

1 **Higher-taxon and functional group responses of ant and bird assemblages to**  
2 **livestock grazing: a test of an explicit surrogate concept**

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16 Running head: Testing biodiversity surrogates

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20 **ABSTRACT**

21 Biodiversity monitoring programs are routinely established to quantify changes in biotic  
22 communities in response to land management. Surrogacy is implicitly used in many such  
23 monitoring programs whereby the measurement of a component of biodiversity is used to  
24 infer responses of broader biodiversity. Yet rarely is this surrogacy validated by  
25 demonstrating that measured variables and the target variable of interest have matching  
26 responses to management treatments. Here we examined the responses of higher-taxon and  
27 functional groupings of ants and birds (our surrogate variables) two years after the  
28 implementation of experimental livestock grazing treatments, and compared these with the  
29 responses of total ant and bird species richness (our target variables) to the same treatments.  
30 We found significant and strong correlations between surrogate and target variables, but this  
31 did not predict corresponding similar response to treatments. For ants, we found that the  
32 genus *Monomorium* had a negative response to the grazing exclusion treatment, but there was  
33 no matching response of species richness, and so no surrogacy was identified. For birds, total  
34 species richness had a weak positive response to spring/summer grazing exclusion, and the  
35 abundance of honeyeaters (Meliphagidae) showed a similar positive response, suggesting  
36 surrogacy. Our study highlights that correlations among variables do not necessarily lead to  
37 surrogacy, and indeed that different sub-components of biotic assemblages can respond in  
38 ways that contrast with overall species richness. Careful assessment of the matched responses  
39 of surrogate and target variables to management can provide a simple and robust way to  
40 critically assess biodiversity surrogacy.

41

42 **Keywords:** biodiversity conservation, grazing, insect, indicator, modified landscape,  
43 monitoring

44

## 45 INTRODUCTION

46 Biodiversity monitoring programs are routinely established to quantify changes in biotic  
47 communities in response to different land management practices (Lindenmayer and Likens  
48 2010; Vackar et al. 2012). Acquiring and analysing monitoring data requires considerable  
49 time and effort. Using surrogate variables to make inferences about other unmeasured  
50 variables of interest is one approach to reducing monitoring costs (Caro 2010; Lindenmayer  
51 and Likens 2011). This can be, for example, in the form of higher-taxon surrogacy, where  
52 patterns occurring at a higher taxonomic level, such as family or genus, are used to infer  
53 patterns of species-level responses (Williams and Gaston 1994; Brennan et al. 2006; Driessen  
54 and Kirkpatrick 2017). Functional surrogacy can also be used, whereby individuals are  
55 grouped by their shared ecological attributes, such as diet or body size, and used to infer  
56 broader assemblage responses to the environment (Gollan et al. 2010; Bhusal et al. 2014;  
57 Barton and Moir 2015). Each of these approaches can offer potentially simple, cheap, and  
58 ecologically meaningful ways to quantify broader biotic patterns, but nevertheless require  
59 proper evaluation before surrogacy can be attributed.

60 Biodiversity surrogates can be used to provide information about the response of biota  
61 to management interventions aimed at conserving broader biodiversity (Lindenmayer et al.  
62 2002; Gonzalez et al. 2013; Barton and Moir 2015). For example, increased abundance of a  
63 particular species following altered land management might be used to infer a broader  
64 community response to management intervention (Gollan et al. 2010; Barton and Moir 2015).  
65 However, it is important to distinguish between studies that identify a simple correlation  
66 between a target and its surrogate from those that show matched responses of these variables  
67 to a shared treatment. This difference is essential to moving beyond establishing an  
68 association and towards establishing surrogacy within a particular context (Barton et al. 2015;  
69 Pierson et al. 2016). The additional step of identifying matched responses is needed because

70 target and surrogate variables may not necessarily respond to an intervention in the same  
71 way, despite themselves being correlated, yet few studies acknowledge or empirically test  
72 this (Pierson et al. 2016).

73 In this study, we used an explicit surrogate concept to guide our evaluation of  
74 surrogates of biodiversity responses to livestock grazing treatments (Fig. 1). This concept is  
75 adapted from the medical sciences (Atkinson et al. 2001; Barton et al. 2015) and shows how  
76 a surrogate variable is placed between a treatment and its target, while accounting for  
77 covariates. Monitoring of different taxa was subsequently undertaken to assess the effects of  
78 grazing treatments on biodiversity, and this provides the basis of our current study. We  
79 examined the responses of a suite of higher-taxon and functional groupings of ants and birds  
80 (our surrogate variables) and see if any match the response of overall species richness (our  
81 target variables) to the livestock grazing treatments. Our questions were: (1) Which surrogate  
82 and target variables respond to the grazing treatments? (2) Which surrogate and target  
83 variables are correlated? (3) Which variables are both strongly correlated *and* show similar  
84 responses to the grazing treatments? These analyses provide the basis for an objective  
85 assessment of matched responses of surrogate and target variables to a common treatment  
86 and are hence a simple, but important, test of surrogate validity.

