

1 **Robustness of habitat-based surrogates of animal diversity: a multi-**
2 **taxa comparison over time**

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17 **ABSTRACT**

- 18 1. Many animal taxa respond strongly to spatial and temporal variation in vegetation structure
19 and floristic composition, suggesting that changes in vegetation could be a cheap and
20 readily observable surrogate for changes in animal assemblages. Yet there is considerable
21 uncertainty about how different taxa respond to vegetation over time, potentially limiting
22 the application of habitat-based surrogates to many areas of applied ecology.
- 23 2. We examined the strength and temporal consistency of habitat-based surrogates of three
24 different vertebrate taxa in a landscape with multiple vegetation types. We used regression
25 models to quantify the relationships between six vegetation attributes (species richness and
26 percentage cover of overstorey, midstorey and understorey) and three measures of bird,
27 mammal and reptile assemblages (abundance, species richness and composition).
- 28 3. We found that overstorey richness and cover had both consistent and strong positive effects
29 on bird assemblages. Vegetation effects were generally weaker and more variable for
30 mammals and reptiles compared with birds. Each taxon displayed different temporal
31 dynamics following fire, with negative effects on birds and mammals, but positive short-
32 term effects on reptiles. Surprisingly, fire increased vegetation effects on birds, but did not
33 consistently alter vegetation effects on mammals or reptiles, indicating a lack of concordant
34 responses among taxa.
- 35 4. *Synthesis and applications.* Empirical testing of habitat-based surrogates of multiple animal
36 taxa is needed to identify reliable and consistent management proxies. Our study suggests
37 that habitat-based surrogates could be useful metrics for quantifying changes in bird
38 assemblages through time and after fire, but that the same metrics could not be applied to
39 mammal and reptile assemblages. The absence of both strong and consistent effects of
40 vegetation attributes across the three groups of vertebrates suggests that taxon-specific

41 habitat surrogates may be required to detect changes over time and after disturbance within
42 heterogeneous landscapes.

43

44 **Key words:** biodiversity, birds, conservation, indicator, landscape, mammals, management,
45 reptiles

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48 INTRODUCTION

49 The enormous complexity of ecosystems presents a great challenge to measuring and
50 understanding changes in biodiversity (Rodrigues & Brooks 2007; Lewandowski, Noss &
51 Parsons 2010; Magurran & McGill 2011). This has resulted in the use of surrogate measures to
52 act as a simpler proxy for changes in biodiversity (Caro 2010; Kessler *et al.* 2011). One such
53 approach is the use of habitat-based surrogates, which are environmental variables that act as an
54 indirect measure of biodiversity (McGeoch 1998; Gollan *et al.* 2009; Banks-Leite *et al.* 2011;
55 Lindenmayer *et al.* 2014).

56 There is a substantial body of evidence showing that animal assemblages respond strongly
57 to spatial and temporal variation in vegetation structure and floristic composition (Tews *et al.*
58 2004; McElhinny *et al.* 2006; Schaffers *et al.* 2008; Qian & Kissling 2010). By extension, these
59 vegetation attributes might be a cheap and readily observable surrogate for the impacts of
60 environmental change on animal populations (Banks-Leite *et al.* 2011). Yet the extent to which
61 vegetation attributes might be used to reliably and consistently reflect changes in animal
62 assemblages from an explicit surrogacy perspective has received little attention (Gollan *et al.*
63 2009; Banks-Leite, Ewers & Metzger 2013).

64 Reliance on habitat-based surrogates for monitoring changes in animal communities has
65 been limited by a number of problems. First, the surrogate group (i.e. that which is measured,
66 typically vegetation) and the target group (i.e. that which the surrogate is a proxy for, often an
67 animal taxon) may respond differently to a particular drivers of change, thus weakening any
68 causal relationship between surrogate and target taxa. Yet, a strong surrogacy relationship is
69 exactly what is required to detect and accurately monitor biotic changes, such as the recovery of
70 biodiversity following a disturbance. Second, any given surrogate may be more effective for one
71 target taxon than another, but the taxonomic breadth of surrogacy relationships is rarely tested or

72 elucidated (Gollan *et al.* 2009; Caro 2010; Kessler *et al.* 2011; Larsen *et al.* 2012). Thus it is
73 unclear to what extent a habitat-based surrogate might accurately reflect change in one taxon but
74 not another. Finally, surrogacy relationships can vary across spatial scales (Banks-Leite, Ewers &
75 Metzger 2013; Westgate *et al.* 2014), and may be weaker when examined at smaller ‘within-
76 landscape’ scales compared with coarser extrapolated data at regional or continental scales
77 (Rodrigues & Brooks 2007). However, it is at smaller scales where surrogacy relationships have
78 some of their greatest utility as guides to changes in biodiversity and informing management
79 decisions. While some aspects of these problems are well known (Rodrigues & Brooks 2007;
80 Mellin *et al.* 2011; Larsen *et al.* 2012; Banks-Leite, Ewers & Metzger 2013), there have been
81 relatively few empirical evaluations of habitat-based surrogates across distinct vegetation types
82 (Cushman *et al.* 2008), after disturbance (Brennan *et al.* 2006), and over time (Fuller & Rothery
83 2013; Lindenmayer *et al.* 2014). Additional comprehensive studies are therefore needed to
84 identify robust habitat-based surrogates that perform well for monitoring the effects of
85 environmental change across different taxa.

