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Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers

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Running Head: Bird responses to landscape-scale fire

20 **Abstract**

21 **Aim:** To quantify bird responses to a large unplanned fire, taking into consideration
22 landscape-level fire severity and extent, pre-fire site detection frequency, and environmental
23 gradients.

24 **Location:** South-eastern Australia.

25 **Methods:** A major wildfire in 2009 coincided with a long-term study of birds and provided a
26 rare opportunity to quantify bird responses to wildfire. Using Hierarchical Bayesian analysis,
27 we modelled bird species richness and the detection frequency of individual species in
28 response to a suite of explanatory variables including: **(1)** landscape-level fire severity and extent
29 **(2)** pre-fire detection frequency, **(3)** site-level vegetation density, and **(4)** environmental variables
30 (e.g. elevation and topography).

31 **Results:** Landscape-level fire severity had strong effects on bird species richness and the
32 detection frequency of the majority of bird species. These effects varied markedly between
33 species; most responded negatively to amount of severely burned forest in the landscape, one
34 negatively to the amount of moderately burned forest, and one responded negatively to the
35 total area of burned forest. Only one species – the Flame Robin - responded positively to the
36 amount of burned forest. Relationships with landscape-scale fire extent changed over time for
37 one species – the Brown Thornbill - with initially depressed rates of detection recovering
38 after just 2 years. The majority of species were significantly more likely to be detected in
39 burned areas if they have been recorded there prior to the fire.

40 **Main conclusions:** Birds responded strongly to the severity and spatial extent of fire. They
41 also exhibited strong site fidelity even after severe wildfire which causes profound changes in
42 vegetation cover – a response likely influenced by environmental features like elevation and
43 topography.

44 **Keywords:** Community ecology, disturbance, landscape-level fire, mega-fire, site fidelity,
45 succession

46 (A) Introduction

47 Fire has a profound influence on the diversity and distribution of biota worldwide
48 (Bowman *et al.*, 2009; McKenzie *et al.*, 2011). Understanding how species are influenced by
49 fire is a fundamental part of ecology (Johnson & Miyanishi 2008; Valentine *et al.*, 2012;
50 Nimmo *et al.*, 2013a) but relationships between fire and biota can be complex and substantial
51 knowledge gaps remain (Pons & Clavero 2010; Driscoll *et al.*, 2012). The effect on wildlife of
52 very severe fire, where the majority of living biomass is killed (Keeley 2009), and the effects of
53 variation in fire severity, are key knowledge gaps. Severe fire in particular is very poorly
54 studied because long-term studies rarely coincide with a natural severe fire (Whelan 1995;
55 Driscoll *et al.*, 2010). Another knowledge gap is an empirical understanding of how the broad
56 spatial patterns of fire in a landscape affect the diversity and occurrence of species (McKenzie *et*
57 *al.*, 2011). Such landscape context effects are well established in the habitat fragmentation
58 literature (Lindenmayer & Fischer 2006; Collinge 2009) with many studies finding that the
59 amount and condition of vegetation in fragmented landscapes strongly affects biota in habitat
60 patches (Laurance 1991; Viveiros de Castro & Fernandez 2004; Driscoll *et al.*, 2013).
61 However, the ecological effects of the spatial scale and configuration of fire in a landscape
62 have rarely been examined (Zozaya *et al.*, 2012a; Taylor *et al.*, 2012; Nimmo *et al.*, 2013b).

63 We sought to address knowledge gaps on landscape-level fire extent and severity
64 through a long-term, empirical investigation of the responses of birds to the 2009 wildfires in
65 south-eastern Australia. Two features of our study design created an ideal opportunity to
66 address these knowledge gaps: **(1)** Long-term data on the detection frequency of birds collected
67 during repeated surveys at 87 permanent sites before the 2009 wildfires (Lindenmayer *et al.*,
68 2009a). **(2)** Variation in the extent of fire in the landscape surrounding our long-term sites,
69 ranging from 0-100%. Fire severity in these areas surrounding our sites also varied, with some
70 landscapes remaining unburned, others subject to moderate-severity fire, and some
71 experiencing extensive high severity fires, reputed to be the most intense fires ever recorded,
72 reaching 88 000 kW/m (Cruz *et al.*, 2012). These features enabled us to address two inter-

73 linked questions associated with post-fire bird responses to landscape-scale severity and spatial
74 extent of fire.

75 ***Question 1. Does the severity and spatial extent of fire in landscapes affect bird species***

76 ***richness and individual species?*** Many studies have compared the post-fire recovery of biota
77 on burned and unburned areas, but few have quantified the effects of variation in fire severity
78 on biodiversity (although see Smucker *et al.*, 2005; Kotliar *et al.*, 2007; Rush *et al.*, 2012).