87

## 88 **METHODS**

### 89 **Study area and design**

90 Our study was conducted in south-eastern Australia, with sites spanning an area  
91 approximately 100 km east to west, and 150 km north to south (Figure S1). Within this area,  
92 we established 78 sites, each of 40 x 200 m (0.8 ha), across 29 different farms from mid-  
93 2010. All sites were located in temperate grassy woodland, which is characterised by a  
94 patchy distribution of *Eucalyptus* trees in grassland largely dominated by native perennials

95 (Lindenmayer et al. 2012; Barton et al. 2016). Grassy woodland was once widespread in  
96 south-eastern Australia, but has been subject to large-scale clearing or modification due to  
97 agricultural practices including grazing (McIntyre et al. 2014).

98 We grouped the 29 farms into three blocks, each representing a historical ‘business as  
99 usual’ grazing practice of either continuous grazing, short-term rotational grazing (conversion  
100 to rotational grazing practice within the last five years), or long-term rotational grazing  
101 (conversion to rotational grazing practice for greater than 10 years). Farms with continuous  
102 grazing allowed livestock access to sites all year round, whereas farms with rotational  
103 grazing typically rotate higher numbers of livestock through sites, but for a limited duration.

104 Sites were assigned within in each farm to one of three different treatments: (i) all-year  
105 exclusion, (ii) spring/summer exclusion, and (iii) ‘business as usual’. All-year exclusion sites  
106 had little or no grazing by livestock in the year prior to our study. Spring/summer exclusion  
107 sites were not grazed during the six month period of spring and summer prior to our study.  
108 The ‘business as usual’ sites continued grazing in line with the usual grazing practices of the  
109 farm (*viz.* continuous, short-term rotational, long-term rotational). We documented data on  
110 livestock numbers and duration of grazing events for each site as reported by landholders in  
111 the 12 months prior to this study, and provide grazing summary statistics in Table S1.

112

### 113 **Soil and vegetation covariates**

114 Soil and vegetation surveys were conducted on every site during January and February 2012,  
115 approximately two years after the grazing treatments commenced. We established two 20 x  
116 50 m quadrats at 0-50 m and 150-200 m along the centre line of each site (Figure S1). Within  
117 each quadrat, we recorded the number of tree stems > 10 cm in diameter. A 50m transect was  
118 located down the centre of each plot with biometric step-count measurements (Gibbons et al.  
119 2008) taken every metre to assess percentage cover of ground layer native and exotic grass

120 cover, and leaf litter cover. In addition, ground-layer plant biomass was assessed using a  
121 rising plate pasture meter to determine average height of ground cover present (Filip's  
122 Manual Folding Plate Meter, Jenquip, New Zealand (Correll et al. 2003). Vegetation  
123 measures were averaged across the two quadrats to give one measure per site. We also  
124 collected soil cores of 10 cm diameter x 5 cm depth every 16.5 m (n = 12) along the 200-m  
125 centre transect of each site, following the careful removal of any surface plant and litter  
126 biomass present. We then pooled soil samples 1-4, 5-8, and 9-12 for each site to provide three  
127 bulked samples per site (see Figure S1). We air dried samples at 35°C for 48 h prior to  
128 processing, then crushed the dried samples and passed each through a 2-mm sieve. We  
129 quantified total carbon and nitrogen (%) in each sample using Dumas combustion analysis  
130 (Vario Max, Elementar, Germany) (Matejovic 1997), and expressed results as a C:N ratio.  
131 We determined total phosphorus (%) using the Kjeldahl method (Diamond 2006). All soil  
132 measures were averaged to give one value per site.

133

#### 134 **Ant sampling**

135 We sampled ground-active ants using pitfall traps (250 ml plastic jars) dug in flush with the  
136 ground surface and half-filled with a 50% polyethylene glycol solution. Three pitfall traps  
137 were deployed in each site for a two-week period in December 2011 (Figure S1), with ants  
138 removed and pooled to give one sample per site. Our sampling approach deliberately  
139 prioritised spatial replication across many sites over sampling intensity within sites, resulting  
140 in standardised bias towards the more active species of the ant community.

141       Specimens were sorted and identified to subfamily, genus, and species (or  
142 morphospecies) by a taxonomic specialist and assigned a functional group based on their  
143 genus membership using the classification scheme described by Andersen (1995a, 1997) (see  
144 Table S3). We used only the four most abundant functional groups in further analysis: the

145 Dominant Dolichoderinae, Generalist Myrmecinae, Opportunists, and Hot Climate  
146 Specialists. Ant functional groups were first described as a way to improve prediction and  
147 generalisation of ant species responses to disturbance, and have been used previously to  
148 examine responses to livestock grazing (Hoffmann 2010; Barton et al. 2016). The list of ant  
149 species and their functional groupings is given in Table S3.

150

### 151 **Bird surveys**

152 Birds were surveyed during spring of 2011 within a 25m radius at both ends of every site.  
153 Surveys consisted of five-minute point counts with two repeat visits by highly skilled field  
154 staff. All bird species seen or heard during the four counts were pooled to give one sample  
155 per site. There were sufficient data for two families of birds (Acanthizidae and Meliphagidae)  
156 (> 100 individuals) to allow for separate analysis as higher-taxon surrogates. Bird species  
157 also were assigned to their dominant foraging stratum (ground, canopy/shrub, aerial) (Kutt  
158 and Martin 2010), and these were used as our functional group surrogates. The list of bird  
159 species and their functional groupings is given in Table S4.