86 In this study, we examine the extent to which potential habitat surrogates are robust
87 predictors of animal biodiversity over time. We selected a range of habitat variables (percentage
88 cover and species richness of overstorey, midstorey and understorey vegetation strata) as
89 potential surrogates of bird, mammal and reptile assemblages. Our study area consisted of
90 multiple vegetation communities within a single landscape (Lindenmayer *et al.* 2008b; Barton *et*
91 *al.* 2014), and provides a rare opportunity to test habitat surrogacy relationships across a wide
92 gradient in vegetation structure more commonly studied at much larger spatial scales. We
93 assessed the relationship between each vegetation attribute and the abundance, species richness
94 and assemblage composition of each vertebrate taxon, and asked the following questions:

95 1. Which vegetation variables have strong effects on the different animal taxa? At the outset
96 of our investigation, it remained unclear which animal taxon might respond most strongly
97 to the vegetation variables. However, we reasoned that there is likely to be greater
98 concordance among taxa if they shared similar ecologies. We therefore anticipated that
99 mammals and reptiles would exhibit similar responses to vegetation variables due to their
100 occurrence at ground level and close association with understorey vegetation (Fox, Taylor
101 & Thompson 2003; Lindenmayer *et al.* 2008c; Pereoglou *et al.* 2011), whereas birds were
102 likely to have a different response due to their strong association with vertical vegetation
103 structure (MacArthur & MacArthur 1961; Barton *et al.* 2014).

104 2. Which vegetation variables have consistent effects over time and across taxa? Both
105 structural and floristic attributes of vegetation have been shown to change in response to
106 disturbance (Morrison *et al.* 1995; Onaindia *et al.* 2004), which in some cases appear to
107 be the underlying drivers of animal responses to disturbance (Fox, Taylor & Thompson
108 2003; Pereoglou *et al.* 2011; Barton *et al.* 2014). Consequently, we anticipated that
109 changes in vegetation structure and floristic composition would be reflected by change in
110 animal assemblages, but that the precise relationship between plant and animal variables
111 would vary after fire and over time

112 By examining the strength and consistency of vegetation–animal relationships across taxa and
113 over time, our study provides important new insights into which vegetation attributes might be a
114 consistent candidate for use as a habitat-based surrogate of animal biodiversity. Our work also
115 reveals potential weaknesses, such as relying on one taxon over another, that underpin key
116 assumptions of biodiversity surrogates, but which are rarely tested empirically. This has
117 implications for biodiversity management as it can assist with the identification of the limitations
118 and strengths of different candidate surrogate variables.

119

120 **MATERIALS AND METHODS**

121 **Study area and design**

122 We conducted this study in Jervis Bay Territory, approximately 200 km south of Sydney in
123 south-east Australia (150.70° East, 35.15° South). Jervis Bay Territory includes Booderee
124 National Park, which covers 7500 hectares (see Fig. S1 in Supporting Information). A distinctive
125 feature of Booderee National Park is its heterogeneous cover of multiple vegetation communities,
126 ranging from tall eucalypt forest to dry heathland (Taws 1997; Pereoglou *et al.* 2013).

127 In September 2003, 105 permanent study sites were established across the National Park,
128 with the number of sites in each vegetation types generally proportional to the amount of cover of
129 that vegetation. Each site was marked with a 100-metre transect line, with permanent markers
130 placed at 0, 20, 40, 60, 80 and 100 metres. In December 2003, a wildfire burnt approximately
131 50% of Booderee National Park and 50% of the study sites, with a bias towards the eastern side
132 of the park (Fig. S1). This provided an opportunity to conduct a ‘natural experiment’ on the
133 effects of fire on vegetation and fauna in this unique landscape. Of course, it was impossible to
134 randomly allocate fire to the sites in this study after such an event, and we acknowledge the
135 potential for bias in our results as a consequence.

136

137 **Data collection**

138 *Vegetation structure and floristics.* In December 2004, 2006, 2007 and 2009, we measured six
139 attributes of the structure and floristics of the vegetation (hereafter called ‘vegetation attributes’)
140 in two 20 × 20 m plots located at the 20–40 m and 60–80 m points in each site. The attributes
141 were percentage cover and species richness of each of three strata: overstorey (> 10 m),
142 midstorey (2–10 m), and understorey (< 2 m). We took the average of the measures from the two

143 plots to give a single measure for each attribute at each site in each year, and used these data in
144 our subsequent analysis.

145 *Birds.* We completed bird surveys in September 2004, 2006, 2007 and 2009. September is
146 the breeding season for a majority of species in Booderee National Park, and when most summer
147 migrants have arrived. For each survey year, we performed two repeats of bird surveys at the 20
148 m and 80 m markers in each site, resulting in four surveys per site per survey year. We recorded
149 all birds seen or heard within a 50-m radius of the survey points during a 5-minute period,
150 excluding birds flying overhead. We conducted surveys between dawn and mid-morning. Repeat
151 surveys were performed on a different day and by a different observer to incorporate day and
152 observer effects (Lindenmayer, Wood & MacGregor 2009). We pooled the four surveys from
153 each site to give one set of observations per site per year.

154 *Mammals and reptiles.* Surveys of ground-dwelling mammals and reptiles were completed
155 in 2004, 2006, 2007 and 2009 using a standardised combination of traps along the length of the
156 100 m transect of each site: (i) a 380-mm deep \times 300-mm diameter pitfall trap was established at
157 the 0-m, 20-m, 40-m, 60-m, 80-m and 100-m points along each transect, (ii) a black plastic drift
158 fence connected the 0-m and 20-m, 40–60-m and 80–100-m pitfall buckets, (iii) a single 1-m
159 deep \times 80-cm diameter large pitfall trap (a large garbage bin) was established at the 50-m
160 midpoint along each transect, (iv) Elliott traps (Elliott Scientific Equipment, Upwey, Victoria)
161 were placed 0 m, 10 m, 20 m, 30 m, 40 m, 50 m, 60 m, 70 m, 80 m and 90 m along the transect.
162 Each trap was baited with a mixture of peanut butter and rolled oats, (v) small wire cage traps
163 (20 \times 20 \times 50 cm) were placed 20 m, 40 m, 60 m and 80 m along the transect, (vi) a large wire cage
164 trap (30 \times 30 \times 60 cm) was placed at the 0-m and 100-m points along the transect. Surveys at each
165 site involved opening all traps on four consecutive days and nights, except on a very small
166 number of occasions when it rained heavily and traps were closed after three days to reduce the

167 potential for animal mortality from trapping. Sets of scales on each captured reptile, or an ear on
168 each captured mammal, were marked with a semi-permanent white pen so that it would be
169 recognized as a recapture if it were trapped again during the four-day capture period. Surveys of
170 our sites were completed during the warmer months of the year between November and March
171 (Lindenmayer *et al.* 2008a; Lindenmayer *et al.* 2008c). Trapping data were pooled across trap
172 type and the four days of trapping (excluding re-captures) to give a single measure of abundance
173 and richness of mammals or reptiles from each site in each year.

