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

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Abstract

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

50 **Keywords:**

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

53

54 **Introduction**

55 Forest ecosystems worldwide are facing substantial changes in fire regimes (Halofsky et al.
56 2020, Nolan et al. 2020). Severe wildfires are becoming larger and more frequent in many
57 regions, including tropical forests in Brazil (Lizundia-Loiola et al. 2020), dry forests in
58 western U.S.A (Keeley and Syphard 2019), Mediterranean forests in southern Europe (Vitolo
59 et al. 2019) and temperate forests in eastern Australia (Nolan et al. 2020). For example, from
60 2019 to early 2020 in Australia, wildfires burned >12 million ha of forests, destroying >2000
61 homes and putting multiple populations of animals and plants at risk of extinction (Boer et al.
62 2020, Lindenmayer and Taylor 2020, Ward et al. 2020). Much of the area burnt was
63 temperate dry forest (Victorian Government Department of Environment, Land, Water and
64 Planning 2020). Thus, even in dry forests with a long history of fire, there is a need to
65 mitigate the threat of very large and severe wildfires, not only to human life and property but
66 also to prevent detrimental consequences for biodiversity (Ward et al. 2020).

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

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

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

98 Forest plants, in dry forests have evolved a range of traits (e.g. post-fire resprouting, fire-cued
99 germination) that allow populations to persist in fire-prone environments (Pausas et al. 2004).
100 Classifications based on plant functional traits, such as time to maturity and method of
101 persistence, provide a useful framework to understand and predict species' responses to fire
102 (Bradstock and Kenny 2003, Keith et al. 2007, Shedley et al. 2018). Studies in temperate dry
103 forests have shown that the influence of fire on understorey plant species varies between taxa
104 based on species' life-history traits (Penman et al. 2008, Prior et al. 2016) and within taxa
105 based on vegetation type (Foster et al. 2018). Plant regeneration from seed is often associated
106 with species declining over time following fire and vulnerability to increased fire frequency,
107 while post-fire resprouting is associated with species that increase post-fire (Penman et al.
108 2009, Enright et al. 2014). There are exceptions, however, and resprouting species may also
109 be vulnerable to increased fire frequency (Fairman et al. 2017).

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

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

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

132 **Methods**

133 Study location, climate and vegetation

134 The study took place in temperate dry forests, known as ‘foothill forests’, in Victoria, south-
135 eastern Australia (Fig. 1). The generic term ‘foothill forests’ refers to temperate eucalypt
136 forests that cover ~ 75 000 km² in Victoria and occur on the lower- to mid-slopes of the Great
137 Dividing Range. Foothill forests include distinct ecological communities that differ in
138 floristic composition, driven by topographic and climatic variation, ranging from wetter
139 forest types in gullies to drier forests on slopes and ridges. The study area covered ~ 320 km²
140 of the Big River State Forest in the Highlands Southern Fall bioregion (-37.516 S, 146.042 E)
141 where the climate is temperate with a mean annual rainfall of ~ 850 mm. The highest
142 monthly rainfall occurs in winter (August) and the hottest month is February (mean daily
143 maximum ~ 29°C) (Lake Eildon, station no. 083023; <http://www.bom.gov.au/>). The
144 topography is mountainous, often with steep slopes and densely vegetated gullies. Elevation
145 ranges between ~ 450 and 950 m above sea-level.

146 To avoid topographic differences in vegetation composition and structure (i.e. between
147 gullies and ridges), all sites were located within a single vegetation community, ‘herb-rich
148 foothills forest’ (Victorian Government Department of Sustainability and Environment 2004).
149 The canopy of foothill forests reaches heights of 25 m and is often accompanied by a
150 secondary tree layer of *Acacia* spp. The dominant canopy species were messmate stringybark
151 *Eucalyptus obliqua*, mountain grey-gum *E. cypellocarpa*, broad-leaved peppermint *E. dives*

152 and narrow-leaved peppermint *E. radiata*. All four *Eucalyptus* species resprout epicormically
153 following fire. Smaller trees and shrubs constitute the understorey, including blackwood
154 *Acacia melanoxylon*, silver wattle *A. dealbata*, prickly currant-bush *Coprosma quadrifida*,
155 common cassinia *Cassinia aculeata*, and ferns such as austral bracken *Pteridium esculentum*.
156 The ground layer consists of a rich cover of herbs.

157 Fire regime and fire mapping

158 In foothill forests, wildfires typically occur in summer (Dec – Feb). Large wildfires (> 10 000
159 ha) have occurred in the wider foothill forests region in 1939, 1962, 1983, 2003, 2005, 2006,
160 2009, 2014, 2019 and 2020 (Department of Environment, Land, Water and Planning 2015,
161 Nolan et al. 2020). Mapped prescribed fires in the study area date from the 1970s to the year
162 of surveys (Fig. 1). Prescribed fires at the study sites post-1990 were conducted in autumn,
163 but the season of prescribed fires prior to 1990 is not documented. Prescribed fires are ignited
164 from the ground by field officers and generally are smaller than wildfires: the mean fire size
165 at the study sites was 658 ha (range 44 – 1738 ha).

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

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

182 Study design

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

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

202 *Birds*

203 At each site, a 2-ha plot centered over the 250 m transect was established, and surveyed for
204 diurnal birds by a single experienced observer (FR) a total of six times: three times during the
205 austral autumn/winter and three times during spring/summer, between 2017 and 2018.

206 Surveys were conducted in clear weather within four hours of dawn, except for two winter
207 survey rounds during which sites were each surveyed once in the morning and once in the
208 afternoon. Each survey was for a 20-min period and all individuals either heard or seen were
209 identified to species level and recorded. The perpendicular distance (m) to each detection
210 from the transect line was estimated and used to test for differences in detectability between
211 sites (see Appendix S1). Nocturnal birds, raptors and swifts were recorded but excluded from
212 analyses as these groups are not reliably detected by the survey methods.

213 *Understorey plants*

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

225 Data analyses

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

239 *Individual species*

240 For individual species that occurred at $\geq 25\%$ (8/29) of sites last burnt by prescribed fire, we
241 used generalised additive models (GAMs) (Wood 2017) to predict changes in relative
242 abundance (birds) and relative cover (plants) with time since fire. For bird species we used
243 reporting rate, the number of survey rounds (out of 6) during which a species was detected.
244 Variation in reporting rate of species between sites is often a result of variation in the

245 abundance of individuals and so is a reliable proxy for relative abundance (Royle and Nichols
246 2003). For plant species, we used the mean projected foliar cover at sites.

