1 **Conserving focal insect groups in woodland remnants: the role of**

2 **landscape context and habitat structure on cross-taxonomic congruence**

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24   **Abstract**

25   Determining the shared responses of different taxa to landscape modification is a key step for

26   identifying which groups of species are good surrogates for other groups. Yet, surprisingly little is

27   known about the spatial processes that drive cross-taxonomic congruence of diversity or how this

28   knowledge can be used to improve the management of modified landscapes for biodiversity,

29   especially insects. We investigated how assemblages of two ecologically important insect groups,

30   wild bees and beetles, respond to different landscape contexts and habitat structure in an Australian

31   agricultural landscape, and how this, in turn, influenced either group's potential as a surrogate for the

32   other. Bee and ground-active beetle assemblages were sampled in remnant woodland patches in two

33   landscape contexts: woodland patches surrounded by pine plantation and woodland patches

34   surrounded by open grazing land. Bee species richness, and the richness of functionally-defined bee

35   groups did not differ between landscape contexts, in contrast to beetles. We found that landscape

36   context exerted a stronger effect on species composition than species richness of both groups.

37   Although some landscape and habitat variables were useful in predicting the diversity of both insect

38   groups, few were shared. Our findings showed that bee and beetles are poor surrogates for each other

39   in landscapes that are highly modified. Our study highlighted the need to consider: (1) taxon-specific

40   responses to landscape context, (2) the influence of different metrics of cross-taxonomic surrogacy

41   and, (3) dissimilar ecological attributes among insect taxa when selecting insects as biodiversity

42   surrogates. It should not be assumed that agricultural landscapes managed to conserve specific insects

43   (e.g. bees) will necessarily benefit other insects.

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45   **Keywords**

46   Anthropogenic landscapes, Coleoptera, indicator, pollination, remnant vegetation, surrogacy, wild

47   bees

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1. Introduction

Anthropogenic transformation of the world's landscape is a major driver of biodiversity decline (Souza et al. 2015; Lindenmayer et al. 2019). Currently, land used for grazing and animal fodder constitutes half of the world's agricultural land area, and well over 10% of the world's terrestrial surface (Food and Agriculture Organisation 2011). Future expansion and intensification of agriculture is expected to further impact and degrade the world's biodiversity at various scales (Flynn et al. 2009; Le Féon et al. 2010; Tscharntke et al. 2012; Egli et al. 2018). Across Australia, large swaths of landscapes have been irreversibly transformed, with vast areas of native woodland and forests now replaced with cropping and grazing landscapes, , tree plantations and other land uses (Lindenmayer et al. 2010; Lindenmayer et al. 2019), threatening biodiversity and ecosystem services in the process (McAlpine et al. 2002). Therefore, there is an urgent need to identify better ways to conserve and manage biodiversity in anthropogenic and increasingly simplified landscapes (e.g. Henle et al. 2008; Batáry et al. 2010; Landis 2017).

While information on biodiversity is needed to guide conservation decision-making and management, not every component of biodiversity can be cost-effectively measured (Lindenmayer and Likens 2011; Ware et al. 2018). Furthermore, data on many taxa is expensive or difficult to collect due to the high sampling effort required (Favreau et al. 2006; Caro 2012). Conservation practitioners therefore rely on surrogate measures, especially cross-taxonomic surrogates, to quantify suites of biota that are challenging to accurately measure (Caro 2010; Westgate et al. 2014; Lindenmayer et al. 2015; Yong et al. 2018). Cross-taxon surrogate approaches are underpinned by the assumption that patterns of diversity or distributional patterns shown by one taxon (i.e. 'the surrogate') can consistently predict changes in another taxon of interest (i.e. 'the target'), or broader components of biodiversity (Barton et al. 2015; Ware et al. 2018). Determining whether different taxa show similar responses to habitat disturbance and modification (Schulze et al. 2004) or associations in diversity (Kati et al. 2004; Westgate et al. 2014) is critical to identifying cross-taxon surrogates.

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In spite of their immense ecological importance, insects are one particularly challenging component

of biodiversity to document and survey given the poor state of knowledge for many groups and the

limited taxonomic expertise available to study them (Hochkirch 2016). Consequently, the

conservation of insects has received far less attention than vertebrates (Dunn 2005; Guiney &

Oberhauser 2008) despite their recognised roles as pollinators, herbivores, ecosystem engineers and as

prey for many other taxa (Losey and Vaughan 2006; Nichols et al. 2008; Kleijn et al. 2015), and are

sensitive proxies of ecological change (Kremen et al. 1993). Yet, landscape transformation and

fragmentation driven by land-use change can affect insect communities across different levels and

scales (Samways 2005; Hendrickx et al. 2007; Kennedy et al. 2013), and under specific ecological

attributes such as mobility (Marini et al. 2011). Moreover, changes in land-use may modify landscape

and environmental conditions that shape insect diversity (Rösch et al. 2013; Senapathi et al. 2017),

thus driving changes in the functional diversity of other groups (e.g. Tscharntke et al. 2008;

Lindenmayer et al. 2015). Broadly, there is mounting evidence that anthropogenic impacts have

driven the decline of key insect groups, with significant consequences on ecosystem functioning and

human well-being (Dirzo et al. 2014).