174 In sum, our data collection produced species counts for three taxa of animals (birds,
175 reptiles and mammals) from 105 sites across a wide range of vegetation types (see Fig. S1 in
176 Supporting Information). Observations were made on the sites in four years: 2004, 2006, 2007
177 and 2009. Of these sites, 46 were burnt by a wildfire in December 2003.

178

179 **Data analysis**

180 *Response variables.* Abundance, species richness and composition are fundamentally different
181 properties of a biotic assemblage (Magurran & McGill 2011). We calculated abundance and
182 species richness as the sum of individuals or species of each animal taxon recorded within a
183 single site in a particular year. For species composition, we used the Bray-Curtis dissimilarity
184 index applied to $\log_e(1+x)$ transformed species count data to calculate a dissimilarity matrix for
185 each animal taxon. We excluded species that occurred in two or fewer sites (for each year). We
186 then carried out a principal coordinate analysis (PCoA) based on this matrix, deriving an
187 assemblage composition score for each site, using the R function ‘biplot.pcoa’ from the package
188 ‘APE’ (Paradis, Claude & Strimmer 2004). We analysed PCoA site scores from the first axis
189 only, as this accounted for the greatest amount of variation in species composition among sites
190 (19, 37 and 37 percent for birds, mammals and reptiles respectively).

191 *Explanatory variables.* We investigated the effects of untransformed and transformed
192 versions of the six vegetation attributes described above, using $\log_e(x+1)$ for both counts and
193 proportions. Proportions were bounded at 100% as well as at 0%, but examination of plots of the
194 relationships indicated little change in the effect of increasing vegetation near to 100%, so there
195 was no need for a transformation like the logit which respects that boundary. We also
196 investigated differences between Years and between sites of different Burnt status.

197 *Regression models.* We fitted regression models to quantify the relationship between each
198 of the response variables and the full set of explanatory variables described above, including
199 interactions, using the Generalized Linear Mixed Model facilities of GenStat (VSNI 2013). This
200 resulted in nine different regression models (one for each assemblage measure of each taxon).
201 For models of animal abundance and richness, we used negative binomial regression or Poisson
202 regression if there was no detectable aggregation in the counts. Aggregation, also called
203 dispersion, is a measure of heterogeneity in the negative binomial model, with infinite
204 aggregation corresponding to the Poisson model (Hilbe 2011). For assemblage composition data,
205 we used linear models. We fitted 'site' as a random effect in all our models to incorporate
206 repeated measures of sites in different years. We checked the assumption of linearity of effects
207 (on the log scale of species richness and abundance) with additive models (cubic smoothing
208 splines).

209

210 **RESULTS**

211 **Bird, reptile and mammal assemblages**

212 Our surveys across the 105 sites and four different years detected 102 bird species (15 439
213 records), 14 reptile species (1 248 records), and 10 mammal species (3 344 records). Bird
214 assemblage structure (Fig. S2a) varied from sites characterised by the presence of heathland

215 species such as eastern bristlebird *Dasyornis brachypterus* Latham to sites with forest species
216 such as the brown thornbill *Acanthiza pusilla* Shaw and yellow-faced honeyeater *Lichenostomus*
217 *chrysops* Cabanis. Mammal assemblage structure (Fig. S2b) varied from sites characterised by
218 the presence of the habitat generalist long-nosed bandicoot *Perameles nasuta* Geoffroy to sites
219 with forest-dwelling brown antechinus *Antechinus stuartii* Macleay. Reptile assemblage structure
220 (Fig. S2c) varied from sites characterised by the presence of multiple reptile species to sites
221 dominated by the woodland-dwelling delicate skink *Lampropholis delicata* de Vis.

222

223 **Fit of models**

224 We show the estimated aggregation parameters for the models of species richness and abundance
225 in Table 1. For all three animal assemblage variables (abundance, richness and composition),
226 \log_e -transformed vegetation measures were better than the untransformed measures for
227 representing the pattern of the data in the type of model we fitted, and in reducing the deviance of
228 the data (deviance is the extension of the residual sum of squares, appropriate for assessing
229 generalized linear models like negative binomial and Poisson regression). In some cases, there
230 was evidence of nonlinearity in the relationship between response and explanatory variables, but
231 this was usually at the extreme ends of the range of an explanatory variable.

232 In all nine regression models (three response variables by three animal taxa), we found
233 seven instances of a three-factor interaction between Year, Burnt status and any of the vegetation
234 attributes (Table S1). This is slightly higher than that expected by chance for 54 tests, but the size
235 of the effects was small in each case compared to the size of the main effects. There were also
236 seven instances of an interaction between Year and vegetation attributes (Table S1). Due to the
237 lack of these particular interactions, we focus on summarizing our analyses in terms of (i)
238 interactions between Year and Burnt status (adjusting for the effects of all vegetation attributes

239 and their interaction with Burnt status), and (ii) interactions between Burnt status and the
240 vegetation attributes (adjusting for the effect of Year, Burnt status and the interaction between
241 them).