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

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

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

274 *Functional groups*

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

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

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

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

302 *Species diversity and community composition*

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

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

320 Results

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

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

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

338 *Individual species*

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

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

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

365 *Functional groups*

366 The relative abundance or cover of several functional groups, for both birds and plants, was
367 related to time since prescribed fire (Fig. 5). Upper-midstorey foraging birds increased in
368 relative abundance linearly (incline response) with time since fire ($P < 0.05$, deviance
369 explained = 16%, Fig. 5a), lower-midstorey foragers showed a plateau response ($P < 0.001$,
370 deviance explained = 44%, Fig. 5a) and species with low diet versatility ($P < 0.05$, deviance

371 explained = 23%, Fig. 5b) and open-nesting species ($P < 0.05$, deviance explained = 18%,
372 Fig. 5c) both increased linearly (incline response) with time since fire. Facultative-
373 resprouting shrubs ($P < 0.05$, deviance explained = 30%, Fig. 5d) and obligate-seeding shrubs
374 ($P < 0.05$, deviance explained = 25%, Fig. 5f) both showed a bell-shaped response to time
375 since fire.

376 Relative abundance of one bird functional group, lower-midstorey foragers, differed
377 significantly from that of long-unburnt vegetation in the youngest age class ($P < 0.01$, Fig.
378 6a). Relative cover of facultative-resprouting shrubs was greater 3 – 10 years after prescribed
379 fire than in the first three years following prescribed fire ($P < 0.001$, Fig 6c) and that of
380 obligate-resprouting shrubs was significantly greater in long-unburnt vegetation than in the
381 first three years following prescribed fire ($P < 0.05$, Fig 6c).

382 *Species richness and community composition*

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

385 NMDS ordination analyses showed some evidence of successional trajectories of bird and
386 plant communities after prescribed fire (Fig. 8). This influence was stronger for birds ($P =$
387 0.01, PerMANOVA) than for plants ($P = 0.081$). Bird community composition showed most
388 dissimilarity between AC1 (0 - 3 years post-fire) and long-unburnt vegetation (Fig. 8a). The
389 main point of differentiation for plant communities was between AC2 (3 - 10 years post-fire)
390 and long-unburnt (LU) vegetation (Fig. 8c).

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

400 **Discussion**

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

411 *Bird community response to prescribed fire*

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

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

427 *Plant community response to prescribed fire*

428 While some 20% of individual plant species showed a significant response to time since fire,
429 a particularly clear functional effect was a ‘bell-shaped’ response by obligate-seeding shrubs
430 (e.g. mountain hickory wattle *Acacia obliquinerva*) to time since fire. This fire response is
431 typical in short-lived, woody species of Fabaceae and Asteraceae: propagule production
432 reaches a peak at some point in the post-fire succession after which plant cover decreases as

433 adults lose vigor (Keith 2012). For these obligate-seeding species, fire typically kills the
434 mature plant and regeneration occurs from seed stored either in canopy or soil seed banks
435 (Pausas and Keeley 2014). Obligate seeding in forest plants is associated with sensitivity to
436 frequent and infrequent fire (Bradstock and Kenny 2003). Prescribed fire applied at
437 appropriate intervals (~15 – 30 years) would allow enough time for fire-sensitive plants to
438 reach maturity and then stimulate regeneration.

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

448 *A resilient ecosystem?*

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

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

460 Second, the size of a fire and therefore the distance to the burn edge can also influence the
461 post-fire composition of communities (Uys et al. 2006), depending on species' mobility and
462 the rate of post-fire recolonization of sensitive species (Santos et al. 2009). Species'
463 responses to fire may have been influenced by the size (area) of the fire and the species'
464 recolonization ability, with those species with greater dispersal ability able to recolonize

465 more rapidly post-fire. In addition, the interval between multiple fires can have different
466 effects on components of forest vegetation (Penman et al. 2008, Kelly et al. 2017), leading to
467 differential legacy effects from past disturbance. Together, variation in these fire
468 characteristics likely contributed to the relatively high level of variation in the
469 cover/abundance of species within and between sites for a given age-class, and therefore to
470 the muted responses to time since prescribed fire.

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

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

491 The apparent resilience of birds and plants to prescribed fire in this study may also be
492 influenced by several aspects of the study design, including sample size along the post-fire
493 chronosequence, the absence of less-common or rare species for which sample sizes were too
494 low to model that are sensitive to fire, and there may also be species sensitive to fire that have
495 already been greatly reduced in abundance or locally extirpated. However, by pooling species
496 into functional groups, we were able to detect broader effects of prescribed fire on bird and

497 plant communities. These trends were supported by the vectors for influential species in
498 ordination analyses. Given the environmental and ecological characteristics of foothill forests
499 and the patchy nature of prescribed fires, we consider these findings to be a realistic
500 representation for this ecosystem.

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

513 *Implications for management*

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

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

529 ways, and our recommendations relate to the types of prescribed burning that we measured in
530 the present study.

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

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

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

553 *Concluding remarks*

554 By using a comprehensive approach involving analyses of the responses of individual
555 species, functional groups and communities, we identified longer-term effects of prescribed
556 fire on bird and plant communities in a structurally resilient forest ecosystem. In particular,
557 analyses of functional groups gave important insights into the response to time since fire of
558 several groups; notably, understorey-foraging birds, facultative-resprouting shrubs and
559 obligate-seeding plants. These patterns were less evident from analyses of single species or
560 community-wide diversity measures. Overall, bird and plant communities showed relatively

561 high resilience to prescribed fire across a chronosequence of 36 years, which can be
562 attributed to the patchiness of prescribed fires, the prevalence of plant regeneration through
563 resprouting, and the effect of topographic complexity on burn patterns. Application of these
564 findings requires a landscape-scale approach sensitive to forest topography, that will ensure
565 the provision of suitable post-fire habitat for all taxa, both those resilient to fire and those that
566 benefit from longer-unburnt forest vegetation.

567

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575

576 **Supporting Information**

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

578

579 **Data Availability**

580 Data are available in the Dryad Digital Repository (Rainsford 2020):

581 <https://doi.org/10.5061/dryad.ftdz08rd>

582

583 **Literature Cited**

584 Bassett, M., S. W. J. Leonard, E. K. Chia, M. F. Clarke, and A. F. Bennett. 2017. Interacting
585 effects of fire severity, time since fire and topography on vegetation structure after
586 wildfire. *Forest Ecology and Management* 396:26-34.

587 Boer, M. M., V. Resco de Dios, and R. A. Bradstock. 2020. Unprecedented burn area of
588 Australian mega forest fires. *Nature Climate Change* 10:171-172.

