

1 **Vegetation structure moderates the effect of fire on bird assemblages in a**
2 **heterogeneous landscape**

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17 Running title: Fire effects on bird assemblages

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19

20 **Abstract**

21 Ecological theory predicting the impact of fire on ecological communities is typically focused on
22 post-disturbance recovery processes or on disturbance-diversity dynamics. Yet the established
23 relationship between vegetation structure and animal diversity could provide a foundation to predict
24 the short-term effects of fire on biodiversity, but has rarely been explored. We tested the hypothesis
25 that fire effects on bird assemblages would be moderated by increasing vegetation structure. We
26 examined bird assemblages in burnt and unburnt sites at one year and six years after a wildfire, and
27 compared richness and composition responses among and within three structurally distinct
28 vegetation types in the same landscape: heath, woodland and forest. We found that short-term
29 changes in bird assemblage composition were largest in simple heath vegetation and smallest in
30 complex forest vegetation. The short-term change in species richness was larger in forest than in
31 heath. We also found that among-site assemblage variability was greater shortly after fire in heath
32 and woodland vegetation compared with forest vegetation. Our results indicate that complexity in
33 vegetation structure, particularly overstorey cover, can act as an important moderator of fire effects
34 on bird assemblages. Mechanisms for this response include a greater loss of structure in vegetation
35 characterised by a single low stratum, and a proportionally greater change in bird species
36 composition despite a smaller absolute change in species richness. We discuss our results in the
37 context of a new conceptual model that predicts contrasting richness and composition responses of
38 bird assemblages following disturbance along a gradient of increasing vegetation structure. This
39 model brings a different perspective to current theories of disturbance, and has implications for
40 understanding and managing the effects of fire on biodiversity in heterogeneous landscapes.

41

42 **Key words:** conceptual model, community composition, disturbance, habitat complexity, patch-
43 mosaic, succession.

44 **Introduction**

45

46 Understanding the effects of fire in heterogeneous landscapes is of significant interest to ecologists
47 and land managers (Faivre et al. 2011; Kerby et al. 2007; Lindenmayer et al. 2014; Pastro et al.
48 2011; Turner 1987), but accurate prediction of the impacts of fire on animal assemblages is
49 difficult. Much of the theory underpinning fire ecology has centred on patterns of recovery, such as
50 succession and post-fire recolonisation (Franklin et al. 2000; Kelly et al. 2011; Watson et al. 2012).
51 Other theory has been developed to understand how spatial and temporal patterns of fire can
52 influence biodiversity, including the patch-mosaic concept (Bradstock et al. 2005; Parr and
53 Andersen 2006; Pickett and White 1985) and the intermediate disturbance hypothesis (Connell
54 1978; Westgate et al. 2012). This ecological theory has informed many areas of fire ecology, but
55 there remains much to learn about fire impacts (Bradstock et al. 2012). For example, there is mixed
56 support for the intermediate disturbance hypothesis (Fox 2013; Pastro et al. 2011), and some
57 frameworks for understanding post-disturbance succession lack specificity (Keeley et al. 2006;
58 Lindenmayer et al. 2008b; Smith et al. 2012). Further research is required to develop a better
59 understanding of how fire affects different animal assemblages.

60 One potential avenue for further research is the integration of vegetation structure into studies
61 on fauna responses to fire. Fire can have dramatic effects on vegetation structure (Fuhlendorf et al.
62 2006; Santana et al. 2012), and therefore its associated fauna. Vegetation structure is also an
63 important driver of animal species diversity in terrestrial ecosystems worldwide (Bohning-Gaese
64 1997; Tews et al. 2004). For example, empirical studies have shown that bird species richness
65 increases with the vertical height of vegetation (e.g. Kutt and Martin 2010; Lindenmayer et al.
66 2008a; MacArthur and MacArthur 1961). Each additional stratum adds substrates for foraging,
67 nesting, and shelter, thus increasing niche availability, facilitating species coexistence, and driving
68 higher diversity. Previous studies that have linked vegetation structure to animal responses to fire,

69 however, have focused on its role in moderating species recovery (Lindenmayer et al. 2008a;
70 Monamy and Fox 2000), and not as a tool to predict short-term impacts.

71 The heterogeneity of landscapes is strongly influenced by the occurrence of different
72 vegetation types (Forman 1995), and can facilitate or retard the effects of disturbance (Turner
73 1987). When fire occurs across multiple vegetation types, the differences in structure may be
74 critical to how faunal assemblages are affected (Kutt and Martin 2010; Lindenmayer et al. 2008a;
75 Monamy and Fox 2000). However, most studies have examined the effects of fire on assemblages
76 in a single vegetation type, such as grassland (Collins and Calabrese 2012; Coppedge et al. 2008) or
77 forest (Clavero et al. 2011; Schimmel and Granstrom 1996). These studies can provide valuable
78 insight into how changes in vegetation after fire can alter faunal assemblages (Barton et al. 2014;
79 Brotons et al. 2004; Faivre et al. 2011; Pastro et al. 2011; Santana et al. 2012), but provide limited
80 information about the relative impact of fire on animals in different and distinct vegetation types
81 within a landscape.