242 Importantly, the six vegetation attributes were partially confounded with each other,
243 particularly within the pairs of measurements (species richness and percentage cover) made in
244 each stratum. We therefore present the effect of each vegetation attribute on its own, ignoring the
245 other five attributes but adjusting for the effects of Year and Burnt status. This gives estimates of
246 the effect of changes in each vegetation attribute, but also includes unspecified effects of other
247 variables. For example, the effect of a change in overstorey cover from 0 to 10% actually
248 represents the effect of that change plus the average changes in the other vegetation measures
249 because of the partial confounding. This approach seemed more useful than estimates of effects
250 for each measure keeping the other measures constant. This is because each of the specified
251 effects corresponds to what an observer might observe and measure in a similar site.

252

253 **Temporal changes in animal assemblages after fire**

254 We found a significant and large interactive effect of year and burnt status on all three animal
255 taxa ($P < 0.05$, except where noted below), even after adjusting for combined vegetation effects
256 (Fig. 1). Table S2 presents summaries of the effects in the models we fitted. These are expressed
257 as changes in each response variable corresponding to a change from 0 to 1 vegetation species or
258 from 0 to 10% vegetation cover (% Change 1), or from 1 to 2 or 10 to 20% (% Change 2), in
259 each of three vegetation strata. Values of % Change 2 are smaller than % Change 1 because of
260 the nature of the $\log_e(1+x)$ transformation. The abundance and species richness of bird
261 assemblages from burnt sites was nearly half that of unburnt sites in 2004, but then returned to
262 similar levels in 2006 and 2007 before returning to a large difference again in 2009. Bird

263 assemblages changed to include more heath-associated species in burnt areas in 2007 and 2009.
264 For mammals, richness and abundance was always lower in burnt sites across all four years of
265 surveys, even though these measures varied considerably from year to year (the interaction of
266 year by burnt status was not significant, richness $P = 0.86$, abundance $P = 0.37$). Mammal
267 composition shifted to include more generalist bandicoots and fewer forest-associated antechinus
268 in 2006 and 2007, but then switched to have more antechinus in 2009. By contrast, reptiles were
269 both more abundant and species rich in burnt sites compared with unburnt sites in 2004, but there
270 was no difference between burnt and unburnt sites in subsequent years. Reptile assemblages
271 shifted to have more woodland-associated delicate skinks in burnt sites in 2004, but much fewer
272 in 2007.

273

274 **Effects of plant species richness**

275 We found several significant effects of plant species richness on animal assemblages, after
276 adjusting for the effects of year and the interaction between year and burnt status. Effects varied
277 in strength and direction depending on stratum and animal taxon. We show these effects in Fig. 2
278 (values given in Table S3), which gives the estimated mean percentage change in the animal
279 assemblage measures corresponding to a change from 0 to 1 plant species in each vegetation
280 stratum (Table S3 also gives the estimated percentage change corresponding to a change from 1
281 to 2 species, for comparison). For birds, we found that the plant species richness of all strata in
282 burnt sites had strong and positive effects on bird assemblages, whereas effects were weaker on
283 unburnt sites, and negative (though non-significant) for the understorey stratum. For example, an
284 increase in overstorey plant richness from 0 to 1 species in burnt sites was associated with a 42%
285 increase in bird species richness and 60% increase in abundance. There were much smaller
286 effects for mammals, although the overstorey effect on abundance was still significant at burnt

287 sites. A positive overstorey effect on composition at burnt and unburnt sites was complicated by
288 an interaction with year: the vegetation effect was significant only in 2006, and was much smaller
289 in other years. There was noticeably more variability in the responses of reptiles, but all three
290 vegetation strata had positive effects on reptile abundance at burnt and unburnt sites (though not
291 all were significant). Both overstorey and understorey vegetation had positive effects on reptile
292 composition.

293

294 **Effects of vegetation percentage cover**

295 There were also several significant effects of vegetation cover on each animal assemblage. We
296 present these effects in Fig. 3 (values given in Table S3), and give the estimated mean percentage
297 change in each animal assemblage corresponding to a change in vegetation cover from 0 to 10%
298 in each stratum (Table S3 also gives the estimated percentage change corresponding to a change
299 from 10% to 0% cover, for comparison). For birds, there was a larger positive effect of
300 overstorey cover in burnt sites than unburnt sites, but larger negative effects of understorey cover.
301 For mammals, the largest effect was from understorey vegetation cover, which was positive in
302 unburnt sites, but negative in burnt sites: this was most apparent for mammal composition. A
303 small but significant positive effect of overstorey cover on mammal composition was again
304 complicated by an interaction with Year, with 2006 again having a larger effect than the other
305 years. For reptiles, there was a positive effect of overstorey and midstorey vegetation cover on
306 richness and abundance, but there were no large differences between burnt and unburnt sites.
307 Understorey cover had a negative effect on these responses at burnt sites.

308

309

310 **DISCUSSION**

311 There are major gaps in our knowledge of whether surrogacy relationships are robust over time,
312 after disturbance, across different taxa, and at scales appropriate to biodiversity management. In
313 this paper, we have tested and compared the responses of multiple animal taxa to identical
314 vegetation attributes within the same landscape, an approach rarely undertaken before. By
315 addressing each of these gaps, our study has revealed that fundamental vegetation attributes have
316 limited utility as strong or consistent surrogates of animal diversity. Further, we found that
317 wildfire altered the relationship between some vegetation attributes and measures of bird and
318 mammal assemblages, while reptile assemblages showed weaker responses to vegetation
319 irrespective of fire. This mix of results highlights the lack of congruent responses of different
320 vertebrate groups to a single vegetation attribute, as well as the highly variable (and sometimes
321 opposite) effects of fire on the relationship between plant and animal covariates. Below we
322 discuss the importance of making the distinction between strong and consistent effects of habitat-
323 based surrogates, and the importance of fire in changing the underlying relationship between
324 vegetation measures and animal assemblages.