- 589 Bradstock, R. A., and B. J. Kenny. 2003. An application of plant functional types to fire
590 management in a conservation reserve in southeastern Australia. *Journal of*
591 *Vegetation Science* 14:345-354.
- 592 Cheal, D. 2010. Growth stages and tolerable fire intervals for victoria's native vegetation data
593 sets. Victorian Government Department of Sustainability and Environment,
594 Melbourne.
- 595 Cheal, D. 2011. Plant vital attributes for ecological fire management. Victorian Government
596 Department of Sustainability and Environment.
- 597 Collins, L. 2020. Eucalypt forests dominated by epicormic resprouters are resilient to
598 repeated canopy fires. *Journal of Ecology* 108:310-324.
- 599 Davis, R. A., T. S. Doherty, E. J. B. van Etten, J. Q. Radford, F. Holmes, C. Knuckey, and B.
600 J. Davis. 2016. Conserving long unburnt vegetation is important for bird species,
601 guilds and diversity. *Biodiversity and Conservation* 25:2709-2722.
- 602 Dickson, B. G., B. R. Noon, C. H. Flather, S. Jentsch, and W. M. Block. 2009. Quantifying
603 the multi-scale response of avifauna to prescribed fire experiments in the southwest
604 United States. *Ecological Applications* 19:608-621.
- 605 Douma, J. C., and J. T. Weedon. 2019. Analysing continuous proportions in ecology and
606 evolution: A practical introduction to beta and Dirichlet regression. *Methods in*
607 *Ecology and Evolution* 10:1412-1430.
- 608 Enright, N. J., J. B. Fontaine, B. B. Lamont, B. P. Miller, and V. C. Westcott. 2014.
609 Resistance and resilience to changing climate and fire regime depend on plant
610 functional traits. *Journal of Ecology* 102:1572-1581.
- 611 Fairman, T. A., L. T. Bennett, S. Tupper and C. R. Nitschke. 2017. Frequent wildfires erode
612 tree persistence and alter stand structure and initial composition of a fire-tolerant sub-
613 alpine forest. *Journal of Vegetation Science* 28:1151-1165.
- 614 Fernandes, P. M. 2018. Scientific support to prescribed underburning in southern Europe:
615 What do we know? *Science of the Total Environment* 630:340-348.
- 616 Flanagan-Moodie, A. K., G. J. Holland, M. F. Clarke, and A. F. Bennett. 2018. Prescribed
617 burning reduces the abundance of den sites for a hollow-using mammal in a dry forest
618 ecosystem. *Forest Ecology and Management* 429:233-243.
- 619 Fontaine, J. B., and P. L. Kennedy. 2012. Meta-analysis of avian and small-mammal response
620 to fire severity and fire surrogate treatments in U.S. fire-prone forests. *Ecological*
621 *Applications* 22:1547-1561.

622 Foster, C. N., P. S. Barton, C. I. MacGregor, J. A. Catford, W. Blanchard, and D. B.
623 Lindenmayer. 2018. Effects of fire regime on plant species richness and composition
624 differ among forest, woodland and heath vegetation. *Applied Vegetation Science*
625 21:132-143.

626 Garnett, S. T., D. E. Duursma, G. Ehmke, P.-J. Guay, A. Stewart, J. K. Szabo, M. A. Weston,
627 S. Bennett, G. M. Crowley, D. Drynan, G. Dutson, K. Fitzherbert, and D. C. Franklin.
628 2015. Biological, ecological, conservation and legal information for all species and
629 subspecies of Australian bird. *Scientific Data* 2:150061.

630 Gonzalez-Benecke, C. A., L. J. Samuelson, T. A. Stokes, W. P. Cropper, T. A. Martin, and K.
631 H. Johnsen. 2015. Understory plant biomass dynamics of prescribed burned *Pinus*
632 *palustris* stands. *Forest Ecology and Management* 344:84-94.

633 Gosper, C. R., S. J. Watson, E. Fox, A. H. Burbidge, M. D. Craig, T. K. Douglas, J. A.
634 Fitzsimons, S. McNee, A. O. Nicholls, J. O'Connor, S. M. Prober, D. M. Watson, and
635 C. J. Yates. 2019. Fire-mediated habitat change regulates woodland bird species and
636 functional group occurrence. *Ecological Applications* 0:e01997.

637 Halofsky, J. E., D. L. Peterson, and B. J. Harvey. 2020. Changing wildfire, changing forests:
638 the effects of climate change on fire regimes and vegetation in the Pacific Northwest,
639 USA. *Fire Ecology* 16:4.

640 Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in
641 count data in ecology and evolution. *PeerJ* 2:e616.

642 Haslem, A., S. W. J. Leonard, M. J. Bruce, F. Christie, G. J. Holland, L. T. Kelly, J.
643 MacHunter, A. F. Bennett, M. F. Clarke, and A. York. 2016. Do multiple fires interact
644 to affect vegetation structure in temperate eucalypt forests? *Ecological Applications*
645 26:2414-2423.

646 Holland, G. J., M. F. Clarke, and A. F. Bennett. 2017. Prescribed burning consumes key
647 forest structural components: implications for landscape heterogeneity. *Ecological*
648 *Applications* 27:845-858.

649 Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R.
650 Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests.
651 *Canadian Journal of Forest Research* 35:877-890.

652 Hutchinson, T. F., R. P. Long, J. Rebbeck, E. K. Sutherland, and D. A. Yaussy. 2012.
653 Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. *Canadian*
654 *Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 42:303-314.

- 655 Hutto, R. L. 2016. Should scientists be required to use a model-based solution to adjust for
656 possible distance-based detectability bias? *Ecological Applications* 26:1287-1294.
- 657 Jacquet, K., and R. Prodon. 2009. Measuring the postfire resilience of a bird–vegetation
658 system: a 28-year study in a Mediterranean oak woodland. *Oecologia* 161:801-811.
- 659 Keeley, J. E., and A. D. Syphard. 2019. Twenty-first century California, USA, wildfires: fuel-
660 dominated vs. wind-dominated fires. *Fire Ecology* 15:24.
- 661 Keith, D. A. 2012. Functional traits: their roles in understanding and predicting biotic
662 responses to fire regimes from individuals to landscapes. *in* R. Bradstock, A. M. Gill,
663 and R. J. Williams, editors. *Flammable Australia: fire regimes, biodiversity and*
664 *ecosystems in a changing world*. CSIRO Publishing, Collingwood, Victoria.
- 665 Keith, D. A., L. Holman, S. Rodoreda, J. Lemmon, and M. Bedward. 2007. Plant functional
666 types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology*
667 95:1324-1337.
- 668 Kelly, L. T., A. Haslem, G. J. Holland, S. W. Leonard, J. MacHunter, M. Bassett, A. F.
669 Bennett, M. J. Bruce, E. K. Chia, F. J. Christie, M. F. Clarke, J. Di Stefano, R. Loyn,
670 M. A. McCarthy, A. Pung, N. Robinson, H. Sitters, M. Swan, and A. York. 2017. Fire
671 regimes and environmental gradients shape vertebrate and plant distributions in
672 temperate eucalypt forests. *Ecosphere* 8.
- 673 Legendre, P., and L. Legendre. 1998. *Numerical Ecology: developments in environmental*
674 *monitoring*. 3rd edition. Elsevier, Amsterdam, The Netherlands.
- 675 Lindenmayer, D. B., and C. Taylor. 2020. New spatial analyses of Australian wildfires
676 highlight the need for new fire, resource, and conservation policies. *Proceedings of*
677 *the National Academy of Sciences*:202002269.
- 678 Lizundia-Loiola, J., M. L. Pettinari, and E. Chuvieco. 2020. Temporal Anomalies in Burned
679 Area Trends: Satellite Estimations of the Amazonian 2019 Fire Crisis. *Remote*
680 *Sensing* 12:8.
- 681 Loyn, R. H., and E. G. McNabb. 2015. Bird population responses to wildfire and planned
682 burns in foothill forests of Victoria, Australia. *Journal of Ornithology* 156:263-273.
- 683 McCarthy, G., K. Moon, and L. Smith. 2017. Mapping fire severity and fire extent in forest in
684 Victoria for ecological and fuel outcomes. *Ecological Management & Restoration*
685 18:54-65.
- 686 Moreira, F., D. Ascoli, H. Safford, M. A. Adams, J. M. Moreno, J. M. C. Pereira, F. X. Catry,
687 J. Armesto, W. Bond, M. E. González, T. Curt, N. Koutsias, L. McCaw, O. Price, J.
688 G. Pausas, E. Rigolot, S. Stephens, C. Tavsanoglu, V. R. Vallejo, B. W. Van Wilgen,