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The two insect groups with the greatest conservation relevance and importance worldwide are bees

(Order Hymenoptera, superfamily Apoidea,) and beetles (Order Coleoptera). Bees are crucial for

delivering pollination services in most ecosystems and are the best-known group of pollinators (e.g.

Hopwood 2008; Kleijn et al. 2015; Winfree et al. 2018). Given their importance to agriculture and the

impending threat of a 'global pollinator crisis' (e.g. Potts et al. 2010), the impact of habitat

modification on pollinating insects is now reasonably well investigated (Le Féon et al. 2010; Kleijn et

al. 2015). By contrast, beetles have received far less attention from conservationists even though they

form a third of all known insect species and perform varied ecological roles (New 2007; Barton et al.

2009; Stork et al. 2015). Because relatively few studies have concurrently examined the response of

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101   multiple insect groups to landscape modification (e.g. Tscharntke et al. 2002; Hendrickx et al. 2007;

102   Gardner et al. 2009), it remains unclear if agricultural landscapes managed to conserve some insect

103   groups (e.g. bees) will also conserve other important groups.

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105   In this study, we compared the responses of two major insect groups, bees and ground-active beetles,

106   to habitat modification in a heavily-transformed landscape that is representative of the plantation and

107   pasture landscapes of south-east Australia (Lindenmayer et al. 2019). In surveying these two groups,

108   we investigated if either can be used as a surrogate for the other by assessing, (1) their responses to

109   different landscape contexts (we subsequently refer to the plantation and grazing land matrix as

110   "landscape contexts") and, (2) cross-taxonomic congruency between the two groups across the whole

111   landscape. We then evaluated landscape and habitat structure as surrogates for insect diversity since a

112   comparative approach can lead to better surrogate identification for conservation management

113   (Lindenmayer et al. 2014; Barton et al. 2015). We structured our questions around a conceptual

114   framework that represents the links between these two insect groups, habitat structure and landscape

115   context (Figure 1). First, we were interested in determining similarities in responses of wild bees and

116   beetles to landscape context. We therefore asked: (1) How does species richness and composition of

117   each insect group respond to different landscape contexts? We then asked: (2) How do groups with

118   similar functional attributes respond to the landscape contexts? We predicted that the response in

119   species richness would be similar, but responses at the species composition level, and between

120   defined functional groups would differ strongly across landscape contexts. This is because studies of

121   insect assemblages have revealed strong responses to habitat structural differences at the functional-

122   group level (Ribera et al. 2001; Purtauf et al. 2005). Next, we were interested in identifying the

123   different components of landscape and vegetation structure that can be used as surrogates of species

124   richness and composition of both insect groups. We therefore asked: (3) What are the landscape and

125   habitat structure variables that best predict bee and beetle species richness and composition?

126   Identification of important habitat components means that easily measured habitat structure variables

127   can be considered independently as surrogates for insect assemblages. Finally, to test if either insect

128 group could be used to predict the diversity of the other group, we asked: (4) Are patterns of bee and

129 beetle species diversity congruent across the study landscape?

130

131 **2. Methods**

132 *2.1. Study sites*

133 Our study was conducted in the Nanangroe region (34°57'54"S, 148°28'46"E) near Jugiong and

134 Gundagai, central New South Wales, Australia. The Nanangroe landscape consists of about 30,000 ha

135 of agricultural (i.e. grazing) land and exotic Radiata Pine *Pinus radiata* plantations (See map: Figure

136 2). Nearly all the original vegetation (i.e. box-gum grassy woodlands) in these landscapes has been

137 cleared in the past two centuries for agriculture and grazing land (Lindenmayer et al. 2008; 2019).

138 The landscape is considered as 'highly variegated' and consists of distinct patches of remnant

139 woodland of varying tree densities and scattered eucalypt trees (McIntyre and Barrett 1992). These

140 woodlands are surrounded by either a matrix of pastures actively grazed by livestock or by

141 monoculture Radiata Pine plantations.

142

143 We identified 52 woodland remnants in four size classes in 1997. In 1998, the landscape matrix

144 surrounding these remnants was transformed with the establishment of dense plantations of the

145 Radiata Pine (Lindenmayer et al. 2008; 2019). A further 56 patches of woodland remnants of

146 matching vegetation classes and sizes were identified in surrounding agricultural land (thereafter

147 referred to as 'woodland remnants in agricultural matrix'). Permanent transects were marked and

148 established at all our study sites prior to the commencement of the study. For this study, a subset of

149 20-23 remnant woodland patches each in the pine plantation and agricultural matrices were randomly

150 chosen to represent the full range of patch size classes (Table 1). Additionally, we selected five sites

151 dominated by Radiata Pine as controls.

