1   *Diversity and Distributions*

2   **Complex responses of birds to landscape-level fire extent, fire severity and**

3   **environmental drivers**

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5   David B. Lindenmayer[1, 2, 3, 4], Wade Blanchard[1], Lachlan McBurney[1, 4], David Blair[1, 4], Sam

6   C. Banks[1,2], Don A. Driscoll[1,2,3], Annabel L. Smith[1,2,3], and A. Malcolm Gill[1]

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8   [1]Fenner School of Environment and Society, The Australian National University, Canberra,

9   ACT 0200 and [2]ARC Centre of Excellence for Environmental Decisions, [3]National

10   Environmental Research Program, [4]Long-term Ecological Research Network, The Australian

11   National University, Canberra, ACT 0200, Australia

12   **Corresponding author:** David Lindenmayer, Fenner School of Environment and Society,

13   The Australian National University, Canberra, ACT 0200, Australia. Tel: +61 2 61250654;

14   Email david.lindenmayer@anu.edu.au

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Abstract

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

Location: South-eastern Australia.

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

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

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

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

(A) Introduction

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

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

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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

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

(A) Results

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

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

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

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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 × 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.

386

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558 Zozaya, E.L., Brotons, L. & Saura, S. (2012b) Recent fire history and connectivity patterns

559   determine bird species distribution dynamics in landscapes dominated by land

560   abandonment. *Landscape Ecology,* **27**, 171–184.

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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.

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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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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).

						Year						Fire		
Variable	Prior	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	++	-		--			++							

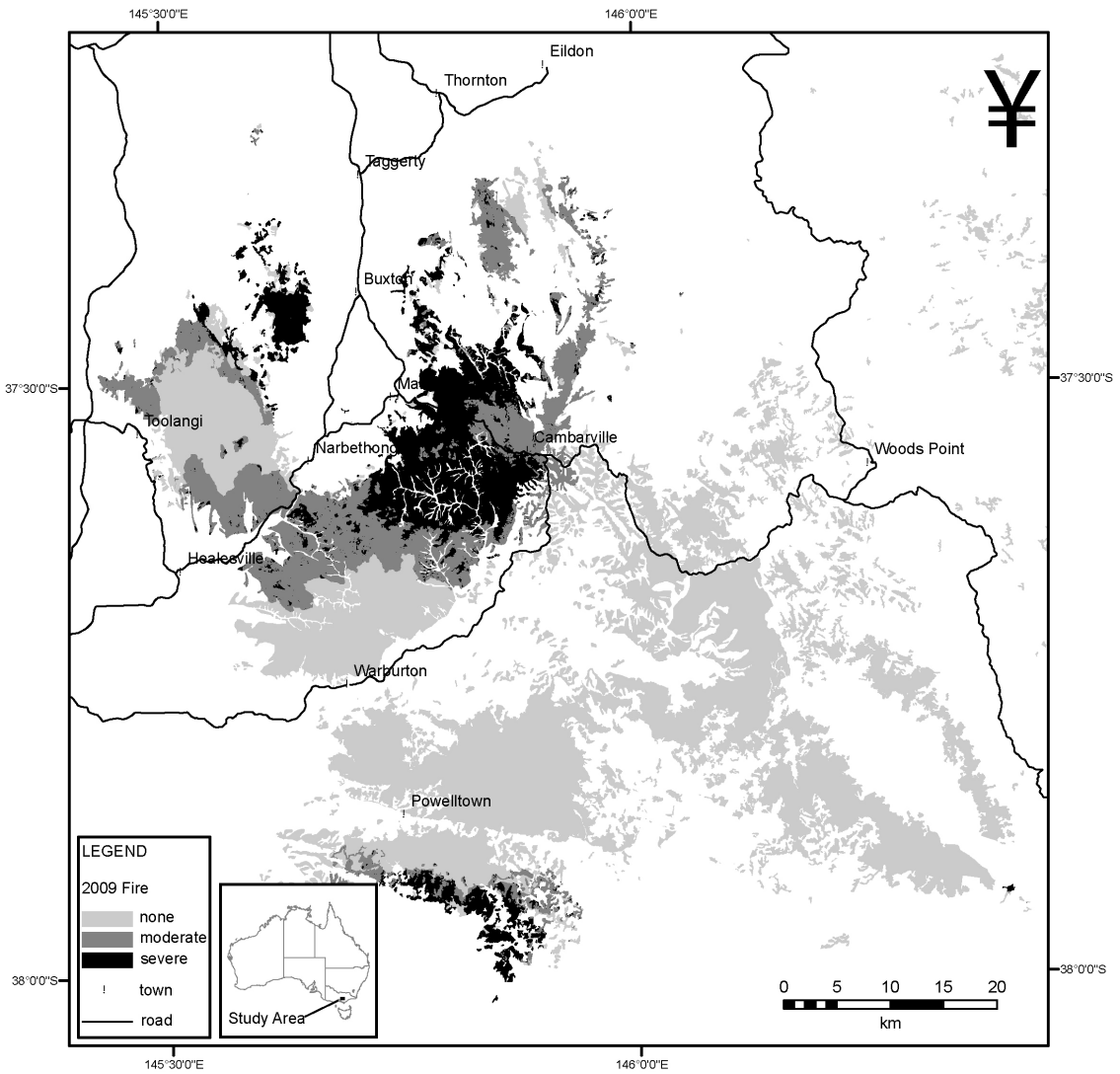| Species											
Striated Pardalote	+++	-	-		+++			---	--			
Spotted Pardalote		---				---	---	---	---			---
Eastern Yellow Robin	++	---				--			-		---	
Eastern Spinebill	++	-	++	--	---	---	---	-	---	--	--	