82 There are contrasting expectations for how vegetation structure might influence the responses
83 of animals to fire. First, many fire-prone landscapes consist of structurally simple vegetation, such
84 as the savannah grasslands of tropical latitudes that rebound rapidly from fire (Murphy and
85 Bowman 2012). This suggests that the impact of fire might be small in structurally simple
86 vegetation. However, studies have also demonstrated show that complex vegetation prior to a
87 disturbance has greater potential to retain structure following a disturbance (Franklin et al. 2002),
88 and that complex vegetation can be more resilient to disturbance (Lavorel 1999). This suggests that
89 the impact of fire might be limited in more complex vegetation. To the best of our knowledge, there
90 have been no previous studies that have examined these contrasting expectations in a single fire-
91 prone and structurally heterogeneous landscape.

92 In this investigation, we test the hypothesis that the impact of fire on bird assemblages would
93 be smaller in structurally complex vegetation compared with structurally simple vegetation. Our
94 study landscape allowed for an explicit comparison of bird assemblage responses to fire among

95 distinct vegetation types, including heath, open woodland and tall forest vegetation. This extends
96 the well-established phenomenon that bird assemblages differ in composition among vegetation
97 types, and instead examines how this general pattern might moderate fire impacts. Our test of
98 whether vegetation structure moderates fire effects on species assemblages places an emphasis on
99 the need for explicit consideration of habitat structural attributes to predict where a fire might have
100 the greatest impact. We use our results to develop a conceptual model for exploring the role of
101 vegetation structure in moderating disturbance effects on animal assemblages in heterogeneous
102 landscapes.

103

104 **Methods**

105

106 **Study area and design**

107

108 We conducted this study in Jervis Bay Territory, approximately 200km south of Sydney in south-
109 east Australia (150.70° East, -35.15° South). The Jervis Bay Territory includes Booderee National
110 Park, which covers approximately 7500 hectares (Fig. 1), and is comprised of several vegetation
111 communities (Lindenmayer et al. 2008a), with forest, woodland and heathland being the three most
112 widespread vegetation types (Fig 1). In September 2003, permanent study sites were established
113 across the National Park as part of a landscape-scale monitoring program (Lindenmayer et al.
114 2008a), with the number of sites in each of the different vegetation types generally proportional to
115 the amount of cover of that vegetation. Each site was 100 metres long, marked with a central 100-
116 metre transect line, and had permanent markers placed at 0, 20, 40, 60, 80 and 100 metres.

117 In December 2003, an unplanned wildfire burnt approximately 50% of Booderee National
118 Park, but occurred unevenly across the different vegetation communities (Fig. 1). This provided an
119 opportunity to conduct a ‘natural experiment’ to test the effects of recent fire on animal
120 assemblages across multiple vegetation types. Active and widespread suppression of fire does not

121 occur in Booderee National Park. Therefore, the experimental ‘treatment’ applied to our sites by the
122 2003 wildfire is compared against a set of ‘unburnt’ sites with a complex fire history. For example,
123 since 1972 the number of fires in any given part of the National Park has varied from none to five
124 (Lindenmayer et al. 2008a), and three of the unburnt sites used in our analyses were burnt once in
125 the ten years prior to the major 2003 wildfire. Our comparison of burnt with unburnt sites in
126 different vegetation types therefore averages across the fire histories of individual sites, and focuses
127 on the short-term responses of birds to vegetation structural changes as a result of the 2003 fire.

128 In this study, we selected 56 sites from the three dominant vegetation types: heath (15 burnt
129 sites, 2 unburnt), woodland (12 burnt sites, 7 unburnt) and forest (11 burnt sites, 9 unburnt).
130 Together, these vegetation types cover approximately 70% of the total vegetative cover of Jervis
131 Bay Territory (Fig. 1, Table S1).

132

133 **Data collection**

134

135 We completed bird surveys in September 2004 and 2009, approximately one year and six years
136 after the 2003 wildfire. September is the breeding season for the majority of bird species in
137 Booderee National Park, and when most summer migrants have arrived. For each survey year, we
138 performed two repeat point counts of birds at the 20 m and 80 m markers in each site, resulting in
139 four point counts in each site per survey year. We recorded all birds seen or heard within a 50 m
140 radius of the marker during a 5-minute period, excluding birds flying overhead. We conducted
141 surveys between dawn and mid-morning. Each site (i.e. both markers) was surveyed on a different
142 day by a different observer to reduce day effects on detection and to overcome potential observer
143 heterogeneity problems (Cunningham et al. 1999). Our survey protocol followed standards that are
144 widely reported in the ecology literature (de Lima et al. 2013; Driscoll and Lindenmayer 2010; Ikin
145 et al. 2013), and helps to correct for false negative errors (i.e. failure to detect a species that is

146 present at the site (Tyre et al. 2003). We pooled surveys at each plot within a site to give one set of
147 observations per site per year.

148 In December 2004 and 2009, we measured six vegetation structural attributes in two 20 x 20
149 m plots located between the 20-40 m and 60-80 m points in every site. The measures were:
150 estimated percentage cover of overstorey, midstorey and understorey vegetation, as well as
151 percentage cover of grass, leaf litter, and bare ground. We defined overstorey as vegetation over 10
152 metres in height, midstorey between 2 and 10 metres, and understorey as less than 2 metres in
153 height. Each stratum was assessed independently of the other, meaning that a site could have, for
154 example, both 80% understorey cover as well as 80% overstorey cover. We took the average of the
155 measures from the two plots to give a single measure for each vegetation attribute at each site, and
156 used these in our subsequent analyses.