152

2.2. Insect sampling

We sampled bees using coloured vane traps. This survey method has increasingly been used in open, temperate landscapes in Australia and North America (e.g. Hogendoorn 2011; Lentini et al. 2012; Joshi et al. 2015). We sampled all 48 sites at the midpoint of each line transect with two traps at each site, located in trees approximately 20m apart. We suspended traps at 1.5-2.0m above ground. Each trap consisted of blue coloured vanes attached to a bright yellow plastic jar. We conducted bee sampling from November to December 2014 during peak bee activity in the austral spring. At the end of the sampling period, we retrieved the traps (81 traps from 43 sites) and preserved all insects caught in 70% ethanol before sorting them to species-level. We assembled bees that were difficult to identify into a reference collection following Droeges (2015), and identified them to species-level using the Pest and Diseases Image Library (PaDIL 2016) and identification keys (e.g. Walker 1995; Michener 2000). Identified bees were then checked by a taxonomist (Michael Batley, Australian Museum). Some bee genera (i.e. *Exoneura* sp.) were classified only to the morphospecies level due to their unstable taxonomy (M, Schwarz. pers comm. 2015).

We used non-baited pitfall traps to sample ground-dwelling beetles. Pitfall traps were placed in four rows, with each row located about 1.0m apart. Each pitfall trap consisted of a plastic container of 5.0cm diameter and 7.5cm depth, and was filled with 100ml of ethylene glycol. In total, we set 384 pitfall traps across 48 study sites. To increase catch rates, we mounted one plastic drift fence (1.0m x 0.2m) along each pair of traps. We conducted beetle trapping from November to December 2014. We recovered 330 traps from 44 sites at the end of the sampling period (with all traps at four sites damaged by livestock, precluding data collection from them). We preserved beetle specimens in 70% ethanol before sorting them to morphospecies level using identification keys (e.g. Matthews 1992; Hangay and Zborowski 2010). We assembled voucher specimens for each morphospecies into a reference collection for comparison. Highly similar morphospecies from speciose families such as

178 Staphylinidae were further validated by an expert familiar with beetle assemblages in similar

179 landscapes (M. John Evans) for accuracy.

180

181 *2.3. Vegetation sampling*

182 To characterize the vegetation structure in our study landscape, we measured a total of 34 vegetation

183 and habitat structural variables at each sampling site (see Supplementary Information Table S4 for full

184 list of variables). We classified woodland remnants on the basis of their constituent tree genera into

185 *Eucalyptus*-dominated and *Casuarina*-dominated sites. In addition, we conducted observational

186 surveys to estimate flowering activity within a 50m radius of the insect traps at the ground, shrub and

187 canopy level. To quantify native tree cover in each woodland remnant, we used tree cover area as

188 measured in a circle (with a 250m and 500m radius) centred at each sampling site. We defined native

189 tree cover to include clusters of trees within habitat patches, as well as the single scattered trees in the

190 landscape. We measured native tree cover area using digitised aerial photographs in ArcGIS version

191 10.1 (Mortelliti and Lindenmayer 2015).

192

193 *2.4. Data analysis*

194 We calculated site-level species richness for both insect groups (Question 1). Because some of the

195 pitfall traps were damaged by livestock, we included only sites that retained the majority of the pitfall

196 traps (at least four of eight traps set) for analysis. Similarly, we used only bee data from traps that

197 were not damaged. We computed species richness estimates using one of three non-parametric

198 estimators (Chao1) (see Walther and Moore 2005). We then plotted sample-based rarefaction curves

199 using 999 random permutations to assess sampling completeness, and compare species richness for

200 both groups in different landscape contexts (Gotelli and Colwell 2001). We performed this analysis

201 using the function 'specpool' in the *vegan* package (Oksanen et al. 2016).

202

203   We calculated Moran's I to assess the effect of spatial autocorrelation on observed species richness

204   for both insect groups (Legendre 1993) using the *ape* package available in R (Paradis et al. 2004).

205   Moran's I assesses the relationship of the dependent variable against a matrix of weights (i.e. the

206   neighbourhood matrix is calculated based on pairwise Euclidean distances across all site

207   combinations). We then fitted generalised linear models to test if mean site-level species richness was

208   related to landscape context. Because the dependent variable (observed species richness) involved

209   count data, we fitted models with a Poisson-error distribution and a log-link function. If species

210   richness was found to be spatially correlated, we accounted for this in the model by fitting 'site' as a

211   random effect while 'landscape context' was retained as a factor with three levels. We conducted

212   these analyses using the 'glmer' function in the package *lme4* (Bates et al. 2014).