325

326 **Consistent versus strong effects of vegetation within and across taxa**

327 Overstorey vegetation richness and cover nearly always had a positive effect on the abundance,
328 richness and composition of each animal taxon, indicating that canopy vegetation had a
329 consistent effect across multiple taxa (Table 2). However, some of these effects were only
330 moderate or weak (and non-significant) for mammals and reptiles, and the strongest effects were
331 for birds. This confirms our initial expectation that birds would respond to overstorey vegetation
332 (MacArthur & MacArthur 1961; Barton *et al.* 2014). The finding that overstorey had both
333 consistent and strong effects on bird assemblages suggests that broad habitat classifications that

334 distinguish between canopy cover and extent, which has been attempted at landscape scales
335 (Oliver *et al.* 2004; Cushman *et al.* 2008), is an effective surrogate of bird assemblage diversity
336 even at relatively small scales.

337 Mammals and reptiles often showed strong responses to understorey vegetation cover,
338 which again agreed with our initial expectation of their stronger association with ground-layer
339 variables. There was also a surprising change in the direction of the effect of understorey cover
340 on mammal assemblage composition after fire, with an increase in the prevalence of bandicoots
341 among assemblages from burnt sites. This has been reported in previous work (Lindenmayer *et*
342 *al.* 2008a), but our study suggests this may be driven by an increase in understorey cover.
343 Notably, the effect of understorey cover was consistently negative across all three animal taxa,
344 but this was only in sites burnt by fire and effects were mostly weak. Nevertheless, understorey
345 cover could be a useful surrogate for the loss of diversity of multiple vertebrate taxa after fire
346 (Table 2).

347 Reasons for why most of the six vegetation measures did not have consistent or strong
348 effects on mammal and reptile assemblages might be related to the influential role of other key
349 habitat variables such as food or nesting resources. Further, the relatively high spatial
350 heterogeneity of vegetation types within our study landscape, and the close proximity of many of
351 our sites, may be a critical factor driving the absence of concordant responses among taxa.
352 Further, the use of different sampling methods of mammals and reptiles (compared with birds) is
353 also a potential explanation for the different responses observed, with trapping being a very
354 different survey technique than real-time point counts of birds.

355 Importantly, the effects of the number of plant species and percentage cover of vegetation
356 on the animal assemblages were confounded, and difficult to disentangle. For example, the
357 addition of a single tall tree species to a heath or open woodland site will necessarily increase

358 both the amount of cover and the richness of the overstorey stratum. Such confounding among
359 variables has been reported previously (Cade, Noon & Flather 2005; Banks-Leite, Ewers &
360 Metzger 2013), and shows that causal mechanisms linking habitat variables to changes in animal
361 assemblages may be difficult to identify.

362

363 **The effect of fire on habitat-based surrogates**

364 After adjusting for combined vegetation effects, we found that fire had large negative effects on
365 bird and mammal richness and abundance, but positive effects on reptile richness and abundance.
366 This highlights the overwhelming effect that fire has on animal assemblages beyond the effect of
367 vegetation. However, fire also dramatically altered the effects of the vegetation attributes on
368 animal assemblages. This was most evident with the significantly stronger effects of vegetation in
369 all strata on bird assemblages in burnt sites. The enhanced vegetation effects on bird assemblages
370 in burnt sites may have been due to the loss of vegetation structure. In the absence of normal
371 levels of cover, what cover remained appears to have had a disproportionate effect on
372 determining the spatial occurrence of birds across our sites, and suggests that animals respond
373 more strongly to vegetation in a recently burnt environment. Few studies have examined habitat-
374 animal associations specifically from an applied surrogacy perspective after intense disturbances
375 such as fire (Brennan *et al.* 2006). This makes our result important because it demonstrates that
376 particular vegetation attributes are not only robust to disturbance, but could improve their
377 surrogacy potential, at least for birds.

378 Our analyses suggested that the lack of an effect of fire on the majority of vegetation
379 effects on mammals and reptiles may be due to these taxa having less strong associations with
380 these variables in the first place. However, we did detect strong effects of fire *per se*, which
381 might be due to direct mortality, changed food availability or elevated predation rates in the

382 immediate post-fire environment (Erwin & Stasiak 1979; Rochester *et al.* 2010). The increase in
383 captures of reptiles immediately after fire, however, might be due to a combination of increased
384 mobility as they search for more scarce resources, or release from predation by birds or small
385 mammals that decreased in these areas (Lindenmayer *et al.* 2008c).

386 Many studies have demonstrated the effect of fire on vegetation structure (e.g. Taylor
387 2010; Russell-Smith, Edwards & Price 2012), and subsequent effects on associated fauna
388 (Fuhlendorf *et al.* 2006; Lindenmayer *et al.* 2008b; Barton *et al.* 2014). Thus, we anticipated that
389 a habitat attribute used as a surrogate of animal diversity might be vulnerable to disturbance
390 effects, and an altered or weaker relationship with associated fauna. Overall, however, we found
391 that bird assemblages were more strongly affected by vegetation, whereas mammals and reptiles
392 exhibited only limited changes in responses to vegetation after fire. Mixed responses to fire
393 among different taxa is not unusual (Pastro, Dickman & Letnic 2011), but we show that these
394 mixed results are also reflected in their responses to habitat-based surrogates.

395

396 **Applications to biodiversity management**

397 Rigorous empirical testing is needed to evaluate and identify robust surrogacy relationships.

398 Although many studies have identified vegetation attributes associated with the diversity and
399 composition of vertebrate assemblages (Tews *et al.* 2004; McElhinny *et al.* 2006; Schaffers *et al.*
400 2008; Qian & Kissling 2010), very few studies have made an explicit comparison among
401 multiple taxa in response to identical vegetation measures within the same landscape. Our study
402 provides new evidence of the variable effectiveness of habitat-based surrogates of three important
403 vertebrate taxa.