689 G. Xanthopoulos, and P. M. Fernandes. 2020. Wildfire management in
690 Mediterranean-type regions: paradigm change needed. *Environmental Research*
691 *Letters* 15:011001.

692 Nolan, R. H., M. M. Boer, L. Collins, V. Resco de Dios, H. Clarke, M. Jenkins, B. Kenny,
693 and R. A. Bradstock. 2020. Causes and consequences of eastern Australia's 2019–20
694 season of mega-fires. *Global Change Biology* 26:1039-1041.

695 Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin,
696 R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H.
697 Wagner. 2019. *vegan: Community Ecology Package*. R Foundation for Statistical
698 Computing, Vienna.

699 Ooi, M. K. J., R. J. Whelan, and T. D. Auld. 2006. Persistence of obligate-seeding species at
700 the population scale: effects of fire intensity, fire patchiness and long fire-free
701 intervals. *International Journal of Wildland Fire* 15:261-269.

702 Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in
703 relation to fire in crown-fire ecosystems. *Ecology* 85:1085-1100.

704 Pausas, J. G., and J. E. Keeley. 2014. Evolutionary ecology of resprouting and seeding in
705 fire-prone ecosystems. *New Phytologist* 204:55-65.

706 Pausas, J. G., and C. L. Parr. 2018. Towards an understanding of the evolutionary role of fire
707 in animals. *Evolutionary Ecology* 32:113-125.

708 Penman, T. D., D. L. Binns, T. E. Brassil, R. J. Shiels, and R. M. Allen. 2009. Long-term
709 changes in understorey vegetation in the absence of wildfire in south-east dry
710 sclerophyll forests. *Australian Journal of Botany* 57:533-540.

711 Penman, T. D., D. L. Binns, R. J. Shiels, R. M. Allen, and R. P. Kavanagh. 2008. Changes in
712 understorey plant species richness following logging and prescribed burning in
713 shrubby dry sclerophyll forests of south-eastern Australia. *Austral Ecology* 33:197-
714 210.

715 Penman, T. D., L. Collins, T. D. Duff, O. F. Price, and G. J. Cary. 2020. Scientific evidence
716 regarding effectiveness of prescribed burning. Pages 99 - 111 in A. J. Leavesley, M.
717 Wouters, and R. Thornton, editors. *Prescribed Burning in Australia: The Science and*
718 *Politics of Burning the Bush*. Australasian Fire and Emergency Service Authorities
719 Council, East Melbourne.

720 Pons, P., and M. Clavero. 2010. Bird responses to fire severity and time since fire in managed
721 mountain rangelands. *Animal Conservation* 13:294-305.

- 722 Pope, T. L., W. M. Block, and P. Beier. 2009. Prescribed Fire Effects on Wintering, Bark-
723 Foraging Birds in Northern Arizona. *Journal of Wildlife Management* 73:695-700.
- 724 Price, O. F., T. D. Penman, R. A. Bradstock, M. M. Boer, and H. Clarke. 2015.
725 Biogeographical variation in the potential effectiveness of prescribed fire in south-
726 eastern Australia. *Journal of Biogeography* 42:2234-2245.
- 727 Prior, L. D., G. J. Williamson, and D. M. J. S. Bowman. 2016. Impact of high-severity fire in
728 a Tasmanian dry eucalypt forest. *Australian Journal of Botany* 64:193-205.
- 729 R Development Core Team (2018) R: A Language and Environment for Statistical
730 Computing. R Foundation for Statistical Computing, Vienna, Austria.
- 731 Rainsford, F. 2020. How does prescribed fire shape bird and plant communities in a
732 temperate dry forest ecosystem? Dryad, data set.
733 <https://doi.org/10.5061/dryad.fttdz08rd>
- 734 Rainsford, F. W., L. T. Kelly, S. W. J. Leonard, and A. F. Bennett. 2020. Post-fire
735 development of faunal habitat depends on plant regeneration traits. *Austral Ecology*
736 doi:10.1111/aec.12896.
- 737 Raunkiaer, C. 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford
738 University Press, London.
- 739 Royle, J. A. and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence
740 data or point counts. *Ecology* 84:777-790.
- 741 Robinson, N. M., S. W. J. Leonard, A. F. Bennett, and M. F. Clarke. 2016. Are forest gullies
742 refuges for birds when burnt? The value of topographical heterogeneity to avian
743 diversity in a fire-prone landscape. *Biological Conservation* 200:1-7.
- 744 Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests
745 and woodlands: history, current practice, and challenges. *Frontiers in Ecology and the*
746 *Environment* 11:E15-E24.
- 747 Santos, X., V. Bros, and À. Miño. 2009. Recolonization of a burned Mediterranean area by
748 terrestrial gastropods. *Biodiversity and Conservation* 18:3153.
- 749 Santos, X., E. Mateos, V. Bros, L. Brotons, E. De Mas, J. A. Herraiz, S. Herrando, À. Miño,
750 J. M. Olmo-Vidal, J. Quesada, J. Ribes, S. Sabaté, T. Sauras-Yera, A. Serra, V. R.
751 Vallejo, and A. Viñolas. 2014. Is response to fire influenced by dietary specialization
752 and mobility? A comparative study with multiple animal assemblages. *PLoS One*
753 9:e88224-e88224.
- 754 Shedley, E., N. Burrows, C. J. Yates, and D. J. Coates. 2018. Using bioregional variation in
755 fire history and fire response attributes as a basis for managing threatened flora in a

756 fire-prone Mediterranean climate biodiversity hotspot. *Australian Journal of Botany*
757 66:134-143.