213

214   To compare site-level species composition across different landscape contexts (Question 1), we

215   performed non-metric multi-dimensional scaling (NMDS) to ordinate site-level counts in species

216   space for both insect groups. We first square root-transformed data on the raw abundance of all

217   species to reduce the influence of highly abundant species. We then used the multiple response

218   permutation procedure (MRPP) as a non-parametric test to assess for pairwise differences in species

219   composition across the two landscape contexts and pine contrasts. Each MRPP analysis yields the

220   effect size statistic *A* which measures within-class heterogeneity with the Bray-Curtis dissimilarity,

221   which we assessed using 1,000 permutations (McCune and Grace 2002), and is often used alongside

222   NMDS ordinations, although permutational procedures such as PerMANOVA) could also be used

223   with robust outcomes.

224

225   To test if ecological attributes influenced responses of both bee and beetle species assemblages to

226   landscape context (Question 2), we compared species richness and composition of groups defined by

227   their shared functional attributes. Past studies found that life history traits of bee species, particularly

228   nesting strata (location of nesting: above versus below ground) significantly influenced their

229 responses to various types of habitat change such as habitat loss and agricultural intensification (e.g.

230 Cane et al. 2006; Williams et al. 2010). Consequently, traits that influenced how a species responds to

231 environmental conditions could prove useful for understanding fine-scale community responses

232 (Greenleaf et al. 2007; Barton et al. 2013a). We partitioned the bee dataset into two groups based on

233 data on species-specific nesting requirements available in Dollin et al. (2000) and Michener (2000),

234 and further checked by an expert. We identified bee species that nest in cavities or plant parts (e.g.

235 *Exoneura* sp.) and defined them as 'above-ground' nesting species (*sensu* Williams et al. 2010). The

236 remainder were classified as ground-nesting species (e.g. *Amegilla*, *Lasioglossum* sp.). We carefully

237 checked each individual beetle morphospecies from our reference collection with a stereo microscope.

238 We classified a morphospecies as being flightless if the elytra were fused or if wings were absent. We

239 classified all other beetle species flight-capable.

240

241 We first fitted a series of generalised linear models with a Poisson-error distribution to compare

242 species richness of each functionally-defined species group across the landscape contexts. Because of

243 spatial autocorrelation in the bee dataset detected earlier in the Moran's I test, we fitted 'site' as a

244 random effect in models for both functionally-defined groups. To compare species composition for

245 each group across pairs of landscape contexts, we used MRPP tests with 1,000 permutations. We then

246 performed Spearman's rank correlation, to test if a group defined by a shared functional attribute was

247 a useful predictor of species richness in other groups. We used Spearman's rank correlation because

248 the sample size (number of study sites) was low and did not meet parametric assumptions needed for

249 Pearson's correlation.

250

251 Next, we evaluated the influence of habitat and landscape variables on species richness and species

252 composition (Figure 1; Question 3). For species richness, we fitted a series of generalised linear

253 models that related species richness to six explanatory landscape variables. We excluded highly

254 correlated variables (Pearson's $r > 0.5$) from the analysis after inspecting a correlogram matrix of all

255   habitat variables. We transformed three categorical variables, 'forest type', 'topography' and 'water

256   body' into factors. We applied a Poisson error distribution and logarithmic link function in the models

257   rather than log-transforming our data (O'Hara and Kotze 2010). We fitted two sets of candidate

258   models using Bayesian Model Averaging (BMA). We implemented BMA to account for model

259   uncertainty in the model selection process by taking the average of the best candidate models based

260   on their posterior model probability (Wintle et al. 2003). We ranked the best five models in each

261   candidate set by the Bayesian Information Criterion (BIC) and their posterior probability. We

262   completed model selection using the *BMA* package (Raftery et al. 2015).

263

264   To compare the effects of different habitat structure on bee and beetle species composition, we fitted

265   vectors for selected habitat structures variables into our NMDS ordination results. The full set of

266   variables were first assessed using a correlogram matrix and retained for analysis only if they were

267   found not to be strongly correlated (Pearson's $r < 0.5$). The function 'envfit' available in 'Vegan'

268   computes factor averages or vectors for each habitat structural variable fitted to the ordination matrix

269   (Oksanen et al. 2016). After excluding highly correlated variables (Pearson's $r > 0.5$), we compared

270   the remaining 15 habitat variables. We assessed the significance of the fitted vectors for each habitat

271   structure variable using 999 permutations.

272

273   In earlier questions, we focussed on the responses of the two insect assemblages to different landscape

274   contexts. Here, we aimed to assess how congruent diversity patterns of these two groups were across

275   the study landscape (Figure 1; Question 4). To assess for congruency of bee and beetle species

276   richness, we performed Spearman's rank correlation using site-level species richness. We used the

277   Spearman's correlation coefficient as a measure of correlation strength because our dataset was found

278   to be non-normally distributed using the Shapiro-Wilk test. To assess for congruency in species

279   composition, we used partial Mantel tests implemented on the package *Ecodist* (Goslee and Urban

280   2013). We used Partial mantel tests as the strength of correlation between two matrices conditioned

281 on a third matrix of geographic distances allowed the effects of space to be accounted for (Goslee and

282 Urban 2007), thus partitioning out the variation due to space. We assessed the statistical significance

283 of each partial Mantel tests using 999 permutations. We conducted all statistical analyses using R v.