160

### 161 **Statistical analysis**

162 We first used principal components analysis (PCA) to identify collinearity among the nine  
163 soil and vegetation measures. PCA generated three new variables (notation of PC1, PC2,  
164 PC3) that each represented an environmental gradient among our sites (Table S2). These  
165 variables accounted for a combined 67% of variation in our environmental data. The first  
166 component represented a gradient from under trees out to improved pasture/grassland sites.  
167 The second component represented a gradient of exotic perennial to native annual grass  
168 cover. The third component represented a gradient of increasing native perennial grass cover.

169 We selected species richness of each taxon as the target variable of interest, with this  
170 variable being the most commonly used measure of diversity in applied ecology and  
171 conservation (Fleishman et al. 2006; Magurran and McGill 2011). We next considered  
172 overall abundance of each taxon, richness of families or genera, abundance of individuals  
173 within key families or genera, and abundance of individuals within functional groups as our  
174 surrogate variables. We focused on abundance within higher taxonomic or functional groups  
175 because it is often correlated with species richness (Bock et al. 2007; Magurran and McGill  
176 2011), but much easier to measure than species-level richness.

177 To address **Question 1** (Which surrogate and target variables respond to the grazing  
178 treatments?), we designed a statistical model that could be used to test for the effects of  
179 grazing treatments on our suite of target and surrogate variables for each taxon. We used a  
180 generalised linear mixed model (Bolker et al. 2009) to test for the main effects of farm  
181 grazing history (three levels: continuous, short rotational, long rotational), and the nested  
182 interaction of the applied grazing treatments (three levels: all-year exclusion, spring/summer  
183 exclusion, business as usual) within their associated historical grazing practice. To account  
184 for potential correlation among sites within an individual farm, we used farm as a random  
185 effect and structured our models as follows:

186 (a) *response variable* ~ *grazing history* + *grazing history:grazing treatment* +  
187 *random(farm)*

188 Next, we ran a second set of models testing for the effects of the three environmental  
189 covariates derived from our PCA (PC1, PC2, PC3). This was so we could compare the effects  
190 of the grazing treatments *per se* where environmental variation is accounted for in the  
191 experimental design, with the effects of environmental variation where the grazing treatments  
192 and experimental design are ignored. We again used farm as a random effect, and structured  
193 our models as follows:



194 (b) *response variable* ~ *PC1 + PC2 + PC3 + random(farm)*.

195 The full list of response variables examined with our models are given in Table 1. We  
196 used a negative binomial error distribution due to overdispersion of the data. We ran our  
197 models with the ‘glmmTMB’ function in glmmTMB (Magnusson et al. 2017) using R  
198 statistical software (R Development Core Team 2017). We wanted to compare the direction  
199 and magnitude of grazing effects on both target and surrogate variables to visually identify  
200 matched responses of variables to each treatment. Effect estimates were therefore plotted of  
201 each nested grazing treatment on each surrogate and target variable. Effect estimates of  
202 spring/summer exclusion and all-year exclusion were calculated relative to the ‘business as  
203 usual’ grazing treatment. Effects plots provide a quantitative estimate of the difference between  
204 two groups. We used 95% confidence intervals to indicate important effects – i.e. if an effect  
205 confidence interval crossed the zero-effect line, then the effect size was not considered to be  
206 significant.

207 To answer **Question 2** (Which surrogate and target variables are correlated?), we  
208 calculated Pearson correlation coefficients between species richness (the target) and all  
209 higher-taxon and functional surrogate variables listed in Table 1. Both ant and bird target and  
210 surrogate variables were different measures of the broader assemblage, so some correlations  
211 were expected. However, we wanted to know if the strength of correlation ( $r$ ) between target  
212 and surrogate variables was a useful predictor of the correspondence between surrogate and  
213 target responses to the grazing treatments and environmental covariates. To answer **Question**  
214 **3** (Which variables are both strongly correlated *and* show similar responses to the grazing  
215 treatments?), we ranked surrogate variables in order of correlation strength, and noted against  
216 each one the direction and significance of the effect of the grazing treatments and  
217 environmental covariates.

218

## 219 RESULTS

### 220 *Effects of grazing treatments on ants and birds*

221 No significant effects of historical grazing context was found for any of our ant or bird  
222 assemblage measures, and we therefore focused on the grazing treatments. For ants, we found  
223 no significant effect of any grazing treatment on ant species richness (our target variable)  
224 (Fig. 2). However, we did find a significant negative effect of grazing exclusion on the ant  
225 genus *Monomorium* from farms with a short-term rotational grazing history (Fig. 2). Notably,  
226 we found that, for birds, the spring/summer exclusion treatment had a near-significant (0.06,  
227 see Table S6) positive effect on species richness on farms with a history of continuous  
228 grazing, and this corresponded with a significant positive effect on the abundance of canopy  
229 and shrub foraging birds (Fig. 3). A significant negative effect of spring/summer grazing  
230 exclusion was found for bird species richness on farms with a history of long-term rotational  
231 grazing, and this corresponded with a similar response of birds in the family Meliphagidae  
232 (Fig. 3). There were no effects of grazing exclusion on any measure of the bird community.