404 From a management perspective, our results support the use of overstorey vegetation as a
405 surrogate for bird assemblages. Both plant species richness and percentage cover of overstorey

406 vegetation had strong effects on the abundance and richness of bird assemblages, and these
407 effects were enhanced at sites burnt by fire. In contrast, our data do not support the nomination of
408 any vegetation attributes as consistent surrogates of mammal or reptile assemblages. This
409 suggests that taxon-specific habitat-based surrogates may be required. However, this would
410 require additional surveys of vegetation, and raises the issue of cost in terms of both time and
411 effort. In this case, the direct assessment of each taxon through dedicated surveys could provide
412 greater accuracy of measured changes in richness and abundance than the use of indirect
413 vegetation measures (Lindenmayer & Likens 2011). Such direct measurement of animal
414 populations is also likely to have greater robustness to temporal variability and disturbance.

415 We build on previous research that has suggested habitat-based surrogates may be a
416 superior class of surrogate relative to other classes of surrogates. This is, in part, due to their
417 potential efficiency and practical value to resource managers and policy makers (Lindenmayer,
418 Margules & Botkin 2000; McElhinny *et al.* 2005). Our detailed assessment of several potential
419 habitat surrogates has highlighted the contrasting responses of different taxa, and revealed that
420 birds were the only taxon with both consistent and strong responses. Management decisions
421 based only on bird data, however, may be inappropriate as a guide to management aimed at
422 biodiversity more broadly. Although habitat-based surrogates may be appealing from a practical
423 or cost perspective (Banks-Leite *et al.* 2011), the different ecologies of multiple taxa are difficult
424 to account for with a single, easily-measured vegetation attribute. Targeted research to identify a
425 single habitat attribute associated with multiple taxa may prove to be difficult, but might focus on
426 a limiting resource that is shared across taxa. This is because a focus on a shared resource will
427 help to identify links between different taxa and their habitat through a common functional
428 dependence in a key habitat attribute. If this attribute is limiting, then changes in this resources
429 are more likely to be reflected by dependent animal assemblages.

430

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437

438 **DATA ACCESSIBILITY**

439 Dryad Digital Repository. <http://dx.doi:10.5061/dryad.s7d2d>

440

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573 **Supporting Information**

574 Additional supporting information may be found in the online version of this article.

575 **Fig. S1.** Location map of study area.

576 **Fig. S2.** Ordination plots of bird, mammal and reptile PCoA scores.

577 **Table S1.** Summary of regression models for three measures of bird, mammal and reptile
578 assemblages (species richness, abundance, composition), and six attributes of vegetation

579 **Table S2.** Mean (with 95% confidence limits) species richness, abundance and composition for
580 each animal taxon by year and burnt status.

581 **Table S3.** Effects of each vegetation attribute (with 95% confidence limits) on species richness,
582 abundance and composition of each animal taxon.

583

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585

586 **Table 1.** Estimated aggregation parameters for abundance and species richness count data of
587 birds, mammals and reptiles

Taxon	Response	Aggregation	S.E.
Birds	Richness	∞ (Poisson)	–
	Abundance	6.2	0.5
Mammals	Richness	∞ (Poisson)	–
	Abundance	32.9	11.5
Reptiles	Richness	∞ (Poisson)	–
	Abundance	5.0	1.0

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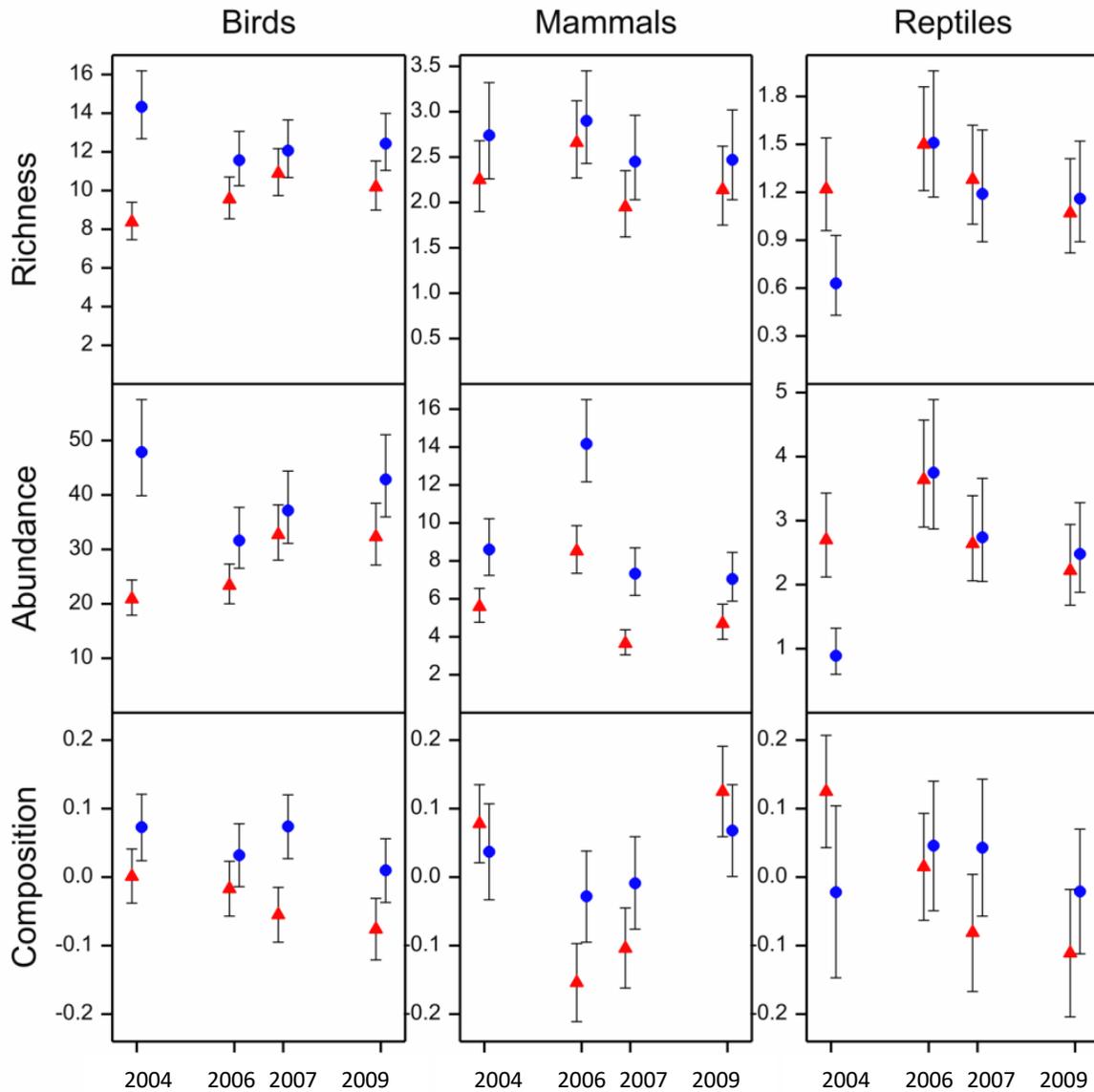
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591 **Table 2.** Summary of strong vs consistent effects of vegetation on the three animal taxa