157

158 **Data analysis**

159

160 Gradients in vegetation structure

161

162 We quantified vegetation attributes at each site to compare structure across the three vegetation
163 types. We used principal components analysis (PCA) to summarise the major gradients in
164 vegetation structure using a co-variance matrix of percentage cover of the six vegetation attributes.
165 We used the first two components of the PCA as response variables in a linear mixed model to
166 compare the changes in vegetation structure within and among vegetation types in GenStat 14
167 (VSNI 2013). We fitted fire (burnt, unburnt), vegetation type (forest, woodland, heath), and time
168 since fire (1 year, 6 years) as fixed factors, and site as a random factor to account for repeated
169 measures of each site.

170

171 Bird species richness

172

173 We used the software EstimateS 9.1 (Colwell 2013) to estimate ‘true’ species richness of birds from
174 our study sites and assess the thoroughness of our bird surveys. We calculated estimates using the
175 abundance-based coverage (ACE) estimator and the Chao 1 estimator, and compared the estimated
176 number of species with the observed number of species. These two estimators consider the number
177 of rare species in a sample (counts from a site) and were the most appropriate for our data
178 (Magurran and McGill 2011). We calculated separate species richness estimates for each vegetation
179 type in 2004 and 2009.

180 We tested for differences in bird species richness among burnt and unburnt sites in each
181 vegetation type using a generalised linear mixed model with a Poisson error distribution (estimated
182 dispersion = 0.91) and log-link function in GenStat 14 (VSNI 2013). We fitted burnt status,
183 vegetation type, and time since fire as fixed factors. We also fitted site as a random factor to
184 account for temporal autocorrelation due to repeated measures of each site. The significance of
185 effects was determined using Wald tests. We tested for spatial autocorrelation in model residuals
186 using the ‘correlog’ function in the ‘ncf’ package in R (Zuur et al. 2009), but found no evidence of
187 this for species richness among sites in close proximity.

188

189 Bird assemblage composition

190

191 We examined differences in bird assemblage composition among burnt and unburnt sites in each
192 vegetation type using three different multivariate approaches. For all tests, bird abundance data
193 were square root transformed to reduce the influence of abundant species. We used a Mantel test to
194 examine the correlation between pairwise site dissimilarity in bird assemblage composition (Bray-
195 Curtis), and pairwise site dissimilarity in vegetation structure (Euclidean) across all sites. . We
196 repeated the test for each survey year to determine whether the correlation was different at one year

197 after the wildfire compared with six years after wildfire. Significance was determined using 9999
198 permutations of the data in PC-Ord 5 (McCune and Grace 2002).

199 We used canonical analysis of principal coordinates (Anderson and Willis 2003) to examine
200 how bird assemblage composition responded to fire within each vegetation type. We constrained
201 the ordination with regard to the two gradients in vegetation complexity identified in the PCA
202 above. We plotted mean scores in an ordination diagram, and grouped sites according to their
203 vegetation type, burnt status, and time since fire. This allowed us to compare the interactive effects
204 of vegetation type and fire on changes in bird assemblage composition. We examined the strength
205 of the correlation between the two vegetation structure gradients and the first two constrained
206 ordination axes, and identified bird species that contributed strongly to the multivariate patterns ($r \geq$
207 ± 0.3). We used 9999 permutations of the data to test for the significance of correlations between
208 the two vegetation gradients and the first two constrained ordination axes.

209 We used Permutational Analysis of Multivariate Dispersion (Anderson et al. 2006) to test for
210 differences in among-site variability in assemblages from each vegetation type between one and six
211 years after the wildfire. This test calculates the average distance to the centroid of a group of
212 samples projected in multivariate space, with a greater distance to centroid indicating greater
213 among-sample variability (Anderson et al. 2006). Statistical significance was determined from
214 10,000 permutations of the data.

215

216 **Results**

217

218 **Gradients in vegetation structure**

219

220 Our principal components analysis produced two new axes that accounted for a combined 73% of
221 the variation in vegetation structure (Table S2). The first axis (PC1) had high loadings for leaf litter
222 and overstorey cover, representing a gradient of increasing overstorey density, i.e. increasing

223 vertical structure (Fig. S2). The second axis (PC2) had high positive loadings for understorey cover
224 and negative loadings for bare ground, representing a gradient of increasing understorey density, i.e.
225 increasing horizontal structure (Fig. S2). The contrasting vertical and horizontal structure of the
226 three vegetation types can be seen clearly in Figure 1. We found a significant interactive effect of
227 fire, vegetation type and time on site vertical structure (PC1) scores (Wald₂ = 11.61, P = 0.005,
228 Table S3). Vertical structure of unburnt heath vegetation, but not burnt heath vegetation, increased
229 from one year to six years after the wildfire (Fig. S3). For horizontal structure (PC2), we found no
230 interactive effect of fire, vegetation type and time (Wald₂ = 1.97, P = 0.380), but there was a
231 significant interaction between fire and time (Wald₁ = 51.40 P < 0.001). There was a large decrease
232 in horizontal structure for all vegetation types one year after the fire, with the largest being evident
233 for heath vegetation. We found no difference in horizontal structure between burnt and unburnt sites
234 after six years (Fig. S3).