233

### 234 *Effects of environmental covariates on ants and birds*

235 Several significant effects of the environmental covariates on ant and bird assemblages were  
236 found. For ants, PC1 (tree- to grassland-dominated) had a significant positive effect on ants  
237 in the genus *Rhytidoponera* and Opportunists (Fig. 4), and a negative effect on the genus  
238 *Monomorium* and the Generalist Myrmecines (Fig. 4). Only PC2 (gradient from exotic  
239 perennials to native annuals) had a significant positive effect on species richness, which  
240 corresponded with a positive effect on genus richness and the abundance of the genus  
241 *Pheidole* (Fig. 4). For birds, none of the covariates had an effect on species richness.  
242 However, PC1 had a negative effect on the abundance of Acanthizidae and Meliphagidae, as  
243 well as the abundance of aerial and canopy/shrub foragers (Fig. 4). PC2 had a significant

244 positive effect on the abundance of Acanthizidae. PC3 (gradient of increasing native  
245 perennials) had a significant positive effect on the abundance of Meliphagidae.

246

#### 247 *Correlations between surrogates and targets*

248 Genus richness of ants and family richness of birds were most strongly correlated ( $r > 0.8$ )  
249 with their target variable of species richness (Table 2, Table 3). Abundance of key families  
250 (birds), genera (ants), or functional groups had weaker (but often still significant) correlations  
251 with species richness (Table 2, Table 3). We found only two instances of a significant  
252 correlation being matched by a similar response, both for birds. This included a positive  
253 response of bird species richness and abundance of canopy and shrub foragers to  
254 spring/summer exclusion grazing in farms with historical continuous grazing, and a matched  
255 negative effect of spring/summer exclusion grazing on species richness and abundance of  
256 Meliphagidae in farms with long-term rotational grazing (Table 3). Interestingly, we found an  
257 instance of no correlation but matched positive response to environmental covariate PC2 for  
258 abundance of the ant genus *Pheidole* and total species richness (Table 2). There were also  
259 some strong correlations between surrogate and target variables (e.g. total abundance and  
260 family richness of birds) and a matched *absence* of response to grazing and environment  
261 (Table 3).

262

## 263 **DISCUSSION**

264 We examined the responses of different measures of ant and bird assemblages to livestock  
265 grazing treatments and environmental covariates to demonstrate a way to identify and  
266 validate biodiversity surrogate responses to environmental change. We approached the  
267 problem by using a clear conceptualisation of treatment–surrogate–target relationships  
268 (Barton et al. 2015). We found that few surrogate responses matched those of the target

269 (overall species richness), thus invalidating their surrogacy in terms of indicating an effect of  
270 grazing or the environment on ant or bird assemblages. Although there were several strong  
271 correlations between target and surrogate variables, this did not provide additional insight  
272 into whether they had matched responses to the grazing treatments or environment. The  
273 correlations between some surrogate and target variables and their matched lack of response  
274 to grazing might also suggest potential surrogacy for ineffective treatments. Our approach  
275 demonstrates the value of using a clear surrogacy concept for straight-forward validation of  
276 biodiversity surrogates.

277

### 278 *Corresponding effect sizes as a way to validate surrogacy*

279 Testing the hypothesis of no correspondence between target and surrogate provided a starting  
280 point for the validation of a surrogate variable, and is routinely used in the medical sciences  
281 (NIH Definitions Working Group 2000; Atkinson et al. 2001). For ants, we found no  
282 response of species richness to the grazing treatments, and therefore no surrogacy for  
283 treatment effects was identified. The abundance of the genus *Monomorium*, however, showed  
284 a strong negative response to grazing exclusion, but was surprisingly the only ant response to  
285 grazing. However, we did find that abundance of the genus *Pheidole* corresponded with  
286 species richness in their positive response to environmental covariate PC2, which represented  
287 an environmental gradient from exotic-dominated to native-dominated grassland. Higher-  
288 taxon abundance, therefore, appears to be a plausible surrogate for species richness responses  
289 to environment gradients. This is consistent with other studies showing higher-taxon  
290 approaches to surrogacy in insects (Cardoso et al. 2004; Rosser and Eggleton 2012; Driessen  
291 and Kirkpatrick 2017), and the prominent role of environmental gradients in structuring  
292 insect communities by acting on key species groups (Bernadou et al. 2015; Gutierrez-  
293 Canovas et al. 2015). This has been shown repeatedly for ants, where different genera are

294 known to respond quite differently to the environment (Andersen 1995a; Bestelmeyer and  
295 Wiens 2001; Barton et al. 2016).

296 In contrast with ants, bird species richness responded to the grazing treatments.  
297 Specifically, there was a modest decrease in bird species richness in spring/summer grazing  
298 exclusion sites on farms with a history of long-term rotational grazing, and this was matched  
299 by a decrease in the abundance of Meliphagidae (honeyeaters). There also was a near-  
300 significant increase in species richness on sites with the recent application of a  
301 spring/summer grazing exclusion regime. This was matched by an increase in canopy and  
302 shrub foraging birds. From an ecological perspective, continuous grazing can negatively  
303 affect bird diversity (Eldridge et al. 2016), and it is a good outcome to find that  
304 spring/summer grazing exclusion practices led to a small increase in overall richness. It is  
305 intriguing, then, to find that spring/summer grazing exclusion had a negative effect on farms  
306 that already practice restricted grazing. Other studies of rotational grazing have shown no  
307 effect on birds (Dorrough et al. 2012) or negative effects on birds (Ranellucci et al. 2012)  
308 relative to continuous grazing. Changes to grazing regimes will alter seed, nectar and insect  
309 resources for birds, and even within the short time-frame of our study appear to have had  
310 effects on components of the bird community. From a surrogacy perspective, our results  
311 show there are two plausible surrogate bird variables for the assessment of grazing treatments  
312 in our study region. Identifying both Meliphagidae and canopy/shrub foragers as surrogates  
313 of total species richness, albeit in different grazing contexts, is an important finding. Long-  
314 term monitoring of biodiversity in our study sites (i.e. >10 years), including canopy/shrub  
315 foragers in spring/summer grazing exclusion sites and honeyeaters in exclusion sites, will be  
316 critical to testing of the temporal robustness of these surrogates further, and their ability to  
317 detect biotic changes over time (Barton et al. 2014).