758 Sitters, H., F. Christie, J. Di Stefano, M. Swan, P. Collins, and A. York. 2014. Associations
759 between occupancy and habitat structure can predict avian responses to disturbance:
760 Implications for conservation management. *Forest Ecology and Management*
761 331:227-236.

762 Sitters, H., J. Di Stefano, F. Christie, M. Swan, and A. York. 2016. Bird functional diversity
763 decreases with time since disturbance: Does patchy prescribed fire enhance ecosystem
764 function? *Ecological Applications* 26:115-127.

765 Smith, P., and J. Smith. 2017. Influence of fire regime and other habitat factors on a eucalypt
766 forest bird community in south-eastern Australia in the 1980s. *Australian Journal of*
767 *Zoology* 64:312-326.

768 Stephens, S. L., L. N. Kobziar, B. M. Collins, R. Davis, P. Z. Fulé, W. Gaines, J. Ganey, J.
769 M. Guldin, P. F. Hessburg, K. Hiers, S. Hoagland, J. J. Keane, R. E. Masters, A. E.
770 McKellar, W. Montague, M. North, and T. A. Spies. 2019. Is fire “for the birds”?
771 How two rare species influence fire management across the US. *Frontiers in Ecology*
772 *and the Environment* 17:391-399.

773 Trauernicht, C., B. W. Brook, B. P. Murphy, G. J. Williamson, D. M. J. S. Bowman. 2015.
774 Local and global pyrogeographic evidence that indigenous fire management creates
775 pyrodiversity. *Ecology and Evolution* 5:1908-1918.

776 Uys, C., M. Hamer, and R. Slotow. 2006. Effect of burn area on invertebrate recolonization
777 in grasslands in the Drakensberg, South Africa. *African Zoology* 41:51-65.

778 Victorian Government Department of Environment, Land, Water and Planning. 2020.
779 Victoria’s bushfire emergency: biodiversity response and recovery. Preliminary report
780 – version 1. Victorian Government Department of Environment, Land, Water and
781 Planning.

782 Victorian Government Department of Sustainability and Environment. 2004. EVC/Bioregion
783 benchmark for vegetation quality assessment: Highlands – Southern Fall bioregion,
784 EVC 23: Herb-rich Foothill Forest. Victorian Government Department of
785 Sustainability and Environment.

786 Vitolo, C., C. Di Napoli, F. Di Giuseppe, H. L. Cloke, and F. Pappenberger. 2019. Mapping
787 combined wildfire and heat stress hazards to improve evidence-based decision
788 making. *Environment International* 127:21-34.

789 Ward, M., A. I. T. Tulloch, J. Q. Radford, B. A. Williams, A. E. Reside, S. L. Macdonald, H.
790 J. Mayfield, M. Maron, H. P. Possingham, S. J. Vine, J. L. O'Connor, E. J.
791 Massingham, A. C. Greenville, J. C. Z. Woinarski, S. T. Garnett, M. Lintermans, B.
792 C. Scheele, J. Carwardine, D. G. Nimmo, D. B. Lindenmayer, R. M. Kooyman, J. S.
793 Simmonds, L. J. Sonter, and J. E. M. Watson. 2020. Impact of 2019–2020 mega-fires
794 on Australian fauna habitat. *Nature Ecology & Evolution*.

795 Watson, S. J., R. S. Taylor, D. G. Nimmo, L. T. Kelly, A. Haslem, M. F. Clarke, and A. F.
796 Bennett. 2012. Effects of time since fire on birds: How informative are generalized
797 fire response curves for conservation management? *Ecological Applications* 22:685-
798 696.

799 Wood, S. N. 2017. *Generalized additive models: an introduction with R*. 2nd Ed. Chapman
800 and Hall/CRC, New York.

801 Zeileis, A., F. Cribari-Neto, B. Gruen, I. Kosmidis, A. B. Simas, and A. V. Rocha. 2020.
802 'betareg'. R Foundation for Statistical Computing, Vienna

803

804 **Tables**

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

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

806

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

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

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

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

811 **Figure captions**

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

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

820 Figure 3. Responses bird and plant species to time since prescribed fire in foothill forests. (a)
821 Percentage of plant and bird species for which the modelled response to time since prescribed
822 fire resembled different types of generalized response-curves (after Watson et al. 2012). 'NS'
823 refers to non-significant relationships. (b) Explanatory power of generalized additive models
824 of the relative abundance of bird ($n = 22$) and relative cover of plant ($n = 39$ species) species
825 as a function of time since prescribed fire. Points represent the deviance explained (%) of
826 models. Notch plots indicate the median, upper and lower quartiles and 95% confidence
827 intervals for each taxonomic group. (c - f) Models of selected bird (orange lines) and plant
828 (green lines) species to time since prescribed fire. Lines are fitted models. Shaded areas are
829 95% confidence intervals. $P = P$ -value, $D =$ deviance explained.

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

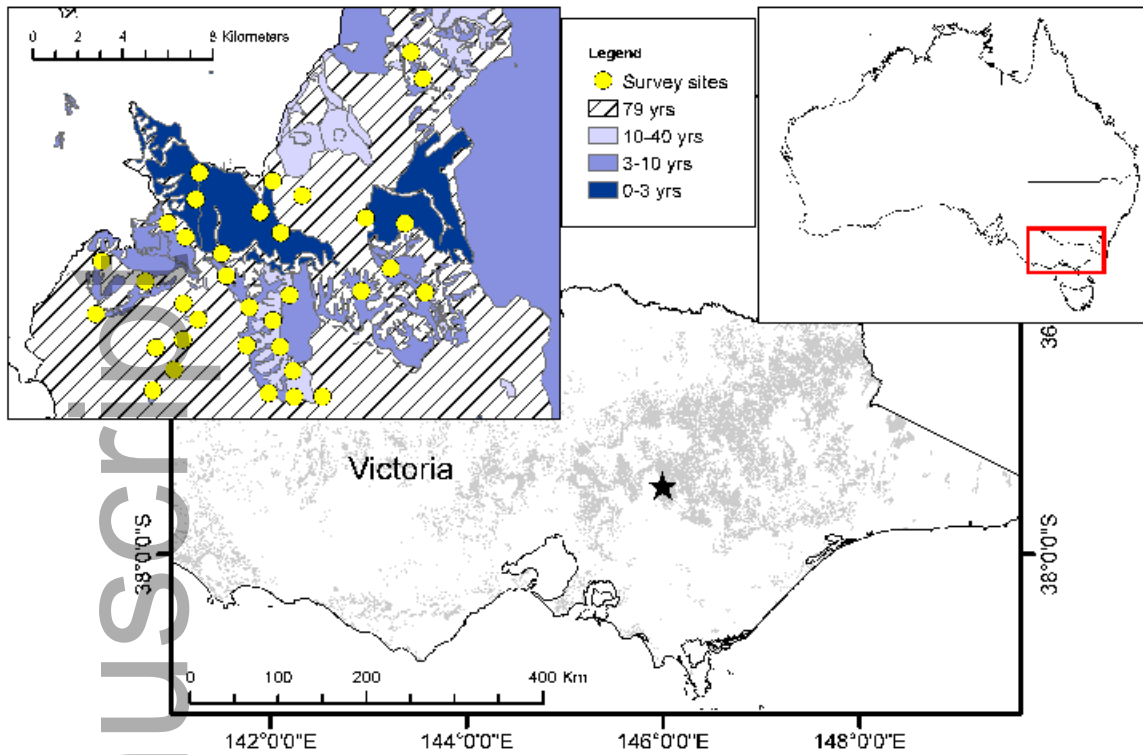
837 Figure 5. Response of functional groups of bird and (a – c) plant (d – f) species to time since
838 prescribed fire in foothill forests. Birds were grouped according to (a) foraging location
839 (upper-midstorey: $n = 20$ species, lower-midstorey: $n = 5$, throughout: $n = 6$), (b) diet
840 versatility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