235

236 **Bird species richness**

237

238 We recorded 4,181 birds from 68 species during our surveys in 2004 and 2009 (Table S4). Our
239 surveys were thorough, ranging from 68-97 % in our 2004 surveys, and 88-97% in our 2009
240 surveys (Table S5). We detected no interactive effects of fire, vegetation type and year on bird
241 species richness (Wald₂ = 1.93, P = 0.387). However, we found a significant main effect of
242 vegetation type (Wald₂ = 35.97, P < 0.001, see Table S6), with species richness of birds lowest in
243 heath and highest in forest (Fig. 2). Although no significant interaction was detected, the difference
244 in richness between burnt and unburnt vegetation was greater in woodland and forest than in heath
245 at one year after the fire. These apparent differences were absent six years later.

246

247 **Bird assemblage composition**

248

249 We found a significant positive correlation between pairwise bird assemblage dissimilarity and
250 vegetation structural dissimilarity, and that the magnitude of the correlation increased from one year
251 after the fire ($r = 0.218$, $P = 0.0003$) to six years after the fire ($r = 0.304$, $P < 0.0001$). This indicated
252 that sites with similar vegetation structure shared similar bird assemblages, but that this relationship
253 was weaker after recent fire.

254 The first two axes of the principal coordinate analysis explained 20.1% and 11.5% of the
255 variance in bird assemblage composition, respectively (Fig. 3). Ordination of constrained site scores
256 showed that bird assemblages were clearly differentiated *between* vegetation types along a gradient
257 of increasing vertical structure, represented by axis one (Fig 3a, $P < 0.001$). Bird assemblages were
258 also differentiated *within* each vegetation type along a gradient of increasing horizontal structure,
259 represented by axis two (Fig 3a, $P < 0.001$). Sites burnt one year after the wildfire always had bird
260 assemblages that changed in composition in the direction of decreasing horizontal structure.
261 Further, the magnitude of the difference in bird composition between burnt and unburnt sites was
262 greatest in heath vegetation, followed by woodland, and smallest in forest vegetation.

263 Several bird species were strongly correlated with the canonical ordination axes (Fig 3b). Two
264 heath specialists, the southern emu-wren (*Stipiturus malachurus*) and eastern bristlebird (*Dasyornis*
265 *brachypterus*), were each strongly correlated with low vertical structure (i.e. heath vegetation), but
266 also were correlated with high horizontal structure (i.e. dense understorey). In contrast, two forest
267 specialists, the grey fantail (*Rhipidura albiscapa*) and eastern spinebill (*Acanthorhynchus*
268 *tenuirostris*), were correlated with high horizontal and vertical structure (i.e. forest with dense
269 understorey). The crimson rosella (*Platycercus elegans*) was strongly correlated with low horizontal
270 structure and high vertical structure (i.e. forest with open understorey).

271 We found a significant overall difference in spatial variability of bird assemblages among
272 vegetation types at one and six years after the wildfire ($F = 4.34$, $P < 0.001$). Post-hoc comparisons
273 indicated that variability among sites within each vegetation type was significantly higher one year

274 after fire compared with six years for heath and woodland, but not forest vegetation (Fig 4). All
275 vegetation types had similar levels of among-site variability six years after fire.

276

277 **Discussion**

278

279 Heterogeneous landscapes provide distinct challenges to understanding the effects of disturbance on
280 biodiversity (Barton et al. 2014; Fuhlendorf et al. 2006; He and Mladenoff 1999; Lindenmayer et al.
281 2014; Turner 1987). Our study of the effects of fire in a landscape with a mix of different vegetation
282 communities revealed an interacting role of vertical and horizontal vegetation structure in
283 moderating bird assemblage responses to fire. Our results supported our hypothesis that increased
284 vegetation structure would reduce the effects of wildfire on bird assemblages, although we found
285 this only for composition changes and not richness changes. Below we discuss the links between
286 vegetation structure and bird assemblage responses, and then develop our findings into a conceptual
287 model to provide a framework to link vegetation structure with fire disturbance effects on animal
288 assemblages.

289

290 **The moderating influence of vegetation structure**

291

292 We have shown how vertical and horizontal structure is associated with bird assemblage patterns
293 among different vegetation types. Effects of vegetation structure on bird communities are
294 commonly reported (e.g. Barton et al. 2014; Bohning-Gaese 1997; Davis et al. 2000; MacArthur
295 and MacArthur 1961; Montague-Drake et al. 2009), but the separate effects of vertical and
296 horizontal structure are less well understood. For example, we found higher species richness of
297 birds in forest vegetation compared with woodland or heath vegetation. This was due to greater
298 overstorey cover, which was a strong driver of the occurrence of the grey fantail and eastern
299 spinebill, for example. It is hypothesised that greater overstorey cover generates greater resource

300 availability in the form of foliage, branch and trunk foraging substrates, as well as shelter from
301 predators for a range of species (Montague-Drake et al. 2009; Recher et al. 1985). Although vertical
302 structure was important for determining differences in bird assemblages *between* vegetation types,
303 horizontal structure in the lower stratum was associated with changes in bird assemblage
304 composition *within* vegetation types. The variation in horizontal structure was due to changes in
305 understorey shrub cover, and was a strong driver of the occurrence of heath specialists such as the
306 eastern bristlebird and southern emu wren (Lindenmayer et al. 2008a).