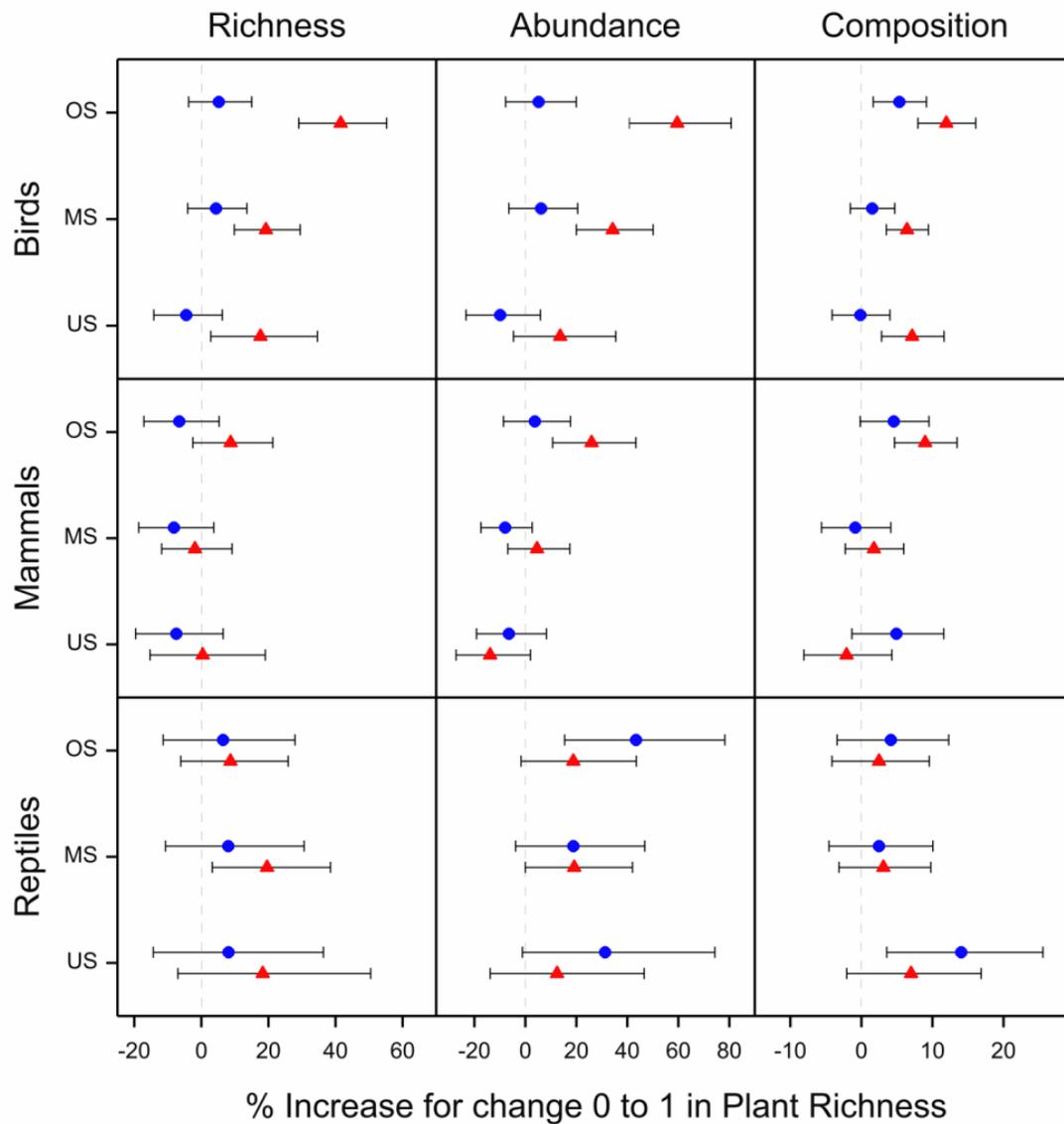
	Strength of effect	Consistency of effect	Recommendation
Overstorey	<ul style="list-style-type: none"> • Strong effects on bird richness, abundance and composition, especially in burnt sites. • Strong effect on reptile abundance only, especially in unburnt sites. • Weak effects on mammals. 	<ul style="list-style-type: none"> • Effects were consistently positive for all three animal taxa. 	<ul style="list-style-type: none"> • Effects of OS cover and richness were consistently positive across taxa, but only strong for birds. • OS vegetation cover is effective surrogate for bird diversity.
Midstorey	<ul style="list-style-type: none"> • Moderate effects on bird abundance, especially in burnt sites. • Generally weak effects on mammals and reptiles. 	<ul style="list-style-type: none"> • Some differences between taxa. 	<ul style="list-style-type: none"> • Effects were both inconsistent across taxa, and only moderate or weak. • MS vegetation cover is not an effective surrogate.
Understorey	<ul style="list-style-type: none"> • Strong effects on mammal assemblage composition, but direction of effect depends on disturbance. • Moderate effects on reptile richness. 	<ul style="list-style-type: none"> • US cover consistently had negative effects on the abundance and richness of all taxa, but only in burnt sites. 	<ul style="list-style-type: none"> • Effects of US cover were consistently negative across taxa, but moderate in strength, and only in burnt sites. • Could be an effective surrogate for loss of diversity after disturbance.