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

847 Figure 6. Response of selected bird (a – c) and plant (d – f) functional groups to post-fire age-
848 classes (AC) in foothill forests. Points indicate mean relative abundance of (a) lower-
849 midstorey foraging birds, (b) birds with low dietary versatility, (c) open nest bird species, and
850 mean relative cover of (d) facultative-resprouting shrubs, (e) obligate-resprouting shrubs and
851 (f) obligate-seeding shrubs in post-fire age-classes. Vertical lines represent 95% confidence
852 intervals. Letters indicate significantly different means ($P < 0.05$) determined by Tukey HSD.
853 AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since prescribed fire, LU: long-unburnt
854 (79 years since wildfire).

855 Figure 7. Response of bird and plant species richness to post-fire age-classes (AC) in foothill
856 forests. Points indicate mean (a) bird and (b) plant species richness. Vertical lines represent
857 95% confidence intervals. Letters indicate significantly different means ($P < 0.05$)
858 determined by Tukey HSD. AC1: 0-3 years, AC2: 3-10 years, AC3: 10-40 years since
859 prescribed fire, LU: long-unburnt (79 years since wildfire).

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



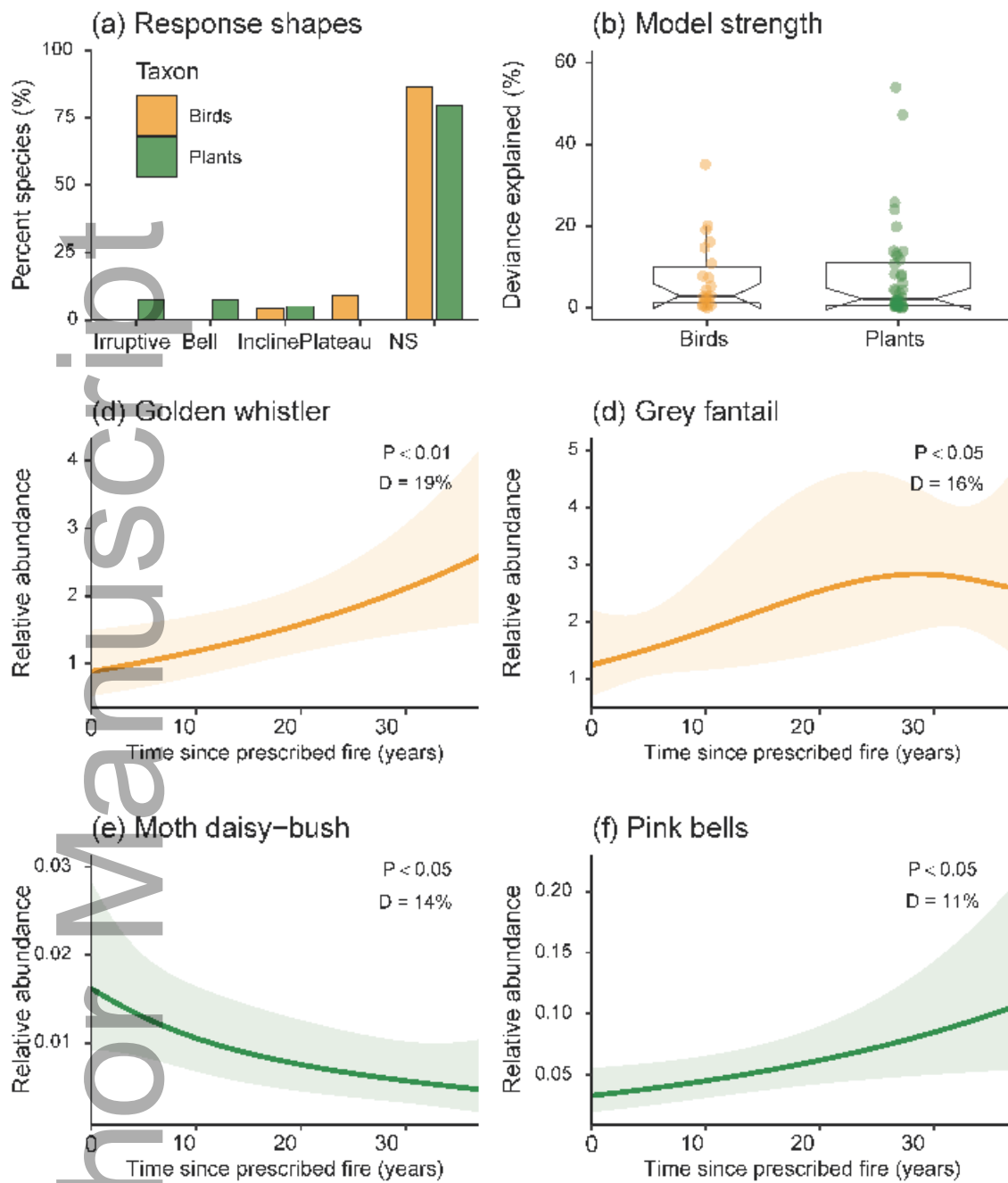
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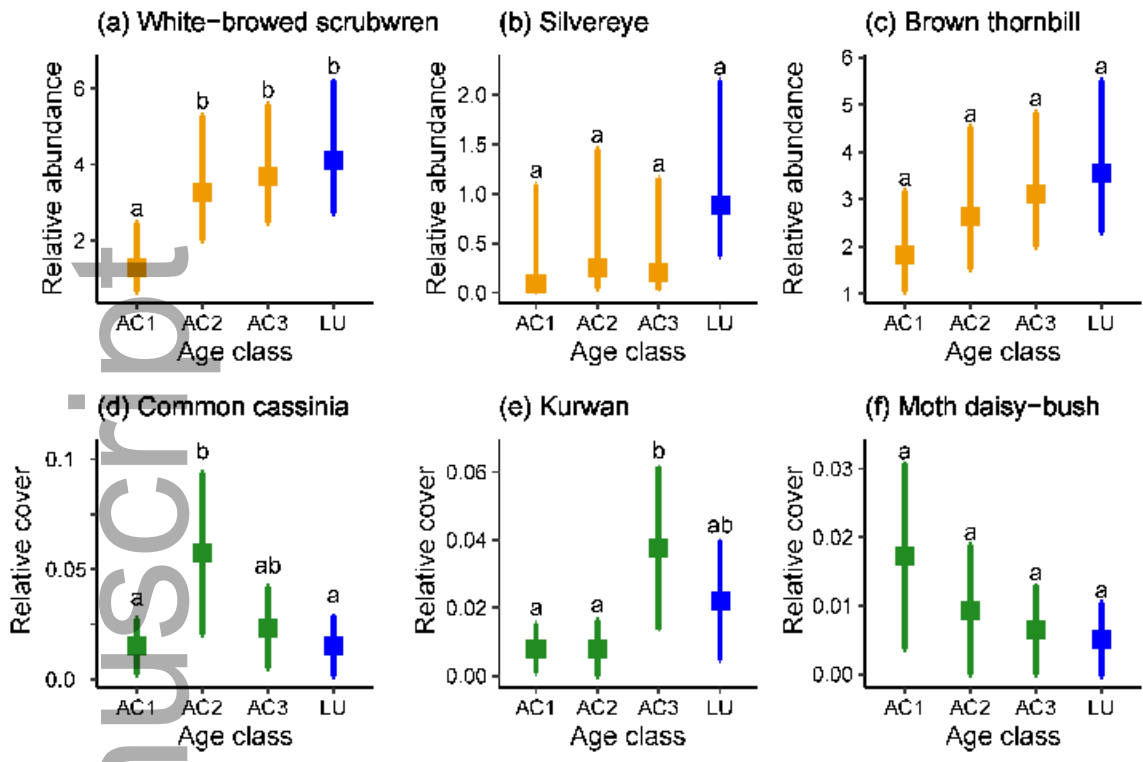