*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
---		+++	+++	+++	

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.
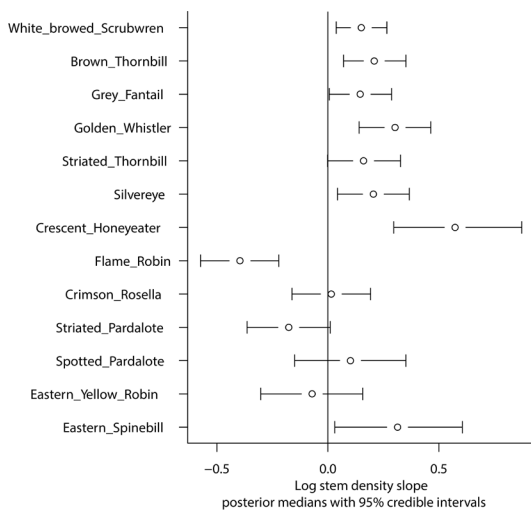

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607 **Fig. 2.** Relationship between species richness and a) extent of severe fire, b) the logarithm of

608 average species richness 2004–2007, and c) the logarithm of stem density. The solid line is

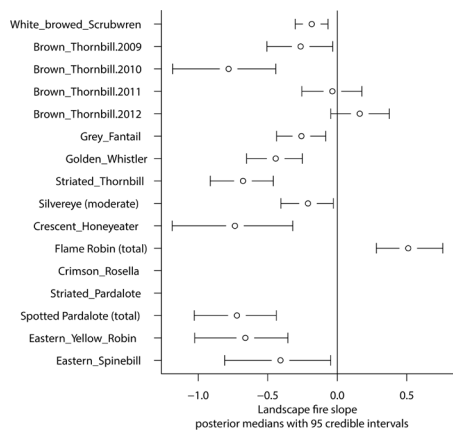609 the posterior median and the dashed lines are the 95% credible limits.
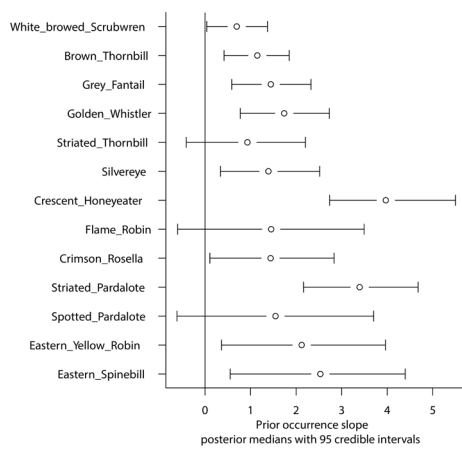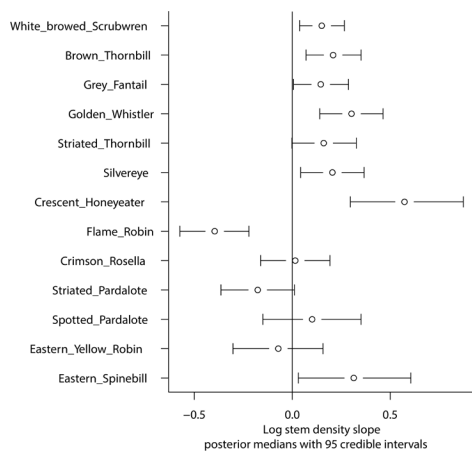
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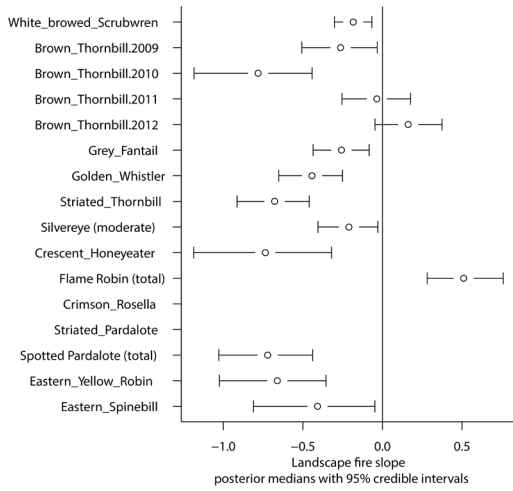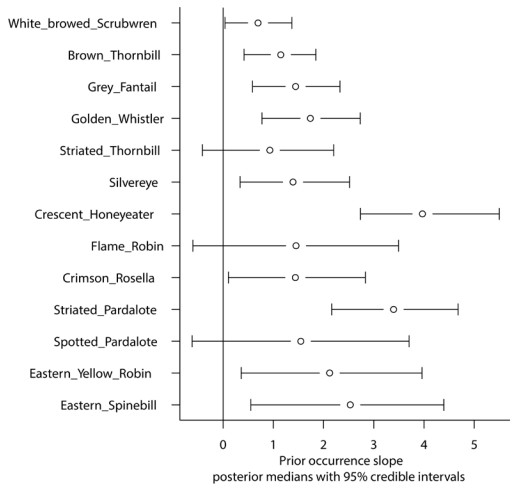
Fig. 3. Posterior medians and 95% credible intervals for the individual bird species and their relationship to a) extent of severe fire, b) the logarithm of average species richness 2004–2007, and c) the logarithm of stem density. The following notes apply to panel: a) the Year x extent of severe fire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

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