307 Notably, we found a loss of horizontal structure in burnt areas of all vegetation types, and this
308 was matched by a corresponding change in bird assemblage composition along this structural
309 gradient. This suggests that a change in the density of shrubs and foliage in this stratum is a key
310 mechanism linking the effects of fire to changes in bird assemblage composition across multiple
311 vegetation types. This can lead to negative impacts on foraging resources and shelter from potential
312 predators for species that use this vegetation layer (Brotons et al. 2004; Davis et al. 2000;
313 Lindenmayer et al. 2009). Further, the magnitude of this change increased when vertical structure
314 was low or absent. This was highlighted by the greater change in assemblage composition in heath
315 compared with forest vegetation. This pinpoints the critical role of vertical structure in moderating
316 the effects of fire in our study system, even after the loss of understorey vegetation.

317 Our study provides a novel example of the moderating effects of vegetation structure in a
318 terrestrial ecosystem. Previous research has identified vegetation structure as an important
319 determinant of the recovery of faunal assemblages after fire, including for reptiles (Lindenmayer et
320 al. 2008b) and mammals (Monamy and Fox 2000). However, these examples have focused on the
321 role of vegetation in moderating the recovery trajectories, and not the initial impacts. Our finding
322 that structurally simple vegetation may be more vulnerable to perturbations than complex
323 vegetation with multiple strata, and experience a more profound short-term change in its associated
324 fauna, suggests that habitat structural attributes may play a key role in moderating the short-term
325 impacts of fire.

326

327 **A conceptual model to explore fire effects on biodiversity in heterogeneous landscapes**

328 Our findings support the hypothesis that increasing vegetation structure moderates the effects of fire
329 on bird assemblages. However, we found that this result was the case only for bird composition
330 changes and not for species richness. This suggests a complex interplay between fire, vegetation
331 structure and bird assemblages, with fire affecting this relationship in different ways for species
332 richness and species composition. From this result, we describe a conceptual model (Fig. 5) that
333 summarises our results into a generalised prediction of the short-term impact of fire on bird
334 diversity across a vegetation gradient of increasing structural complexity. We split bird diversity
335 into its species richness (alpha-diversity) and compositional (beta-diversity) components to
336 highlight the contrasting patterns found in our study. Our model predicts that the short-term change
337 in species richness after fire will be higher in complex vegetation relative to simpler vegetation
338 (compare richness of burnt versus unburnt sites 2004 forest with 2004 heath in Fig. 2). Our model
339 also predicts that fire will cause a greater change in species composition in simple vegetation
340 relative to complex vegetation (compare among-site dissimilarity of sites from 2004 heath with
341 2004 forest in Fig. 4). The contrasting response of species richness and composition to fire is in part
342 due to the underlying relationship between species richness and overstorey cover (see Fig. 2).
343 Complex vegetation characterised by multiple strata contains a greater variety of feeding resources,
344 foraging substrates, and nesting and perching sites, thus enabling greater specialisation among
345 species and driving higher richness in forest vegetation (Recher 1969; Tews et al. 2004). Moreover,
346 this gradient in richness means that structurally simple vegetation, with lower species richness, is
347 susceptible to proportionally greater changes in bird species composition, even though absolute
348 changes in richness can be smaller. The different effects of fire on alpha and beta components of
349 animal diversity has not been explored in detail (Farnsworth et al. 2014), and represents a potential
350 new area for investigation.

351 Our conceptual model has clear links with the recent synthesis of disturbance effects on
352 ecosystems by Peters et al. (2011). These authors describe a framework that outlines three key
353 aspects important to understanding the disturbance cycle, including (i) initial system properties, (ii)
354 disturbance mechanisms and (iii) post-disturbance legacies. Our model addresses the first two of
355 these aspects. Knowledge of the spatial distribution of structurally distinct vegetation types provides
356 valuable information about initial ecosystem properties, and enables better prediction of fire impact
357 on bird communities. Further, the role of vegetation complexity in driving species richness
358 gradients across landscapes provides some information about potential mechanisms of fire effects.
359 Incorporating information about fire severity and frequency in each vegetation type could be an
360 important next step in understanding post-disturbance legacies (Franklin et al. 2000; Peters et al.
361 2011; Whelan 1995). This would complement other conceptual work on periodic disturbances
362 (Tanentzap et al. 2013; Thom et al. 2013), and lead towards better integration of prediction with
363 knowledge of disturbance regimes.

364 We have outlined an example of the relative impacts of fire on animal communities across
365 structurally distinct vegetation types within the same landscape. This provides critical context to our
366 findings, with our conceptual model likely to be most applicable to heterogeneous landscapes
367 comprising a mix of distinct vegetation types, such as is typical in many Mediterranean-climate
368 regions around the world (Cowling et al. 1996; Lavorel 1999). However, a key strength of our
369 conceptual model is that it builds on the well-established relationship between animal species
370 diversity and habitat structure and complexity. Many empirical studies have documented the effects
371 of habitat complexity and heterogeneity on various groups of organisms and in different biomes
372 (e.g. August 1983; Hansen 2000; Heck and Wetstone 1977; Lassau and Hochuli 2004; Tews et al.
373 2004). This rich literature could be used to develop further mechanistic hypotheses about the
374 disturbance response of different taxa in other kinds of ecosystems. For example, the composition
375 and complexity of plant communities has been linked to the diversity and biomass of arthropod
376 communities through resource and habitat provision (Borer et al. 2012). Alternatively, vegetation

377 structure may underpin reptile responses by providing basking opportunities and foraging sites
378 (Pike et al. 2011). Of course, different specific predictions might be tailored for different taxa, as
379 the relative importance of different measures of structure, complexity or heterogeneity will vary.

