.

eastern Australia. However, regeneration of the canopy may not have been complete at 16 years since fire, so the habitat was potentially suboptimal for animals that require the most complex canopy structures possible in these communities. The longest time since fire used in the present study was 16 years, so it is likely that further small increases in canopy cover would accrue after this time, given results obtained in similar systems. In other dry sclerophyll forests of the region, upper canopy cover (>15 m) continued to gradually increase beyond 16 years since fire, while lower canopy cover (4–15 m) increased up to ~30 years post-fire then began to decline (Price and Gordon, 2016). Ongoing post-fire increases in canopy cover were predicted for temperate dry eucalypt forests at higher latitudes, albeit at a reduced rate after 16 years since fire (Haslem et al., 2016).

4.2. Canopy cover and bird occurrence

The responses of most canopy species to canopy cover were positive, and there were no negative responses. Similarly, in a range of coastal vegetation communities of the region, only positive responses to percentage cover of the midstory were recorded among the species for which both direct and indirect effects of time since fire could be distinguished (Lindenmayer et al., 2016). In varied eucalypt forests at higher latitudes, mostly positive links were established among time since fire, vegetation structure and bird species occurrence, but vegetation structure had better predictive capacity than time since fire for most species (Sitters et al., 2014). Of the eight canopy species that were recorded in >20 % and <80 % of sites in the present study, six species consumed fruit, seeds, or both as part of their diet. Four of these granivorous/frugivorous species responded positively to canopy cover, which is consistent with increasing availability of fruit and seeds as the canopy regenerates over time since fire.

In forests around the world, positive avian responses to time since fire have been linked to increasing levels of resources required by birds, while negative responses have been shown to correspond with a post-fire peak then subsequent decline in necessary resources. Avian responses to fire and vegetation structure were investigated in unburnt, burnt and twice-burnt Amazonian forests three years following fire (Hidasi-Neto et al., 2012). Fire history had less influence on the structure of these tropical avian assemblages at the functional trait level than structural attributes of the vegetation, including canopy cover. In mixed-evergreen forests of North America, bird density was greater 17–18 years after fire than at two years after fire, which was attributed to vegetation recovery following fire, but community composition was different owing to the preferences of species for habitat at different successional stages (Fontaine et al., 2009). In conifer forests of western North America, the Black-backed Woodpecker (*Picoides arcticus*) peaks in abundance in the years shortly after fire, then declines, following the post-fire trend in availability of standing dead trees, on which they forage, nest and roost (Tingley et al., 2018).

4.3. Management implications

Birds perform essential ecosystem functions, including regulation of canopy herbivory by insects, pollination, and seed dispersal (Sekercioglu, 2006), so a management focus on maintaining the long-term viability of their populations is necessary. There is potential for increased effectiveness of fire management of fauna in fire-prone forests if their structural habitat preferences are included and considered as complementary to species fire responses (Kelly et al., 2017). Our findings are supportive of forest fire management for avian diversity that includes consideration of canopy cover and time since fire (Sitters et al., 2014). Because there is not a perfect correspondence between canopy cover and time since fire, spatial data for these attributes could be overlaid to refine habitat suitability assessment in the management of natural landscapes for fire-sensitive bird species. Recent processing tools and readily available LiDAR or satellite data products can be used to infer structural attributes of forests (e.g. Queinnec et al., 2021), which increases options for achieving biodiversity objectives in fire planning and management.

4.3.1. Threatened species case study

Wildfires burnt vast areas of forest during the 2019–2020 fire season in south-eastern Australia, which directly impacted populations of many bird species and substantially reduced the amount of habitat within their distributions (Legge et al., 2021). One such species was the Gang-gang Cockatoo (*Callocephalon fimbriatum*), which had been declining in numbers over preceding decades (Cameron et al., 2021). Because their population had been in decline for some time leading up to the recent extensive loss of habitat, in 2022 the Gang-gang Cockatoo was listed as Endangered under the federal Environmental Protection and Biodiversity Conservation Act 1999. We found that the probability of occurrence of the gang-gang Cockatoo increased from 0.13 where canopy cover was 20 %, to 0.52 where cover was 60 %. This result suggests that the management of montane dry sclerophyll forests to support this species would include provision of substantial areas of forest with denser canopy, and consequently older forest, given the positive relationship between canopy cover and time since fire in these communities.

4.3.2. Further research

This study has increased understanding about the relationships among time since fire, canopy cover and canopy bird occurrence, thereby providing options for the application of a range of analytical approaches in subsequent investigations of the topic. We recognize that simpler model structures than those we employed can be used to predict canopy cover using time since fire, or bird species richness/occurrence using canopy cover. However it was more appropriate to use the components of our mediation models to generate predictions, given that they were used to make inferences about direct and indirect effects of time since fire. Subsequent work could measure a range of resources used by birds that may be associated with canopy cover, then map causal relationships in structural equation models of greater complexity to potentially elucidate increasingly nuanced avian responses to fire regimes. Recent remote sensing methods accompanied by ground validation provide options to increase specificity of fire management for canopy birds by enabling estimates of avian resources associated with canopy cover, such as nectar from flowering trees, to be obtained (Law and Chidel, 2008; Dixon et al., 2021). Our methodological approach is applicable in locations with no LiDAR data archives, although traditional field methods or satellite data would need to be used to estimate vegetation cover. For logistical reasons the shortest time since fire included in this study was five years, but the direct effects of fire on birds are presumably stronger in the years immediately following a wildfire. An investigation of the response of canopy birds and canopy cover commencing shortly after fire would fill out our understanding of the relative strength of direct and indirect effects of time since fire.

5. Conclusion

The total number of species, the number of canopy species, and the occurrence of individual canopy species were positively influenced by the effects of a decadal increase in time since that were mediated through forest canopy cover. There was little, if any, direct effect of increasing time since fire from five to 16 years on these birds. This suggests that for these canopy species, at five years since wildfire the forest is accessible to colonizers, and numbers of breeding individuals are adequate to support further population recovery, given ongoing increases in canopy cover. The increased canopy cover at longer time since fire is clearly of vital importance for avian diversity in montane dry sclerophyll forest. Fire management of these forests is faced with the challenge of reconciling the requirements of much of the avifauna for older habitat, with increasing proportions of recently burnt forest, driven by escalating fire activity under climate change.

CRediT authorship contribution statement

Michael J.M. Franklin: Conceptualization, Investigation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Richard E. Major:** Conceptualization, Writing – review & editing. **Ross A. Bradstock:** Conceptualization, Writing – review & editing.

Declaration of competing interest

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

Data availability

The R code for statistical models and input data is available online at https://github.com/mfrnkln/birdstimesincefire1.

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Supplementary data

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