318 We also found that one ant surrogate variable (abundance of *Monomorium*) responded  
319 negatively to grazing exclusion but total ant species richness did not. Ecologically, it is  
320 unclear why this genus responded in this way, but could be due to a preference for more  
321 disturbed sites. Identifying this response to the grazing treatment does not translate to  
322 *Monomorium* being a surrogate for that intervention. In the absence of a target response, the  
323 response of a variable is just a different kind of direct measure and does not perform the  
324 function of guiding inference of the effect of a treatment on a target (Lindenmayer and  
325 Likens 2011; Barton et al. 2015). We suggest that scenarios that demonstrate associations  
326 between variables in the absence of a target cannot be called surrogacy, in the explicit sense  
327 (*sensu* Fig. 1), unless the hypothesis of correspondence is tested in some way.

328

329 *Does surrogate-target correlation predict treatment effect?*

330 Higher-taxon richness was the measure most strongly correlated with species richness for  
331 each taxon. This might be expected as it considered the diversity of organisms, whereas all  
332 other measures considered counts of individuals within groups. For ants, the strongest  
333 correlation was for genus richness, yet this variable did not match the positive response of  
334 species richness to the PC2 environmental covariate. Previous work has shown higher-taxon  
335 richness to be an unreliable surrogate for species richness in Australian ants (Andersen  
336 1995b), so it is interesting that we showed a strong correlation, but no matched response, to  
337 an environmental gradient. Other significantly correlated measures (e.g. overall abundance,  
338 abundance of *Melophorus*) also did not show a similar response as species richness to the  
339 PC2 environmental gradient, with only the abundance of *Pheidole* matching the response of  
340 species richness despite not being correlated. For ants, then, raw correlation between a  
341 surrogate variable (either genus richness or group abundance) and overall species richness is  
342 a poor predictor of surrogacy potential.

343 For birds, total abundance and family richness were the most strongly correlated  
344 measures with bird species richness, and showed a similar lack of response to grazing  
345 exclusion as overall richness relative to all three business as usual contexts. However, even  
346 when our target of species richness did show a response to spring/summer grazing exclusion,  
347 overall bird abundance and family richness did not. This should be troubling, as abundance  
348 can often be a good surrogate for species richness (Bock et al. 2007; Magurran and McGill  
349 2011), and a great deal of emphasis is often placed on correlation as a pre-requisite to  
350 surrogacy (Westgate et al. 2014; Yong et al. 2016). Yet, both these assumptions were to  
351 shown to be false in our study of livestock grazing.

352

### 353 *Conclusions*

354 We have shown that a recently applied ecological intervention (i.e. altered livestock grazing)  
355 induced changes in species richness of the bird community, but not the ant community. Some  
356 components of the bird community responded in a similar way, and thus could be plausible  
357 surrogates. In contrast, only a single genus in the ant community responded to grazing but  
358 cannot be regarded as a surrogate for our target. Instead, our candidate surrogate variables  
359 that had a response to grazing or the environment, but did not match the target response,  
360 provide different kinds of information useful to understanding biotic responses to  
361 environmental change more broadly. Our study also highlights that coarse measures such as  
362 community species richness can be a poor target measure for different sub-components of a  
363 community to act as biodiversity surrogates. Our choice of surrogate variables was loosely  
364 based on requiring less effort to measure than the target of species richness, whilst being  
365 informative. It could be argued that richness of species within key genera, families, or  
366 functional groups rather than abundance, might be more informative. But this negates the  
367 intrinsic purpose of a surrogate variable being easier to measure, and species level

368 identification of ants, in particular, is time and expertise intensive. If this were to be done  
369 then simple direct measurement of the target (i.e. species richness of ants and birds) could  
370 have been performed, and surrogacy not required (Lindenmayer and Likens 2011).  
371 Nevertheless, we have demonstrated how an explicit approach to surrogate validation can  
372 provide a robust way to critically assess surrogacy for biodiversity responses to  
373 environmental change.

374

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517 **Table 1.** List of surrogate variables for each taxon, grouped into higher-taxon and functional  
 518 surrogates.

<b>Surrogate variable</b>	<b>Ants</b>	<b>Birds</b>
Higher-taxon richness	Genus richness	Family richness
General abundance	Overall abundance	Overall abundance
Higher-taxon abundance	Abundance of <i>Iridomyrmex</i> Abundance of <i>Melophorus</i> Abundance of <i>Monomorium</i> Abundance of <i>Nylanderia</i> Abundance of <i>Pheidole</i> Abundance of <i>Rhytidoponera</i>	Abundance of Acanthizidae Abundance of Meliphagidae
Functional abundance	Abundance of hot climate specialists Abundance of generalist myrmecines Abundance of dominant Dolichoderinae Abundance of opportunists	Abundance of Ground foragers Abundance of Canopy and Shrub foragers Abundance of Aerial foragers
Target	Species richness	Species richness

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522 **Table 2.** Surrogate ant variables ranked in order of correlation strength with their target of  
 523 ant species richness, and the corresponding effects of grazing treatments.