79 Fire severity is defined as the effects of fire on the vegetation (Keeley 2009) and in this study
80 it corresponded to the amount of scorch and consumption in the ground, shrub and overstorey
81 layers. Understanding the effects of fire severity is necessary to enable accurate predictions of
82 the response of fauna to changes in fire regimes and fire management practices (Driscoll *et*
83 *al.*, 2010). We postulated that species richness and the detection frequency of individual
84 species would be lower on sites where the surrounding landscapes had experienced high-
85 severity fire, than on sites where the surrounding landscapes experienced moderate-severity
86 fire or remained unburnt. Such responses might occur if fire affects regional populations of
87 species (Askins *et al.*, 1987), source-sink population dynamics (Pulliam *et al.*, 1992) or
88 metapopulation dynamics (*sensu* Hanski 1999). We also postulated that the effects of
89 landscape fire severity would dissipate over time as the vegetation regenerated, consistent with
90 post-disturbance succession theories (Johnson & Miyanishi 2008).

91 ***Question 2. Do pre-fire species richness and individual species detection frequency influence***

92 ***post-fire levels of those variables?*** Most studies of fire effects on animals have been post-hoc,
93 space-for-time investigations which lack pre-fire site occupancy data (Whelan 1995;

94 Bradstock *et al.*, 2012). Yet this information is important as a species might be present or
95 absent from an area for reasons that may be independent, or partially independent, of fire.

96 These reasons include environmental conditions like slope and aspect (Huggett & Cheeseman
97 2002) or behavioural patterns of sociality and long-term site affinity in animals (Allee 1931;
98 Gill 1995). Taking account of pre-fire detection frequency is therefore necessary to accurately
99 predict how animals might respond to fire. We postulated that post-fire species richness and

100 the detection frequency of individual species would be related to pre-fire levels in those
101 variables. This was based on earlier investigations in our study area indicating that bird
102 species richness and the occurrence of individual species were strongly related to key
103 environmental drivers like elevation and topography (Lindenmayer *et al.*, 2009b) which
104 remain unchanged by fires.

105 Our investigation took advantage of the opportunity provided by the intersection of a major
106 wildfire with a pre-existing long-term study to quantify biotic responses to fire. Insights
107 generated by investigations like this one are important to better determine the effects of fire
108 on the persistence and viability of populations of individual species (Kotliar *et al.*, 2007; Hutto
109 2008; Swanson *et al.*, 2011) as well as better quantify the role of fire as a key ecosystem process
110 (Turner *et al.*, 2003; Bowman *et al.*, 2009).

111 **(A) Methods**

112 **(B) Study region**

113 Our study region was the Central Highlands of Victoria, approximately 120 km north-
114 east of Melbourne, south-eastern Australia (Fig. 1). Our study sites were located in montane
115 ash forests dominated by either Mountain Ash (*Eucalyptus regnans*) or Alpine Ash (*E.*
116 *delegatensis*) trees which are up to 100m and 70m tall, respectively. Mountain Ash and
117 Alpine Ash are obligate seeders, meaning that wildfires can kill trees and the forest
118 regenerates only from seed (Smith *et al.*, 2013). The mean fire return interval in montane ash
119 forests has been estimated at 75 years (McCarthy *et al.*, 1999) but ranging from 30-300+
120 years depending on the location of an area in the landscape (Lindenmayer 2009).

121 **(B) 2009 fire severity variables**

122 The February 2009 wildfires burned 72 000 ha of montane ash in our study region
123 (Gibbons *et al.*, 2012) (Fig. 1). Within four weeks of the fires, we completed on-ground
124 surveys of 87 survey sites distributed throughout the study region (Fig. 1) to quantify fire
125 severity (see Lindenmayer *et al.*, 2010). Each site was assigned to one of three categories: **(1)**
126 no fire (43 sites), **(2)** moderate-severity fire characterised by the ground and understorey layer

127 being killed and/or consumed while the overstorey remained intact (28 sites), and **(3)** high-
128 severity fire in which plants in the ground, shrub and understorey layers were killed and
129 crowns of overstorey trees consumed (16 sites).

130 Using spatial data on forest cover following the 2009 fires (from the Government of
131 Victoria), we calculated the area of forest (ha) that had been burned within a 500 m and 1 km
132 radius circle surrounding each survey site. Within these circles, we calculated the total area
133 burned at any severity, the area burned at moderate severity, and the area of burned at high
134 severity. We did not examine circles with a radius larger than 1 km as this resulted in
135 overlapping polygons that were no longer spatially independent of one another.

136 During preliminary analyses, we found a strong relationship between site-level and
137 landscape-level fire severity. For example, there was a point bi-serial correlation of 0.862
138 between site-level severe fire and landscape-level severe fire (Appendix S1). However, some
139 of our landscapes included severely or moderately burned forest surrounding field sites that
140 remained unburned (Appendix S1). Given these levels of correlation, we focused our
141 statistical analyses only on landscape-level fire. We also identified limited differences in bird
142 responses between the 500 m and 1 km polygons for landscape-level fire during preliminary
143 analyses. We therefore presented results only from the 1 km radius circle.