284 2.15.1 (R Project for Statistical Computing, http://www.r-project.org).

285

286 **3. Results**

287 *3.1. Overview*

288 We collected a total of 3,717 beetles representing 274 morphospecies in 36 families, and 1,714 bees

289 representing 32 species in four families through our field sampling. The number of bee species in the

290 four families were highest in the Halictidae (18 species), followed by Apidae (8 species),

291 Megachilidae (5 species) and Colletidae (1 species) (Table S1). Among beetle families, the most

292 species-rich were the rove beetles (family Staphylinidae, 35 morphospecies), scarabs (family

293 Scarabeidae, 33 morphospecies) and ground beetles (family Carabidae, 30 morphospecies) (Table

294 S2). Our sampling effort was consistent for both insect groups, detecting 64.0-77.8% of predicted bee

295 diversity, and 61.5-71.1% of predicted beetle diversity (see Supplementary Figure S1). We found that

296 bee species richness was spatially weakly correlated between woodland remnants across the landscape

297 (Moran's I = 0.0998, P = 0.004). We found no such patterns for beetle species richness (Moran's I = -

298 0.00185, P = 0.649).

299

300 *3.2. How do bee and beetle assemblages respond to different landscape contexts? (Question 1)*

301 We found that bee species richness was highest in woodland remnants in the agricultural matrix

302 (Chao1 estimate: 43 species), followed by remnants in the pine plantation matrix (Chao1 estimate: 27

303 species) (Figure 3a). However, predicted beetle species richness was higher in woodland remnants in

304 the pine plantation matrix (Chao1 estimate: 281 species) than woodland remnants in the agricultural

305 matrix (Chao1 estimate: 237.5 species) (Figure 3b). Predicted species richness was lowest in the pine

12

306   plantation sites for both bees (Chao1 estimate: 12 species) and beetles (Chao1 estimate: 75 species)

307   (Figure S1). However, bee species richness was not significantly different between woodland

308   remnants in either the pine plantation or agricultural matrix (mean difference = -0.0905, Z = -0.395, P

309   = 0.693) after accounting for variation due to random effects (variance = 0.0668). Similarly, there

310   were no differences in bee species richness between woodland remnants in either the pine matrix

311   (mean difference = -0.236, Z = -0.950, P = 0.342) or agricultural matrix (mean difference = -0.326, Z

312   = 1.111, P = 0.267), and the pine plantation sites. Conversely, beetle species richness was

313   significantly different between pairwise comparisons of all landscape contexts. Beetle species

314   richness was significantly different between woodland remnants in both landscape contexts (mean

315   difference = -0.215, Z = 3.370, P < 0.001) (Table S3). Pine plantation sites were significantly poorer

316   in beetle species richness than both kinds of woodland remnants (mean difference = -0.274, Z = -

317   2.337, P = 0.0194).

318

319   We found that the species composition of both bee and beetle assemblages was significantly different

320   between landscape contexts with the bee assemblage in pine sites weakly nested within that of

321   woodland remnants in pine (Figure 4, Table 2). However, species composition of the beetle

322   assemblages was more dissimilar across the landscape contexts than the bee assemblages (Table S5).

323   Pairwise comparisons of beetle species composition were always stronger when compared with

324   pairwise comparisons for bees. For instance, beetle species composition differed more strongly

325   between woodland remnants in the agricultural matrix and pine plantation sites (A = 0.0794, P =

326   0.001), than that for bees (A = 0.0430, P = 0.010).

327

328   *3.3. How do bee and beetle groups with similar functional attributes respond to the landscape*

329   *contexts? (Question 2)*

330   We found that neither landscape contexts had a significant effect on species richness of ground-

331   nesting bees (mean difference = -0.0264, Z = -0.139, P = 0.890) and above-ground nesting bees

13

332   (mean difference = -0.159, Z = -0.340, P = 0.734) after accounting for variation due to random effects

333   (Figure 5b, Table S3). However, no species of above-ground nesting bee occurred in the pine-

334   dominated sites even though ground-nesting species occurred at these sites (mean richness = 4.4

335   species). We found that the species richness of flightless beetles differed across landscape contexts

336   (mean difference = -0.515, Z = -2.714, P < 0.01) (Figure 5c, Table S3), but not between remnants in

337   either landscape context and pine plantation. Similarly, woodland remnants in the pine matrix

338   supported a significantly higher richness of flight-capable beetles than remnants in the agriculture

339   matrix (mean difference = 0.318, Z = 4.637, P < 0.001). Species richness of flight-capable beetles

340   between the pine contrast sites and woodland remnants in pine were significantly different (mean

341   difference = 0.553, Z = 4.415, P < 0.001) but not between woodland remnants in agriculture.