380

381 **Implications**

382

383 The moderating effect of vegetation structure has significant implications for fire management and
384 biodiversity conservation. Altered disturbance regimes can lead to simplification of landscapes and
385 the loss of variation in vegetation structure and composition (Grossmann and Mladenoff 2007;
386 Vandvik et al. 2005). From the perspective of our study, such simplification may also lead to a loss
387 of variation in faunal responses to disturbance among different vegetation types, and may diminish
388 the resilience of heterogeneous landscapes to major ecological disturbances such as fire. In such
389 landscapes, meta-population and meta-community dynamics among vegetation patches are critical
390 to their functioning, and contribute to landscape-scale biodiversity patterns (Aauri and de Lucio
391 2001; Biswas and Wagner 2012; Tschardt et al. 2012). Our finding that habitat heterogeneity is
392 linked to the differential responses of birds to fire within a landscape, provides further evidence that
393 local-scale processes underpin the maintenance of biodiversity within landscapes (Barton et al.
394 2013; Brotons et al. 2004). It also supports theory that landscape heterogeneity can moderate the
395 effects of disturbance more generally (Turner 1987, 2010).

396 Much of the current thinking about managing the effects of fire on biodiversity is dominated
397 by the patch-mosaic concept where a diversity of fire histories is considered important for
398 generating ecosystem heterogeneity (Kelly et al. 2012; Parr and Andersen 2006). Our finding that
399 vegetation structure can moderate the impacts of fire on bird assemblages goes beyond the domain
400 of the patch-mosaic concept and suggests that fire management needs to incorporate vegetation
401 attributes in addition to fire history attributes. This is because the short-term impacts of fire on
402 fauna will vary depending on vegetation structure, thus driving heterogeneity in faunal assemblages

403 independent of spatial patterns of fire history (Stirneman et al. 2014). This will enable the
404 prediction of the relative impact of fire in heterogeneous landscapes with variable vegetation.
405 Where fire occurs across multiple vegetation types, this requires careful consideration of the
406 potential for more pronounced effects on structurally simple vegetation, and associated changes in
407 faunal assemblages. This perspective is somewhat counter-intuitive, as fire management practices
408 may need to be concerned about both the structurally complex and species-rich places in a
409 landscape, as well as the less complex or less diverse parts of a landscape. Our model provides a
410 predictive framework to investigate in more detail the effects of fire and other disturbances on
411 faunal assemblages, and the moderating role of vegetation structure in heterogeneous landscapes.

412

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414

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419

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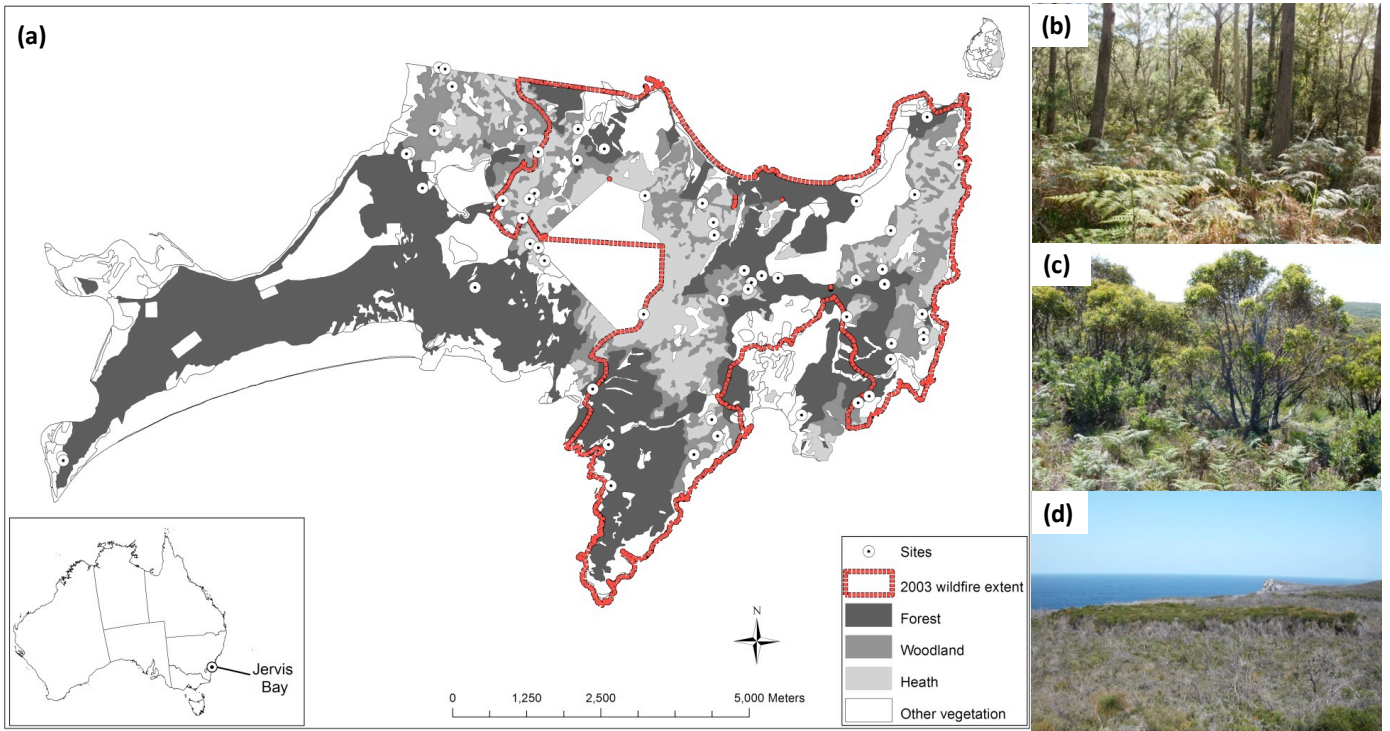
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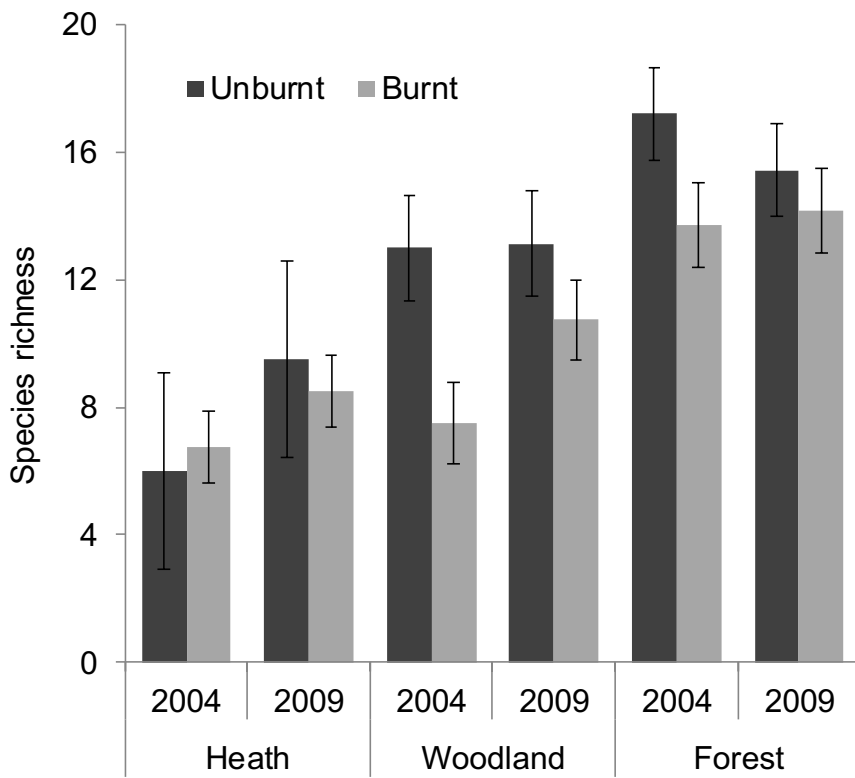