144 **(B) Other covariates**

145 Our 87 field sites were distributed throughout the study region and covered a wide
146 range of variation in environmental conditions. Using ground-truthing and maps, we derived
147 environmental variables for each site that are known to influence the occurrence of birds in
148 montane ash forests (Lindenmayer *et al.*, 2009b). These included elevation (220–1040 m),
149 topographic position (gully, midslope, ridge) and aspect (assigned to one of two categories:
150 northerly-westerly and southerly-easterly).

151 We also included a measure of stem density in our analysis, calculated from post-fire
152 vegetation surveys conducted annually on each site. We established three 10 x 10 metre
153 permanent plots at each site and assigned every stem to one of 11 diameter at breast height

154 classes (ranging from 0–5 cm to 180 cm+) and one of seven height classes (ranging from 2–5
155 m to 60 m+). We identified the species of each stem and recorded its condition (burnt,
156 coppicing, dead or live). We defined stem density as the number live or coppicing stems in
157 the 2–5 m and 6–10 m height classes of all species.

158 **(B) Bird surveys**

159 In 2003, we established 87 one hectare permanent bird monitoring sites. We
160 conducted surveys in 2004, 2005, 2007, 2009, 2010, 2011 and 2012, giving three pre-fire and
161 four post-fire surveys for each site (Lindenmayer *et al.*, 2009b). We completed all surveys in
162 late November which is the breeding season for the majority of species and when summer
163 migrants have arrived. Our standardised protocol entailed repeated 5 minute point interval
164 counts (*sensu* Pyke & Recher 1983) at the 0 m, 50 m and 100 m points along a central 100 m
165 transect at each site. In each year of our surveys, each site was surveyed by two different
166 highly experienced ornithologists on different days to account for observer heterogeneity
167 (Cunningham *et al.*, 1999; Lindenmayer *et al.*, 2009c) and day effects (Field *et al.*, 2002;
168 Lindenmayer *et al.*, 2009c). We pooled counts across the 0 m, 50 m and 100 m plots and also
169 pooled data across observers and days. Thus, we amalgamated our data within each site to
170 give the number of recordings of each species from the maximum possible six observer-by-
171 plot combinations for any given survey year. We combined the individual records for each
172 species on a site to form an index that we call the (species) frequency of recording. That is,
173 the number of opportunities (out of six) on a given transect at which we detected that species.

174 **(B) Statistical analysis**

175 To quantify the effect of landscape-level fire severity, fire extent and covariates on
176 bird species richness (total number of species per site per year), we used a Bayesian
177 hierarchical (multi-level) Poisson regression model with a log-link function (Appendix S2).
178 To quantify the effects of landscape-level fire severity, fire extent, and covariates on the
179 detection frequency of individual bird species, we used a Bayesian hierarchical (multi-level)
180 logistic regression model. For both the species richness and individual species analyses, we

181 report the posterior median (PM), 95% credible intervals and Bayesian P-value for model
182 parameters on the log-odds scale. Credible intervals that do not include zero are indicative of
183 an effect.

184 We constructed statistical models for 13 individual species recorded 200 or more
185 times between 2009 and 2012 (Appendix S3). We used this number of records for individual
186 species to take a conservative approach and for consistency with our previous (pre-fire) work
187 on birds (Lindenmayer *et al.*, 2009b).

188 Model selection is a difficult process and several competing approaches exist. This
189 issue is particularly difficult for hierarchical random effects models as there are problems
190 with both the Deviance Information Criterion (DIC) and with approximating the integrals
191 required for computing the Bayesian Information Criterion (BIC) (Müller *et al.*, 2013). We
192 therefore chose the model with the lowest BIC from among a candidate set of models without
193 the hierarchical structure (Appendix S2) and also computed the DIC for the hierarchical
194 version of the models to check for consistency between the two methods. The base model for
195 species richness consisted of the following variables: elevation, stem density, aspect,
196 topographic position, post-fire survey year modelled as a factor variable and pre-fire species
197 richness (averaged between 2004 and 2007). The fire extent variables (moderate, severe,
198 total) and their interactions with year were then added to the base model. This resulted in a
199 candidate set of 11 models. Once the best model was chosen for species richness, it was then
200 fitted in the Bayesian hierarchical fashion (Appendix S2). Our analyses of individual bird
201 species used the same set of eleven models, except we replaced pre-fire species richness with
202 pre-fire frequency of recording (aggregated over 2004–2007).

203 We did not conduct detection/occupancy modelling as there are major problems in
204 fitting such models (Welsh *et al.*, 2013). For example, it is not possible to determine whether
205 the fit from the detection/occupancy model or the fit ignoring the possibility of detection
206 error is the best model (Welsh *et al.*, 2013). In addition, we have accounted for known
207 sources of variation in our surveys in the most appropriate and feasible manner: by using a

208 large number of sites and surveying multiple points per site (local spatial heterogeneity),
209 surveying on multiple days (temporal heterogeneity) and using multiple observers (observer
210 heterogeneity) (Lindenmayer *et al.*, 2009c).