592

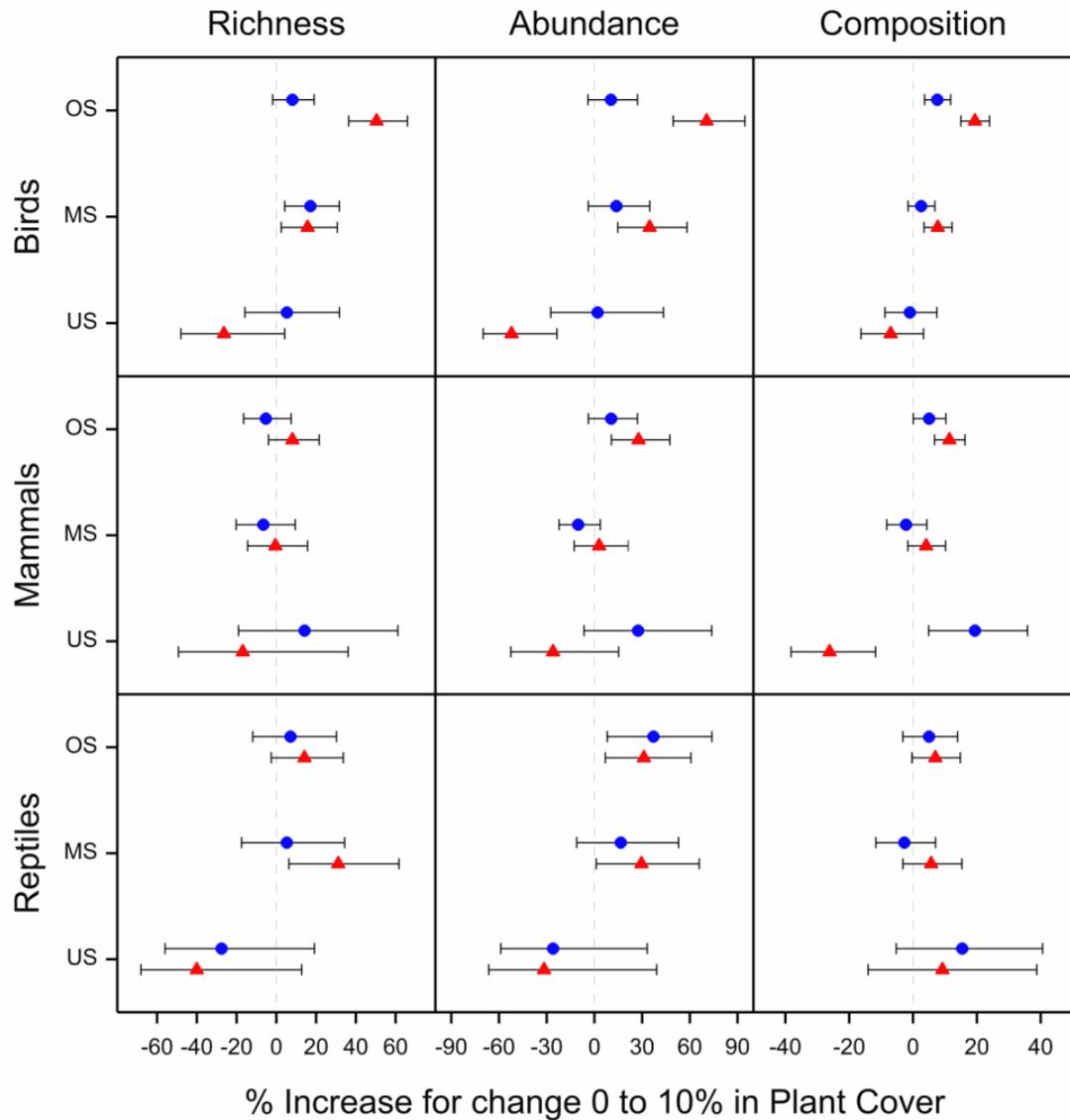
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 595 **Figure 1.** Mean (with 95% confidence limits) species richness, abundance and composition
 596 measures for three taxa over time, by burnt status of sites (red triangles = burnt; blue circles =
 597 unburnt). Means are adjusted for effects of all six vegetation measures and of burnt status, and for
 598 the interaction between the vegetation measures and burnt status.
 599
 600



601
 602 **Figure 2.** Mean percentage increase (with 95% confidence limits) of species richness, abundance
 603 and composition measures for three taxa, corresponding to a change from 0–1 in plant species in
 604 each of three storeys, by burnt status of sites (red triangles = burnt; blue circles = unburnt).
 605 Means are adjusted for effects of year and burnt status, and their interaction, but are not adjusted
 606 for effects of other vegetation measures. OS = overstorey, MS = midstorey, US = understorey.
 607



608
 609 **Figure 3.** Mean percentage increase (with 95% confidence limits) of species richness, abundance
 610 and composition measures for three taxa, corresponding to a change from 0–10% vegetation
 611 cover in each of three storeys, by burnt status of sites (red triangles = burnt; blue circles =
 612 unburnt). Means are adjusted for effects of year and burnt status, and their interaction, but are not
 613 adjusted for effects of other vegetation measures. OS = overstorey, MS = midstorey, US =
 614 understorey.