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589 **Figure 1.** A location map (a) showing the distribution of our survey sites and area burned by the
 590 2003 wildfire in Jervis Bay Territory, south-east Australia. Study sites were established in three
 591 distinct vegetation types including (a) forest, (b) woodland, and (c) heath. These vegetation types
 592 create a heterogeneous landscape and a wide gradient in structural complexity.

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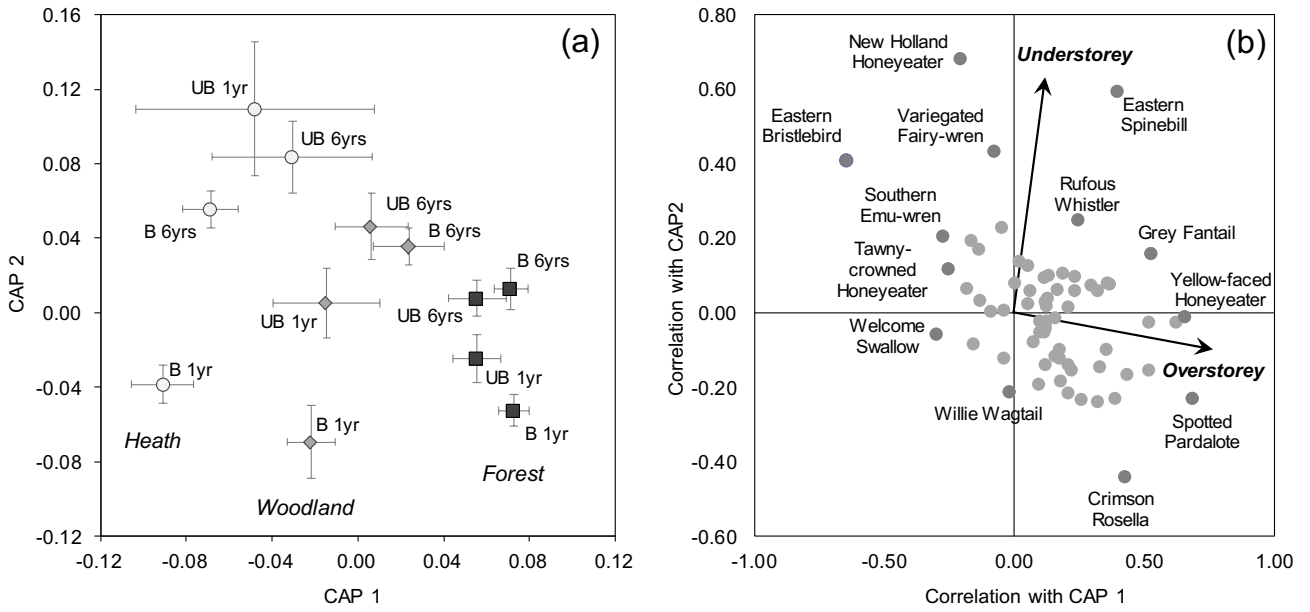