342

343   When we compared the species composition of bee groups defined by functional attributes (Table 2),

344   we found significant differences between above-ground nesting bee assemblages (A = 0.0677, P <

345   0.01) and ground-nesting bee assemblages (A = 0.0411, P = 0.001) among woodland remnants in the

346   pine and agricultural matrix. However, ground-nesting bee assemblages in the pine plantation sites

347   were not significantly different when compared with woodland remnants in either landscape contexts.

348   Species composition of flightless beetles was significantly different for all pairwise comparisons

349   except for that between woodland remnants in the pine matrix and the pine plantation sites (A =

350   0.0079, P = 0.200). However, species composition of flight-capable beetles was significantly different

351   between all pairwise comparisons of sites.

352

353   *3.4. What are the landscape variables that best predict bee and beetle species richness and*

354   *composition? (Question 3)*

355   We summarised the best five of a series of candidate models (bees: 57 models, beetles: 25 models for

356   beetles) based on Bayesian Information Criterion (BIC) values and posterior probabilities. The

357   candidate model that best explained bee species richness incorporated only the intercept (Table 3,

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358   Posterior probability = 0.159). Among landscape variables, we found that native tree cover was

359   relatively the most important covariate even though it was weakly correlated with bee species richness

360   (Supplementary Figure S2), occurring in only 45.2% of the candidate models. Landscape context and

361   topography were the next most important landscape variables, occurring in 25.5% and 26.7% of the

362   models. Generally, woodland remnants in the pine plantation matrix and on slopes were characterised

363   by lower bee species richness.

364

365   The candidate model that best explained beetle species richness (Posterior probability = 0.293)

366   contained elevation, distance to water, and topography as the explanatory variables. We found that

367   elevation was the most important predictor of beetle species richness, occurring in 100% of the

368   candidate models (Table 3; Supplementary Figure S2). Distance to water (58.8% of models), the

369   location of a site on a slope (85.2% of models), and/or a ridge (14.2% of models) were the next most

370   important predictor variables. Distance to water was only weakly associated with higher species

371   richness, while slope and ridge topographies of sites were associated with low species richness.

372   Unlike bees, native tree cover was found to be relatively unimportant for beetles (16.6% of models)

373   and was in fact negatively correlated with beetle species richness.

374

375   We identified four habitat structure variables that were significantly correlated with the NMDS

376   ordination axes describing bee species composition (Table 4): canopy depth (R^2 = 0.189), blackberry

377   cover (R^2 = 0.160), tree crown (R^2 = 0.253) and the extent of exposed rocks (R^2 = 0.279). For beetle

378   species composition, we identified five significantly correlated variables. Basal stem count was the

379   mostly strongly correlated variable (R^2 = 0.473). The other significant variables included tree crown

380   structure, extent of exposed rocks, litter layer and weed cover. Only two of these variables were

381   shared with bees (i.e. crown structure and extent of exposed rocks).

382

15

383   *3.5. Are bee and beetle species richness and composition congruent across the study landscape?*

384   *(Question 4)*

385   We found that site-level species richness for bees was not significantly correlated with the species

386   richness of beetles (Spearman's $\rho = 0.290$; $P = 0.063$) across the study landscape, within each

387   landscape context and among functionally-defined sub-groups. However, bee and beetle species

388   composition were weakly correlated across the study landscape (partial Mantel R = 0.108, $P = 0.024$).

389   When correlations of species composition were considered for each landscape context, all

390   relationships were weak and non-significant.

391

392   **4. Discussion**

393   *4.1. Overview*

394   We found that wild bee and ground-active beetle assemblages from woodland patches differed

395   between landscape contexts. Our findings also showed how functionally-defined attributes can

396   influence an insect group's response to different landscape contexts (e.g. Ribera et al. 2001; Williams

397   et al. 2010). However, the low level of species richness congruence did not improve after functional

398   attributes and different landscape contexts were considered. Given that determining the extent of

399   shared responses to habitat and landscape structure and cross-taxonomic congruency is often a starting

400   point in identifying biodiversity surrogates (Caro 2010; Westgate et al. 2014), our study suggests that

401   bees and beetles are surprisingly poor surrogates for each other despite either groups' ecological

402   importance. Furthermore, our study raise questions about whether the ecological responses of specific

403   arthropod groups to land use change can be used to infer that of other groups. Notwithstanding these

404   findings, we recognise a need to better incorporate insect diversity into the management of landscapes

405   to conserve biodiversity, and identify better surrogates to capture their diversity given their ecological

406   importance (New 1999; Samways 2005; Barton et al. 2009).