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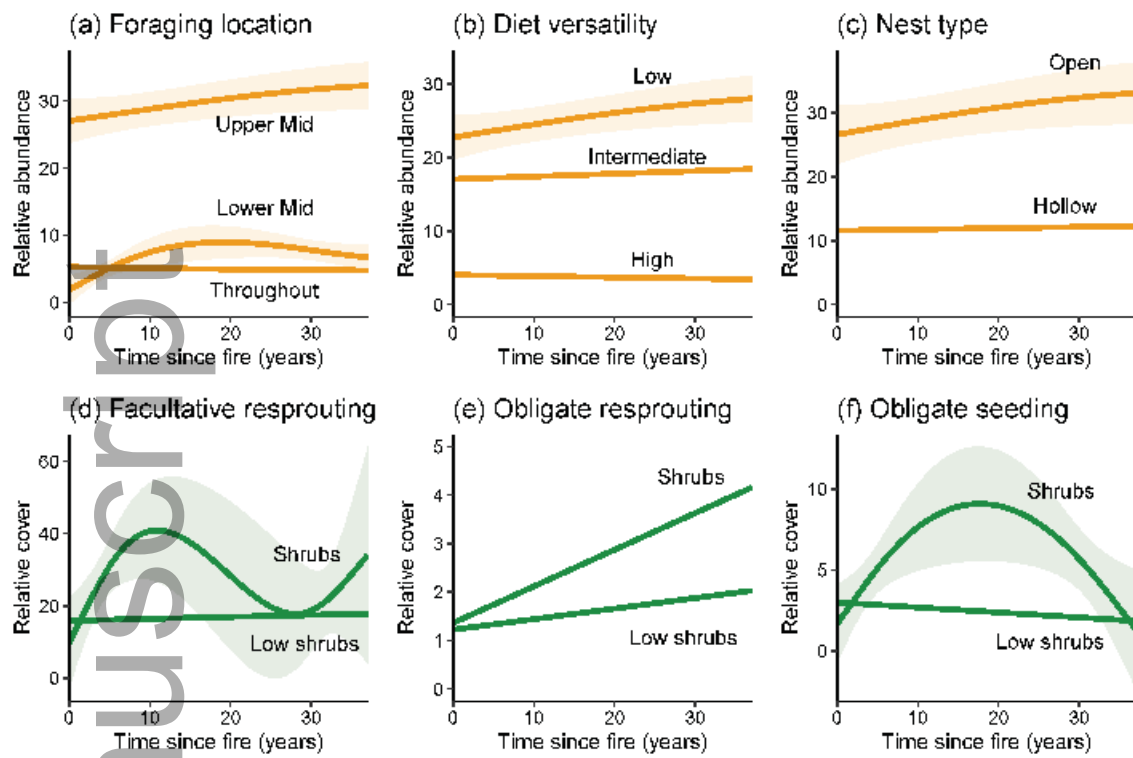
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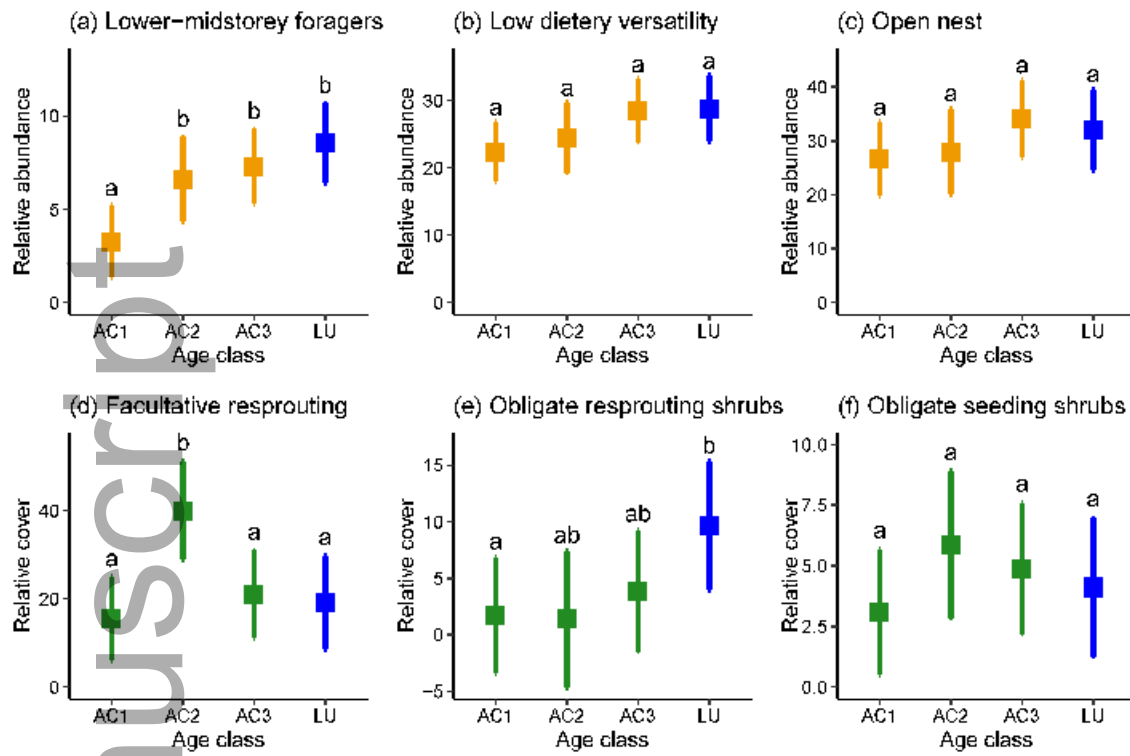