Ant variables	Correlation with species richness	P	Effect of all-year exclusion	Effect of spring/summer exclusion	PC1	PC2	PC3
Total species richness	n/a		-	-	-	+ve	-
Genus richness	0.822	***	-	-	-	-	-
Abundance of hot climate specialists	0.391	***	-	-	-	-	-
Abundance of <i>Melophorus</i>	0.385	***	-	-	-	-	-
Abundance of generalist myrmecines	0.263	*	-	-	-ve	-	-
Total abundance	0.252	*	-	-	-ve	-	-
Abundance of <i>Pheidole</i>	0.202	n.s.	-	-	-	+ve	-
Abundance of <i>Monomorium</i>	0.188	n.s.	-ve	-	-ve	-	-
Abundance of opportunists	0.131	n.s.	-	-	+ve	-	-
Abundance of <i>Nylanderia</i>	0.112	n.s.	-	-	-	-	-
Abundance of dominant Dolichoderinae	0.085	n.s.	-	-	-	-	-
Abundance of <i>Iridomyrmex</i>	0.084	n.s.	-	-	-	-	-
Abundance of <i>Rhytidoponera</i>	-0.008	n.s.	-	-	+ve	-	-

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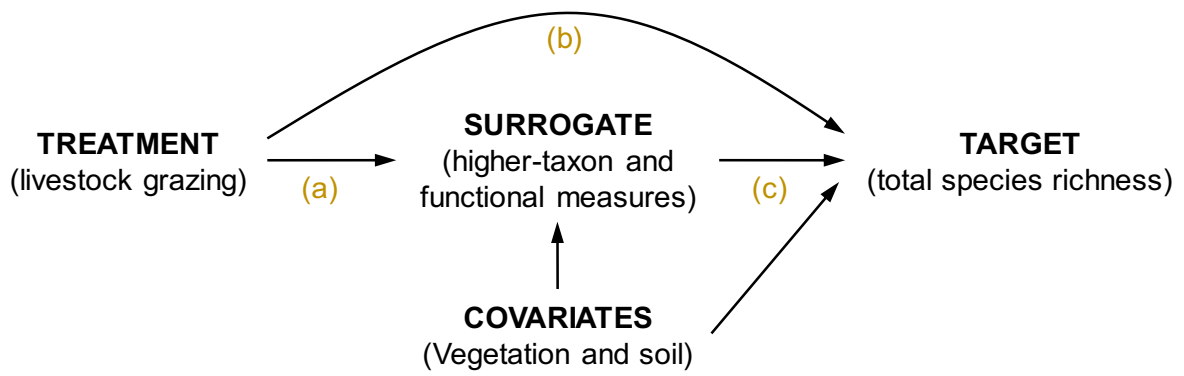
526 **Table 3.** Surrogate bird variables ranked in order of correlation strength with their target of  
 527 bird species richness, and the corresponding effects of grazing treatments. Direction of effect  
 528 and grazing context are given.

Bird variables	Correlation with species richness	P	Effect of all-year exclusion	Effect of spring/summer exclusion	PC1	PC2	PC3
Total species richness	n/a		-	+ve CG, -ve LH	-	-	-
Family richness	0.899	***	-	-	-	-	-
Total abundance	0.802	***	-	-	-	-	-
Abundance of Canopy and Shrub foragers	0.764	***	-	+ve CG	-ve	-	-
Abundance of Aerial foragers	0.587	***	-	-	-ve	-	-
Abundance of Meliphagidae	0.531	***	-	-ve LH	-ve	-	+ve
Abundance of Acanthizidae	0.433	***	-	-	-ve	+ve	-
Abundance of Ground foragers	0.305	n.s.	-	-	-	-	-