407

4.2. How do bee and beetle assemblages respond to different landscape contexts?

Our findings showed that bee and beetle species richness and composition were differently affected by landscape context even though both groups were similarly depauperate in pine-dominated sites (Question 1). Our data suggested that the landscape matrix has a more pronounced effect on beetle assemblages than bee assemblages (which appeared weakly nested, Figure 4), and consistent with similar studies on insects in heavily-transformed landscapes (Öckinger et al. 2012; Kennedy et al. 2013). First, the lower mobility of beetles compared to bees is expected to drive more heterogenous beetle assemblages in our study landscape (Marini et al. 2011a; Marini et al. 2011b; Barton et al. 2013b), and by extension, higher beta-diversity for beetles. Second, the microclimate of woodland remnants in the pine matrix would differ from that of remnants in the agricultural matrix (e.g. Driscoll et al. 2013). By altering the microclimate of the embedded woodland remnants, for instance through reducing wind and light penetration (e.g. Fahy and Gormally 1998; Jukes et al. 2001), cascading effects on soil conditions may arise, creating microhabitats that may influence the compositional heterogeneity of beetle assemblages. Yet, while the matrix can influence the diversity of insect assemblages in the embedded woodland remnants, its transformation (to pine monoculture) could also concentrate bees into 'islands' of woodland remnants embedded in a resource-scarce plantation matrix. Broadly, our study show that differences in the landscape matrix, and particular ecological attributes of insects can drive dissimilar responses from different insect assemblages (e.g. Jauker et al. 2009; Hendrickx et al. 2007; Barton et al. 2013b; Driscoll et al. 2013), and weakening the potential use of any group as a surrogate for other groups.

4.3. How do bee and beetle groups with similar functional attributes respond to the landscape contexts?

We found that bee species assemblages defined by shared functional attributes exhibited different responses to landscape context (Question 2). Ground-nesting species such as *Lasioglossum* sp. remained common across our study landscape, including in pine monoculture sites. Moreover, species

434   richness and composition of ground-nesting bees did not differ between woodland remnants in the

435   pine matrix and pine plantation sites. In contrast, species richness of above-ground nesting bees was

436   diminished in woodland remnants in the pine matrix and no species occurred in pine plantation sites.

437   Such patterns may arise due to changes in fine-scale vegetation structure arising from the

438   transformation of the matrix, which reduced nesting resources. For instance, the dense pine stands in

439   the plantations may limit the growth of hollow-bearing plants at the interface of woodland remnants

440   and the pine matrix, which are depended upon by *Exoneura* and other above-ground bees for nesting

441   (Dollin et al. 2000).

442

443   We found that flight-capable beetles responded to landscape context more strongly than flightless,

444   sedentary species. Such a response was inconsistent with expectations that flightless beetles should be

445   more dispersal-limited (e.g. Assmann 1999) since mobility has been found to influence insect

446   diversity patterns in modified landscapes (Hendrickx et al. 2007; Marini et al. 2011a; Driscoll et al.

447   2013). Studies such as Marini et al (2011a) suggest that relative mobility can explain the observed

448   beta-diversity patterns of some insect groups, with sedentary species accounting for a greater portion

449   of compositional turnover. However, because apterous or brachypterous beetles formed only a small

450   proportion of our total species pool (43 of 274 morphospecies), the effect of landscape context on

451   their diversity may be diluted. Additionally, many ground (carabid) beetle species in our landscape

452   are large-bodied and long-legged, and are thus relatively more mobile (e.g. Horák et al. 2013) and

453   able to respond to changes in habitat structure more quickly, thus driving the higher turnover observed

454   in agricultural landscapes such as ours (Hendrickx et al. 2008). Finally, difference in a species' spatial

455   requirements may also be more strongly influenced other factors such as body size, dietary guild and

456   foraging habits (e.g. Lassau et al. 2005) which were not investigated in our study.

457

458   *4.4. What landscape and habitat structure variables best predict bee and beetle richness and*

459   *composition?*

460   We found that the landscape variables that best predicted the species richness of bees and beetles were

461   markedly different (Question 3). For instance, native tree cover was found to be a relatively important

462   predictor of bee species richness (Table 3), consistent with studies in similar landscapes (e.g. Lentini

463   et al. 2012; Threlfall et al. 2015). However, beetle species richness was more strongly influenced by

464   elevation, distance to water and the topography of the woodland remnants. One explanation for this

465   difference is that foraging bees tend to be limited by floral resources (e.g. Vaudo et al. 2015). In

466   contrast, topography and proximity to water can interact to influence habitat structural components on

467   the ground that are important to beetles, such as the amount of accumulated organic material (e.g.

468   plant debris). Second, through being better dispersers than beetles (Francis and Chadwick 2013), bees

469   can respond to changes in the landscape and its different structural components more rapidly

470   compared to beetles. Third, while beetles are less vagile, they are far more species-rich, than bees.

471   Beetles would therefore exhibit a greater range of microhabitat preferences and respond more strongly

472   to environmental heterogeneity at finer spatial scales (Weibull et al. 2003; Lassau et al. 2005; Barton

473   et al. 2009).