211 **(A) Results**

212 Between 2004 and 2012, we completed 3654 point counts on our 87 sites and
213 recorded 75 bird species. This yielded 7964 individual records of birds pre-fire (2004, 2005
214 and 2007) and 7959 records post-fire (2009, 2010, 2011 and 2012). The DIC yielded the
215 same best model as BIC for species richness and 10 of the 13 individual species (Appendix
216 S4). For the remaining three species, the model chosen by BIC was the second ranked model
217 from DIC (Appendix S4). There was therefore a high level of congruence between the two
218 model selection procedures and we selected our final models using BIC.

219

220 ***Question 1. Does the severity and spatial extent of fire in landscapes affect bird species*** 221 ***richness and individual species?***

222 We found strong evidence of the effects of landscape-level fire severity and fire
223 extent on bird species richness and the detection frequency of the majority of individual bird
224 species (Fig. 2a, Fig. 3). Species richness at a site was negatively associated with the extent
225 of severe fire in the surrounding landscape (PM = -0.22, 95% CI=(-0.18,-0.13)). Seven
226 species responded negatively to the extent of severe fire in the landscape: the White-browed
227 Scrub-wren (PM = -0.18, 95% CI=(-0.30,-0.07)), Grey Fantail (PM = -0.26, 95% CI=(-0.44,-
228 0.08)), Golden Whistler (PM = -0.44, 95% CI=(-0.65,-0.25)), Striated Thornbill (PM = -0.68,
229 95% CI=(-0.91,-0.46)), Crescent Honeyeater (PM = -0.74, 95% CI=(-1.19,-0.32)), Eastern
230 Yellow Robin (PM = -0.72, 95% CI=(-1.03,-0.44)) and the Eastern Spinebill (PM = -0.41,
231 95% CI=(-0.81,-0.05)) (Table 1, Fig. 3a, Appendix S5). Only one species, the Silvereye (PM
232 = -0.21, 95% CI=(-0.41,-0.03)), responded negatively to the amount of forest burned at
233 moderate severity in the landscape (Table 1, Fig. 3a, Appendix S5). The Spotted Pardalote
234 responded negatively to the total amount of burned forest in the landscape (PM = -0.72, 95%

235 CI=(-1.03,-0.44)) whereas the Flame Robin responded positively to the total amount of
236 burned forest in the landscape (PM = 0.51, 95% CI=(0.28,0.76)) (Table 1, Fig. 3a, Appendix
237 S5). The Crimson Rosella and Striated Pardalote exhibited no response to landscape fire
238 variables.

239 We found a landscape fire severity \times year interaction for the detection frequency of
240 just one species – the Brown Thornbill (Table 1, Fig. 3a, Appendix S5). In 2009 (PM = -0.26,
241 95% CI=(-0.51,-0.03)) and 2010 (PM = -0.78, 95% CI=(-1.18,-0.44)), the detection
242 frequency of the Brown Thornbill was substantially lower on sites within landscapes subject
243 to high-severity fire compared with landscapes characterised by moderately burned and
244 unburned forest. This effect was no longer present in 2011 (PM = -0.03 95% CI=(-0.25,0.17))
245 or 2012 (PM = 0.16, 95% CI=(-0.04,0.37)) (Fig. 3a).

246 ***Question 2. Do pre-fire species richness and individual species detection frequency influence***
247 ***post-fire levels of those variables?***

248 We found a strong positive relationship between pre- and post-fire species richness
249 (Fig. 2b), indicating that species rich sites prior to the 2009 fire remained relatively rich in
250 bird species after the fire. We also identified positive relationships between the pre- and post-
251 fire detection frequency of 10 of the 13 individual species (Table 1, Figure 3, Appendix S5).
252 There were no negative relationships between pre- and post-fire detection frequency. The
253 three species for which there were no apparent site fidelity effects were the Flame Robin,
254 Striated Thornbill and the Striated Pardalote (Fig. 3b).

255 **(B) Other effects**

256 We found strong evidence that stem density, elevation, topographic position, and aspect
257 influenced bird species richness and/or the occurrence of individual species (Table 1, Appendix
258 S5). Detection frequencies of eight species (White-browed Scrub-wren, Brown Thornbill, Grey
259 Fantail, Golden Whistler, Striated Thornbill, Silvereye, Crescent Honeyeater and Eastern
260 Spinebill) were positively related to the density of stems on sites following the 2009 fire (Table 1,

261 Fig. 3c, Appendix S5). The occurrence of the Flame Robin was negatively associated with post-
262 fire stem density (Table 1, Fig. 3c, Appendix S5).

263 Species richness and the majority of species were negatively related to elevation, with
264 only the Flame Robin exhibiting a positive response (Table 1, Appendix S5). Species richness
265 and the detection frequencies of the White-browed Scrub-wren, Silvereye, Crimson Rosella and
266 Eastern Spinebill were lower in gullies relative to sites in other topographic positions (Table 1,
267 Appendix S5). One species (the Grey Fantail) was more likely to be detected on warmer and drier
268 (northerly and westerly) aspects (Table 1, Appendix S5).