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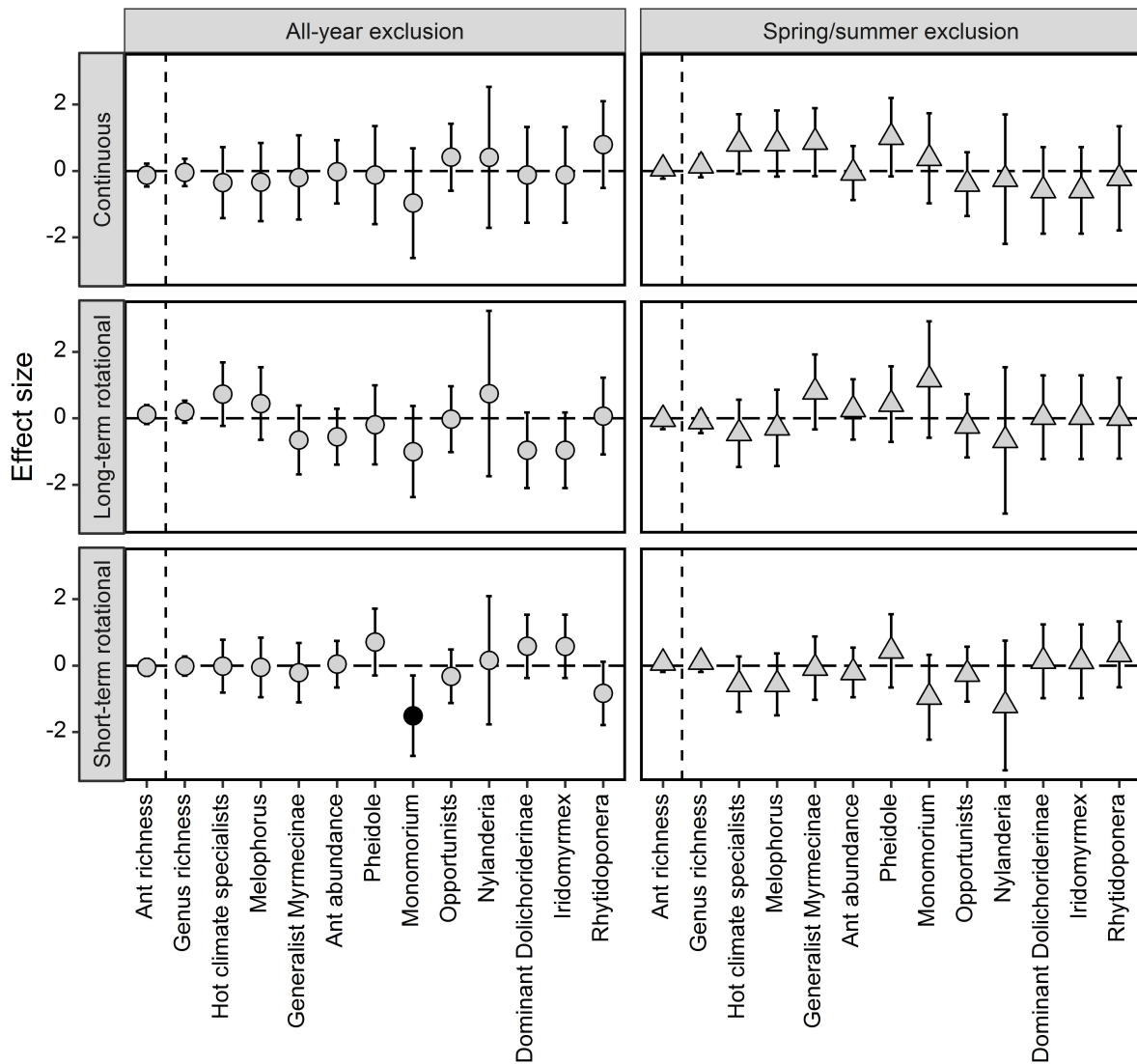
533 **Figure 1.** A surrogate concept that incorporates the relationships between treatment,  
 534 surrogate, and target, as well as covariates. (a) We quantified the effects of the grazing  
 535 treatments on a range of candidate surrogate variables, as well as (b) treatment effects of the  
 536 target for both bird and ant assemblages. Environmental covariates were also considered in  
 537 separate models. (c) We then examined the correlations between surrogate and target  
 538 variables to see if this gave any insight into which surrogate and target responses to the  
 539 treatment were similar.

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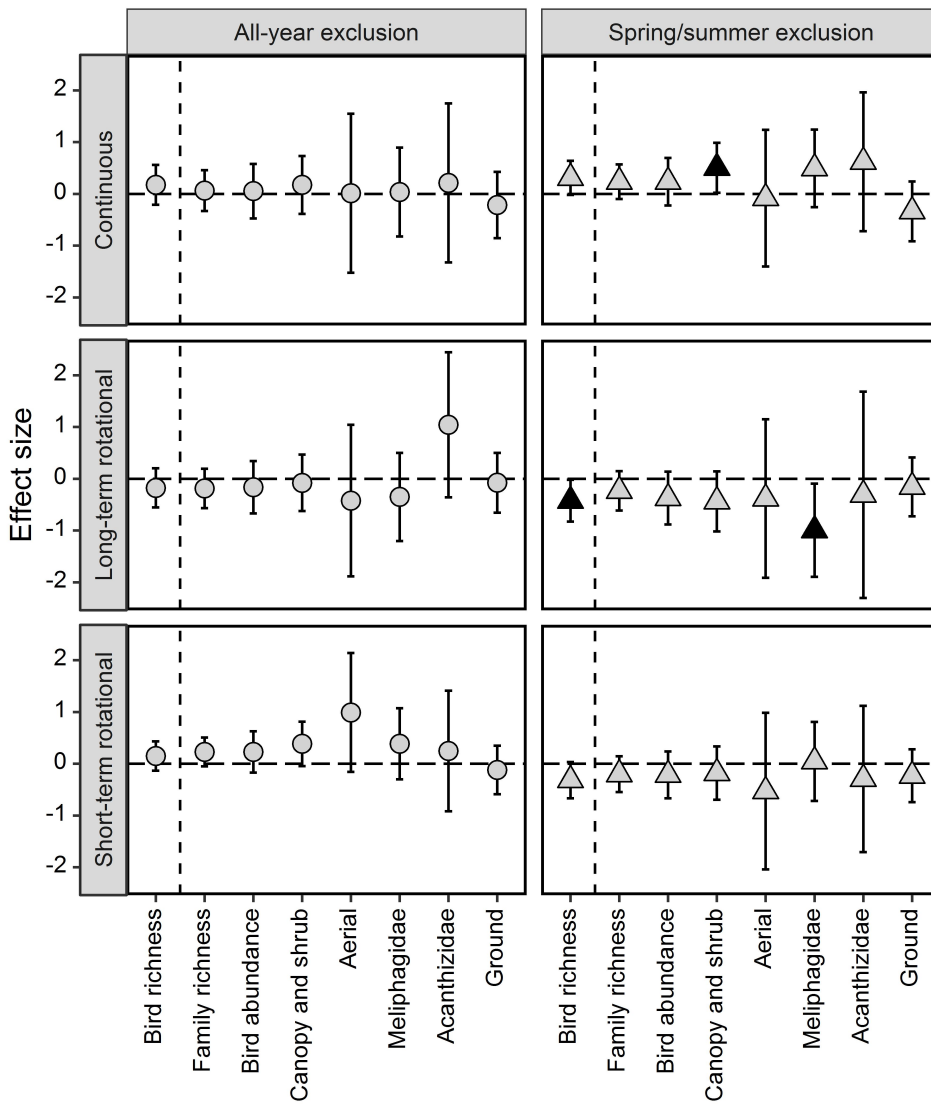
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545 **Figure 2.** Effects of grazing treatments on ant species richness (the target) and various ant  
 546 surrogate variables relative to sites with business-as-usual grazing. Mean effect sizes and  
 547 their 95% confidence intervals are given.