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596 **Figure 2.** Mean (\pm SE) species richness of bird assemblages in burnt and unburnt sites in Heath,

597 Woodland and Forest vegetation at one year (2004) and six years (2009) after wildfire.

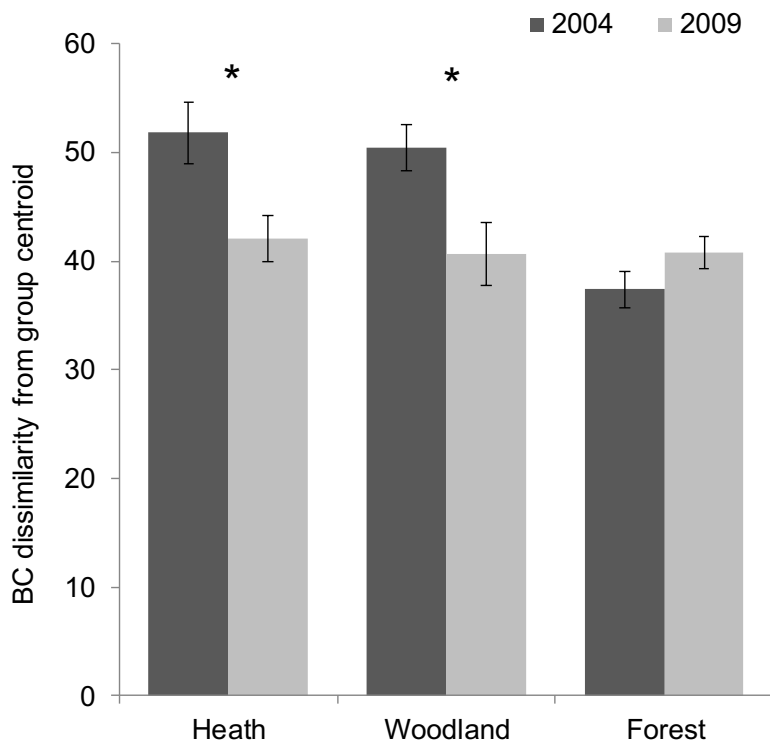
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600 **Figure 3.** Ordination of site scores derived from canonical correlation analysis of bird assemblages
 601 in three vegetation types at 1 year and 6 years after fire. (a) Mean (\pm SE) scores of burnt (B) and
 602 unburnt (UB) sites at one and six years after wildfire. (b) Correlation biplot of bird species (grey
 603 dots) and vegetation structural gradients (Understorey and Overstorey) with canonical axes. Bird
 604 species contributing strongly to patterns are indicated by the dark grey dots (see Table S4 for
 605 scientific names).

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608 **Figure 4.** Differences in among-site dissimilarity of bird assemblage across burnt and unburnt sites

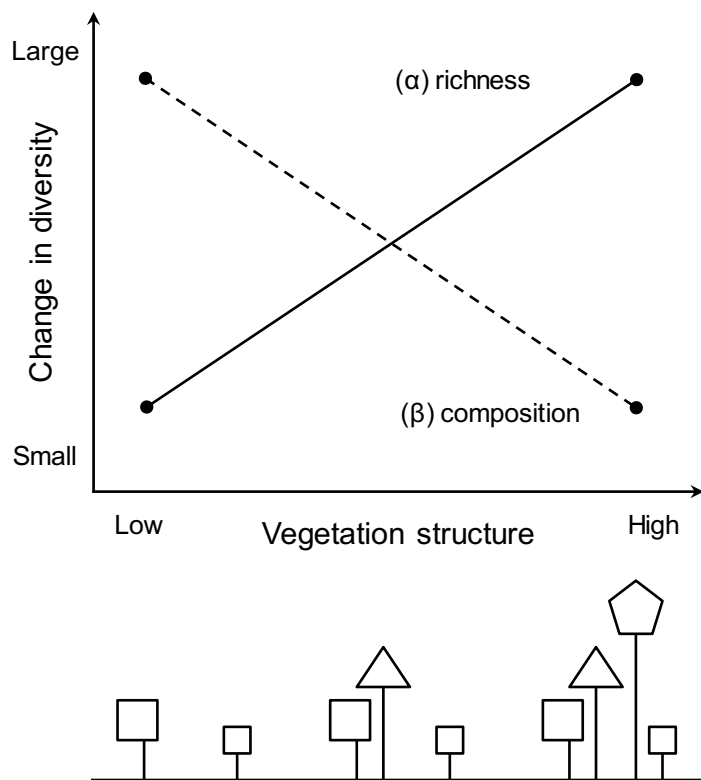
609 between Heath, Woodland and Forest at one year (2004) and six years (2009) after wildfire.

610 *Pairwise differences are significant at $p < 0.05$.

611

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615 **Figure 5.** A conceptual model depicting the expected short-term change in bird diversity after fire
 616 across a gradient of increasing vegetation structure. Species richness (solid line) can be expected to
 617 show the greatest change in structurally complex vegetation and the smallest change in structurally
 618 simple vegetation. In contrast, species composition (dotted line) can be expected to show the
 619 greatest change in simple vegetation and smallest change in complex vegetation.

620