269 There were year-to-year fluctuations (i.e. main effects independent of fire), in species
270 richness and the detection frequency of all individual species (Table 1, Appendix S5) with the
271 exception of the Brown Thornbill which exhibited a strong severe fire x year interaction (see
272 above; Fig. 3a).

273 **Discussion**

274 Our long-term study revealed new insights into the complex responses of birds to
275 landscape-level fire severity and fire extent. These insights included: **(1)** Highly variable
276 inter-specific responses to the extent of moderate and/or severe fire in the landscape
277 surrounding our sites. **(2)** A paucity of interactions between landscape-level fire and survey
278 year, indicating that the negative effects of fire on most species had not dissipated over the
279 four year study period. **(3)** Strong site affinity indicated by positive relationships between
280 pre-fire and post-fire species richness and the detection frequency of individual species, and,
281 **(4)** Impacts of key environmental variables (e.g. elevation) on bird species richness and
282 individual species that were not directly related to fire. We discuss these findings below in
283 relation to the two questions posed at the outset of our work.

284 **(B) Question 1. Does the severity and spatial extent of fire in landscapes affect bird** 285 **species richness and individual species?**

286 Severe fire in the landscape had strong negative effects on species richness and most
287 individual species, consistent with our predictions at the outset of this study and with data

288 from other studies in North America (Kotliar *et al.*, 2007) and Europe (Pons & Clavero
289 2010). Negative responses to moderate severity landscape-level fire were uncommon,
290 possibly because most bird species persist when the overstorey remains intact as opposed to
291 the more extensive vegetation disturbance that occurs during high severity fire. The
292 widespread negative responses to severe landscape fire that we observed may have arisen
293 from a range of inter-related reasons including: **(1)** High levels of direct mortality from the
294 intense conflagration (Keith *et al.* 2002). Burned areas surrounding sites may act as sinks
295 (Pulliam *et al.*, 1992), with higher mortality in severely burned forest. **(2)** Major alteration in
296 forest vegetation structure leading to landscape-scale losses of suitable habitat. This can
297 disrupt the spatial continuity of foraging and/or nesting areas (Askins *et al.*, 1987), increase
298 emigration (Hanski *et al.*, 2002) and impair behavioural patterns like conspecific attraction
299 (Dale *et al.* 2006; Zozaya *et al.* 2012b). And, **(3)** Altered colonisation dynamics, with fewer
300 individuals arriving in unburnt patches as the extent of surrounding burnt forest increased
301 (Hanski 1999). These processes may also explain our finding that virtually all of the species
302 which responded negatively to the amount of severely burned forest burned also responded
303 positively to stem density.

304 Only one species in our study – the Flame Robin – had elevated detection frequency
305 with increasing amount of fire in the landscape. This species also responded negatively to
306 stem density, highlighting its preference for open areas created by fire, irrespective of fire
307 severity. We did not record any new species after the fire that had been absent pre-fire (data
308 not shown). Hence, there appears to be a paucity of early successional specialists in montane
309 ash forests, as the Flame Robin was the only species showing a tendency to occupy this
310 niche. This is unusual as early successional specialists are common in most ecosystems
311 characterised by high-severity disturbances (e.g. the Douglas-fir *Pseudotsuga menziesii*
312 forests of western North America; (Swanson *et al.*, 2011) and Europe (Moreira *et al.* 2001,
313 Pons & Bas 2005, Brotons *et al.* 2008)). An exception is the coniferous montane forests of
314 eastern Asia (Ding *et al.*, 2008).

315 In montane ash forests, very rapid vegetation regeneration and canopy closure on
316 severely burned sites (Ashton 1975) may limit the influx of open-country birds and preclude
317 the evolutionary development of early successional species. This rapid regeneration also may
318 have underpinned the patterns of post-fire occurrence observed for the Brown Thornbill
319 which had recovered from depressed levels of detection frequency by 2011 and 2012.
320 However, it was surprising that no other bird species exhibited a similarly rapid recovery.
321 The historically long fire return interval in montane ash forests ecosystems (McCarthy *et al.*,
322 1999) might favour birds that specialise on older vegetation and such species take longer to
323 recover than the time frame of our study. In addition, montane ash forests are spatially
324 limited and this may discourage the development of specialist early successional avian fauna
325 in this type of forest. Elsewhere in the world, early successional species are often associated
326 with forest types and fire regimes that extend over large areas and therefore at any given
327 time, suitable early successional forest conditions are likely to occur (Hutto, 2008; Pierson *et*
328 *al.*, 2013).

329 Climate change is forecast to lead to altered fire regimes in montane ash forests
330 characterised by more intense and frequent conflagrations (Cary *et al.*, 2012). The paucity of
331 species which specialise on early successional vegetation, coupled with the relatively slow
332 recovery of the majority of bird taxa in the montane ash forests of Victoria, may make the
333 bird assemblages of this ecosystem somewhat more susceptible to fire regime change than
334 those in other ecosystems.