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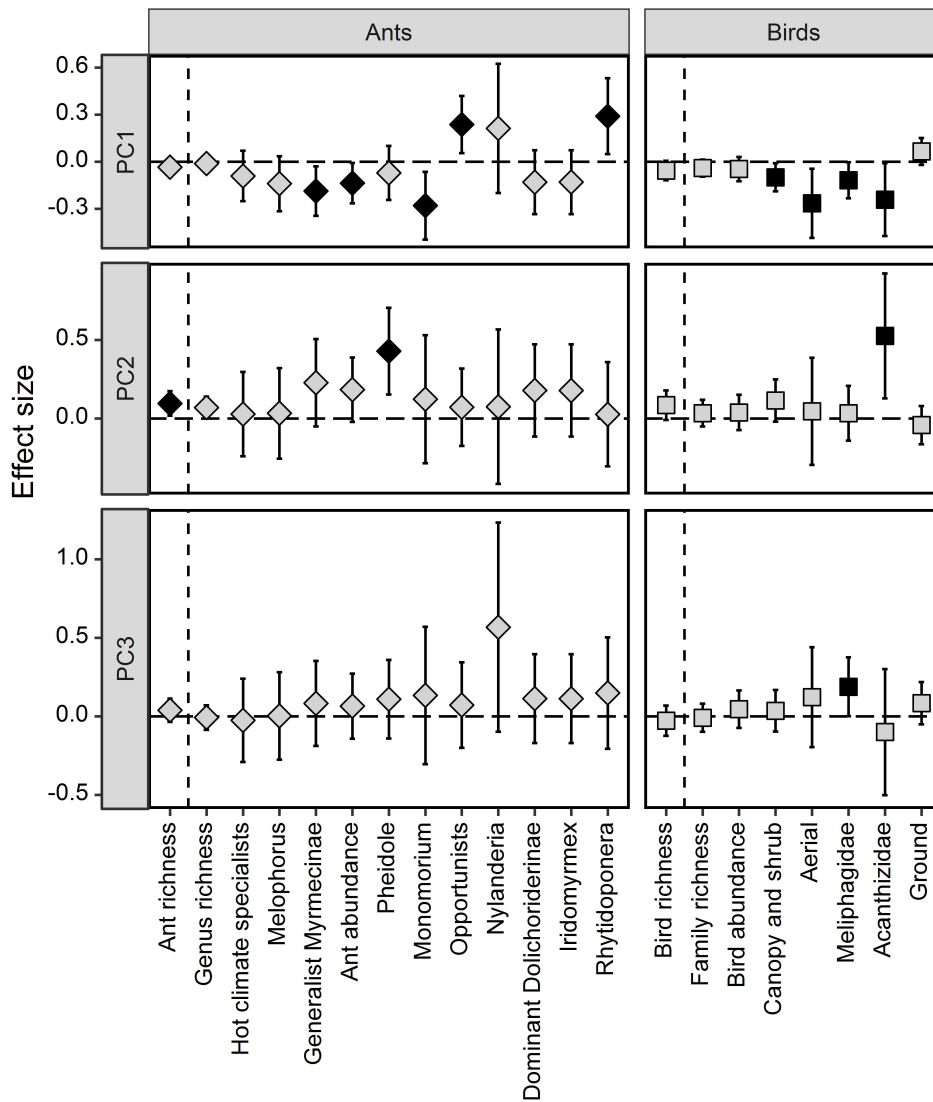


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550 **Figure 3.** Effects of grazing treatments on bird species richness (the target) and various  
 551 surrogate variables relative to sites with business-as-usual grazing. Mean effect sizes and  
 552 their 95% confidence intervals are given.

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556 **Figure 4.** Effects of environmental covariates on ant and bird surrogate variables.

557 Environmental effects are relative to the intercept, with mean effect sizes and their 95%

558 confidence intervals given. PC1 represents a gradient from under trees out to improved

559 pasture/grassland sites. PC2 represents a gradient of exotic perennial to native annual grass

560 cover. PC3 represents a gradient of increasing native perennial grass cover (see Table S2).