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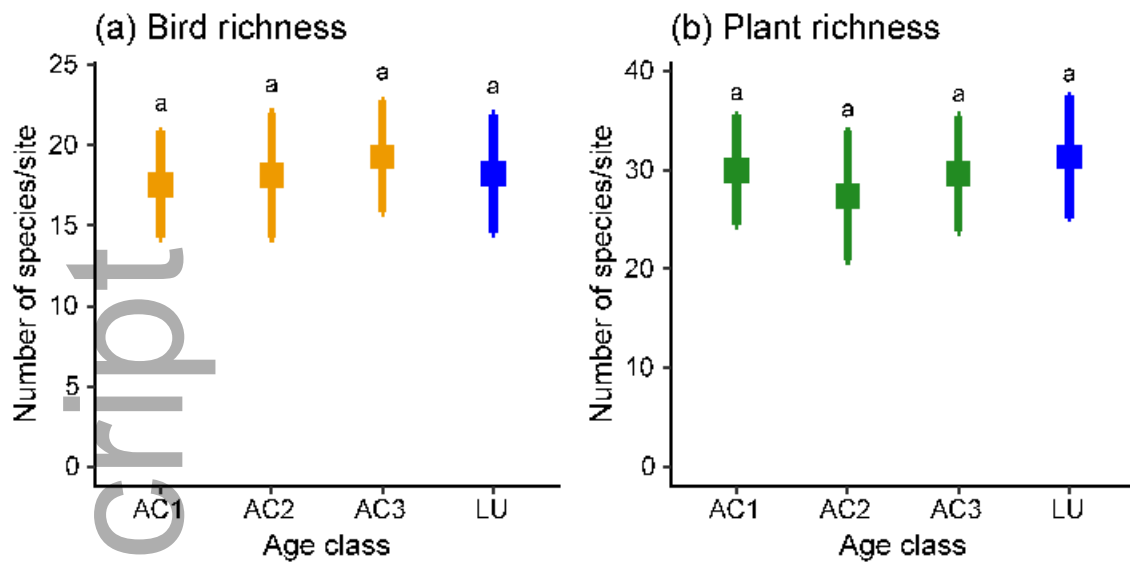
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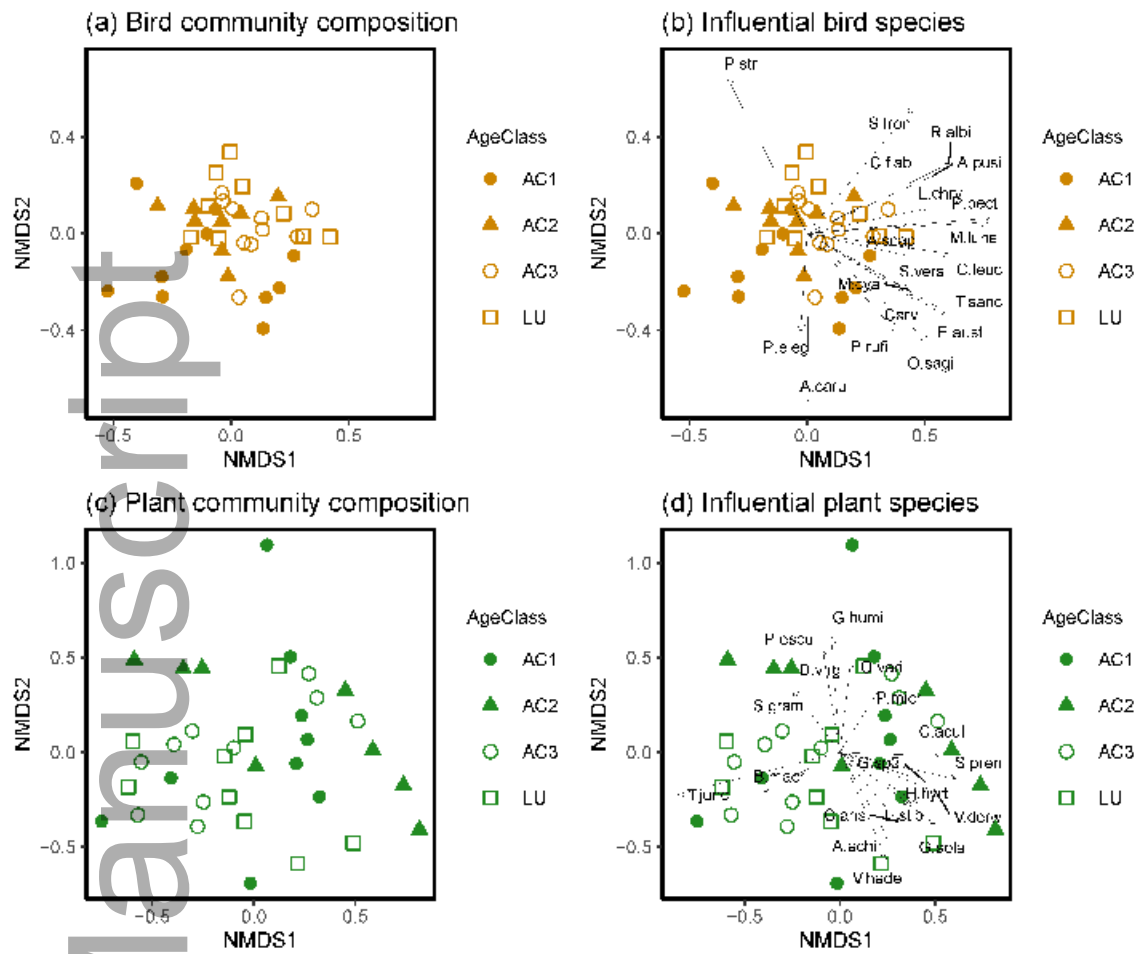
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