335 **(B) *Do pre-fire species richness and individual species detection frequency influence post-fire***
336 ***levels of those variables?***

337 Our results supported the prediction that pre-fire species richness would influence
338 post-fire species richness. We also found that the pre-fire detection frequency of the majority
339 (10/13) of bird species strongly influenced their post-fire occurrence. Sites that were species-
340 rich prior to the fires were more likely to support greater species richness following the fire.

341 Similarly, sites with a high detection frequency for a given species prior to the fires were
342 likely to be characterised by a high post-fire detection frequency for that species.

343 Several, inter-related mechanisms may underpin positive relationships between pre-
344 and post-fire species richness and individual species detection frequency. These include: **(1)**
345 Sites having abiotic characteristics that support more species (e.g. lower elevation or on
346 ridges and gullies; see below). **(2)** Many individual species or groups of species having high
347 levels of site affinity (Gill 1995). Sites may have particular characteristics which allow
348 animals continue to occupy an area, even following disturbance (e.g. Tyndale-Biscoe &
349 Smith 1969) or allow animals to quickly recolonize the area. And, **(3)** High species richness
350 might beget more species through inter- and intra-specific attraction (Smith & Peacock 1990;
351 Catchpole & Slater 1995; Ovaskainen *et al.*, 2010).

352 Our study provides tentative support for the first of the above mechanisms. Bird
353 species richness and the detection frequencies of many individual species were highest at low
354 elevation or outside gullies, suggesting these are important drivers of habitat suitability for
355 birds. Indeed, these responses were similar to those observed for birds prior to the 2009 fire
356 in our study region (Lindenmayer *et al.*, 2009b). A key conclusion arising from our results is
357 that although landscape-scale fires have major impacts on the structure and composition of an
358 ecosystem, abiotic environmental factors such as elevation and topography also exert a
359 substantial influence on bird species richness and detection frequency of many individual bird
360 species.

361 **(B) Other factors**

362 The negative response of species richness to elevation that we observed was broadly
363 consistent with the response seen worldwide (reviewed by Gaston & Spicer 2004). By
364 contrast, our finding for reduced levels of species richness in gullies was opposite to the
365 patterns seen in many ecosystems globally (Huggett & Cheeseman 2002; Palmer & Bennett
366 2006). Gullies in many ecosystems are characterised by higher levels of water, biomass and
367 nutrients than elsewhere in the landscape (Huggett & Cheeseman 2002). However, this may

368 not be the case in our study area because gullies often support Gondwanic rainforest
369 vegetation dominated by Myrtle Beech (*Nothofagus cunninghami*) (Lindenmayer *et al.*, 2000)
370 which may not provide an abundance of food resources for birds such as fleshy fruits, seeds
371 and nectar.

372 **(A) Concluding remarks**

373 Rigorous quantification of the response of biota to fire requires quantifying: **(1)** the
374 extent and severity of fire in the surrounding landscape – even if that site is unburned, and **(2)**
375 the effect of non-fire-related environmental factors (e.g. elevation, topographic position)
376 which can influence the inherent suitability of sites, and, in turn, the importance of measures
377 such as pre-fire species richness for understanding post-fire species richness. Although
378 landscape context effects are often addressed in habitat fragmentation research, our study is
379 one of the first to extend these concepts to fire ecology. We found that the effects of fire
380 severity on birds can operate at broad spatial scales, increasing our understanding of
381 ecosystem responses to disturbance regimes.

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386

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559 determine bird species distribution dynamics in landscapes dominated by land
560 abandonment. *Landscape Ecology*, **27**, 171–184.

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562

563 **BIOSKETCH**

564 General statement of focus of research team: This publication is generated from long-term
565 empirical studies in the Central Highlands of Victoria by the research group at the Fenner
566 School of Environment and Society. For the past 30 years, D.B.L. has conducted long-term
567 empirical studies of vegetation, arboreal mammals, birds, fire effects and management, and
568 the effects of logging in the wet forests of Victoria. The research team includes expert
569 statistical scientists, field-based ecologists dedicated to gathering high-quality field data and
570 ecologists with particular expertise in theory.

571 Author contributions: D.B.L. and W.B. designed the study; W.B. completed the detailed
572 statistical analysis; D.B.L., L.M. and D.B. gathered the field data; D.B.L., W.B. and S.C.B.
573 wrote the paper with significant conceptual and editorial input from D.A.D., A.L.S. and
574 A.M.G.

575

576

577 **SUPPORTING INFORMATION**

578 Additional Supporting Information may be found in the online version of this article:

579

580 **Appendix S1:** Box plot highlighting high levels of colinearity between site-level fire severity
581 and the amount of fire in a 1 km radius surrounding a site

582

583 **Appendix S2:** Statistical details of the multi-level modelling

584

585 **Appendix S3:** Mean values for species richness and percentage detection frequency for
586 individual bird species

587

588 **Appendix S4:** Model selection results (using BIC) for species richness and each of the
589 thirteen individual species across the 7 models of interest (see footnote)

590

591 **Appendix S5:** Detailed posterior summaries of the best models for species richness and each
592 individual species (selected using BIC) showing the lower and upper 95% credible intervals
593 and the Bayesian P-value (BPv).

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597 by the authors. Such materials are peer-reviewed and may be re-organized for online
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Table 1. Summary of important terms for the best fitting model (chosen using BIC) for species richness and each individual bird species. The number of pluses or minuses corresponds to 90%, 95% or 99% credible intervals for a given term, respectively. For categorical variables, a plus (+) indicates that first level is bigger than the second level. For example, for the White-browed Scrub-wren (*Sericornis frontalis*), the +++ for the 2011 versus 2009 comparison indicates that the detection frequency for 2011 was greater than for 2009 (at the 99% credible interval).

Variable	Prior	Year					Fire							
		Elev	SD	Gully	Aspect	10v9	11v9	12v9	11v10	12v10	12v11	Mod	Sev	Mod + Sev
Species Richness	+++	---	++	---			-	--		-			---	
White-browed Scrub-wren	++	---	+++	--			+++	+++	+++	+++	-		---	
Brown Thornbill	+++	---	+++										--	
Grey Fantail	+++		++		+	++		--	---	---	-		---	
Golden Whistler	+++	---	+++				---	---	---	---	---		---	
Striated Thornbill		-	+			+		--	--	---			---	
Silvereye	++	--	++	-			-	--	-	---		--		
Crescent Honeyeater	+++		+++			----	----	---		+++	+++		---	
Flame Robin		++	---			++	+++	+++		++	+			+++
Crimson Rosella	++	-		--			++							

Striated Pardalote	+++	-	-		+++			---	--		
Spotted Pardalote		---				---	---	---	---		---
Eastern Yellow Robin	++	---				--			-	---	
Eastern Spinebill	++	-	++	--	---	---	---	-	---	--	--

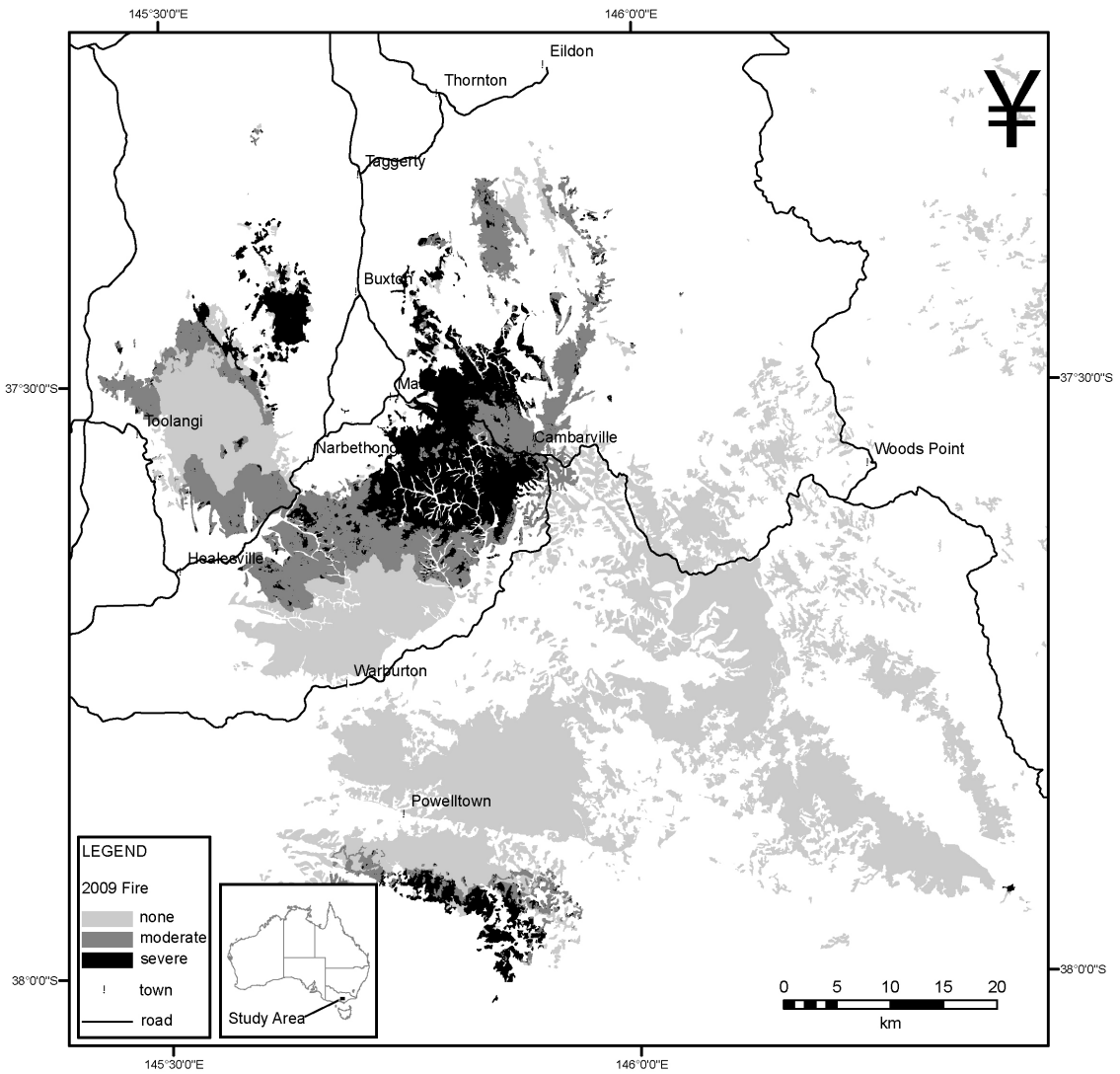
*Brown Thornbill has a severe landscape fire x Year interaction, as shown in the sub-table below.

Severe LF x Year

10v9	11v9	12v9	11v10	12v10	12v11
---		+++	+++	+++	

600 **Figure legends**

601 **Fig. 1.** The location of the montane ash forests in the Central Highlands of Victoria where
602 surveys of forest birds were completed. The hatched area shows the parts of the study region
603 burned in the 2009 fire.

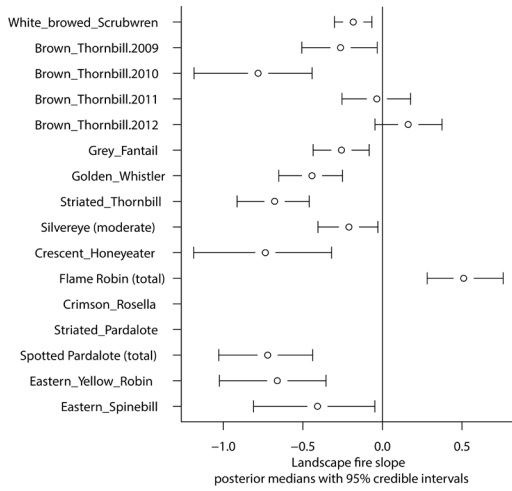


604

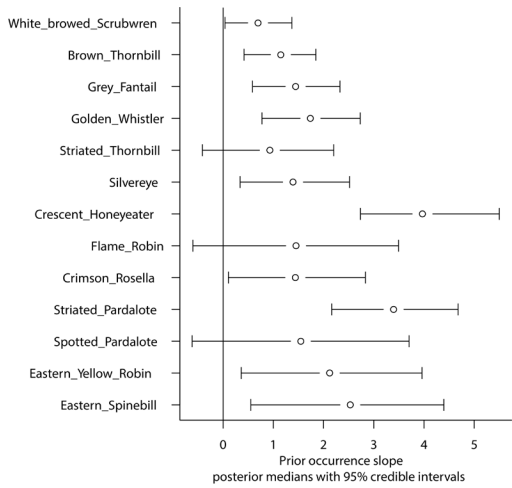
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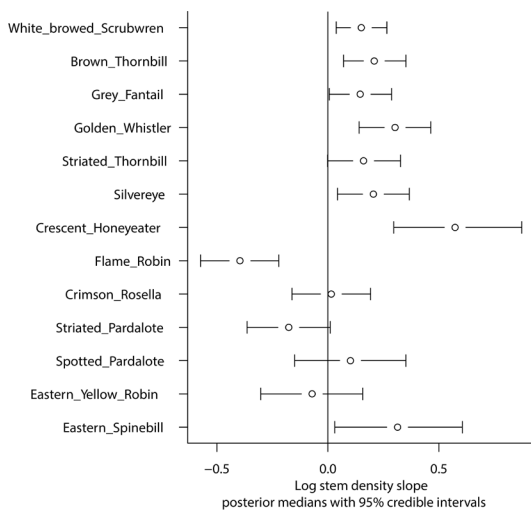
607 **Fig. 2.** Relationship between species richness and a) extent of severe fire, b) the logarithm of
 608 average species richness 2004–2007, and c) the logarithm of stem density. The solid line is
 609 the posterior median and the dashed lines are the 95% credible limits.



610



611



612

613

614 **Fig. 3.** Posterior medians and 95% credible intervals for the individual bird species and their
 615 relationship to a) extent of severe fire, b) the logarithm of average species richness 2004–
 616 2007, and c) the logarithm of stem density. The following notes apply to panel: a) the Year x
 617 extent of severe fire interaction is shown for Brown Thornbill, b) Crimson Rosella and
 618 Striated Pardalote did not have fire included in the final model (see text); and c) Silvereye
 619 responds to extent of moderate fire, while Flame Robin and Spotted Pardalote respond to
 620 extent of total fire.