474

475   We found that beetle species composition was associated with basal stem count, leaf litter, weed cover

476   and the extent of exposed rocks. Not surprisingly, this contrasted strongly with the habitat structural

477   variables most strongly associated with bee composition. These findings suggest that habitat variables

478   useful as surrogates of species diversity for some insect groups may not be useful for others (Question

479   3). For example, the number of trees in each plot (as determined by basal stem counts) may affect the

480   ground layer by contributing fallen leaves and deadwood. This, in turn, creates a diversity of habitat

481   types for ground-dwelling, saproxylic beetles (e.g. Barton et al. 2009), but not necessarily so for bees

482   (e.g. Roulston and Goodell 2011).

483

484   *4.5. Are bee and beetle species assemblages congruent across the study landscape?*

485   We found that congruency of bee and beetle species richness was limited across the study landscape

486   (Question 4). The low level of congruence in species richness did not improve even when functional

487   attributes and different landscape contexts were considered. However, congruency in species

488   compositional similarity performed better than species richness, and consistent with other studies (e.g.

489   Su et al. 2004). These findings are expected since our analyses have shown the importance of

490   different landscape and habitat structure variables to each group. Given that determining the extent of

491   cross-taxonomic congruency is often a starting point in identifying surrogates of biodiversity (Caro

492   2010; Westgate et al. 2014), both bees and beetles have limited use as surrogates for each other. Our

493   findings also highlight the problems of using specific arthropod groups as surrogates for other

494   invertebrate groups (Dauber et al. 2003; Harry et al. 2019), especially bees and other pollinators

495   which are often singled out for conservation prioritisation in agricultural landscapes (Hopwood 2008;

496   Jauker et al. 2009).

497

498   *4.6. Implications for the use of insects as surrogates*

499   Our study demonstrates that well known groups of insects are not necessarily good surrogates for

500   other invertebrate assemblages in agricultural landscapes, and should not be assumed to be so. While

501   it is widely acknowledged that vertebrates are weak surrogates for invertebrates (e.g. Oliver et al.

502   1998; Moritz et al. 2001; Oberprieler et al. 2019), our findings found no support for the hypothesis

503   that specific groups of insect can offer better alternatives as surrogates for other invertebrate fauna

504   (e.g. Ricketts et al. 2002; Lovell et al. 2007). More importantly, and recognising the differing levels of

505   sensitivity of insect taxa to fine-scale habitat structure, our study raise questions on whether diversity

506   responses of specific groups of insects to landscape change can be broadly applied to others.

507

508   Second, our study draws attention to the role of landscape context and its effect on taxon-specific

509   responses across insect assemblages at the species richness and compositional level. Changes in

510   landscape context arising from the transformation of the matrix surrounding woodland patches may

511 alter aspects of habitat structure important to different insect assemblages. Such changes in the matrix

512 can be expected to impact bee and beetle assemblages differently, especially in relation to dispersal

513 and foraging resources (e.g. Holzschuh et al. 2006; Jauker et al. 2009; Driscoll et al. 2013). Put

514 together, cross-taxonomic surrogacy between insect groups can be shaped by the varied differences in

515 the spatial and ecological requirements across different insect taxa, as well as the influence of biotic

516 and bionomic factors on species acting at far smaller scales (Hortal et al. 2010). Such considerations

517 are usually excluded by conservation planning approaches using species data at large spatial scales

518 and resolutions (e.g. Fattorini et al. 2011).

519

520 Our study shows that bee diversity is a poor surrogate for beetles, and even more so when species

521 richness is used as the metric of diversity. However, if cross-taxonomic surrogates are to be

522 considered for managing agricultural landscapes to conserve insects, then measures of compositional

523 (dis)similarity could be more useful (e.g. Su et al. 2004), especially when comparing assemblages

524 across habitats or landscapes. Additionally, sets of landscape and habitat variables can be considered

525 as surrogates of specific insect groups. For instance, native tree cover was a relatively important

526 predictor of bee species richness and thus retaining tree cover in agricultural landscapes can directly

527 benefit wild bee assemblages. In conclusion, our findings demonstrate the low levels of congruency

528 between wild bee and beetle assemblages, and draws attention to the fact that cross-taxonomic

529 patterns of diversity are limited even among the best-studied insect groups (e.g. Ricketts et al. 2002).

530 Against this backdrop, we note that the diversity of many less charismatic (yet ecologically important)

531 insects such as flies (order Diptera) and springtails (order Collembola) remain poorly understood in a

532 conservation planning context. Therefore, there remains a need to investigate how diversity and

533 abundance patterns of better known insects groups co-vary with other insect groups to broaden

534 conservation actions targeting invertebrate assemblages (New 1999; Lovell et al. 2007; Barton et al.

535 2009). Insights from such studies will underpin the identification of more effective surrogates for

536 insect diversity (Samways 2007), which in turn can better guide insect conservation in agricultural

537 landscapes.

21

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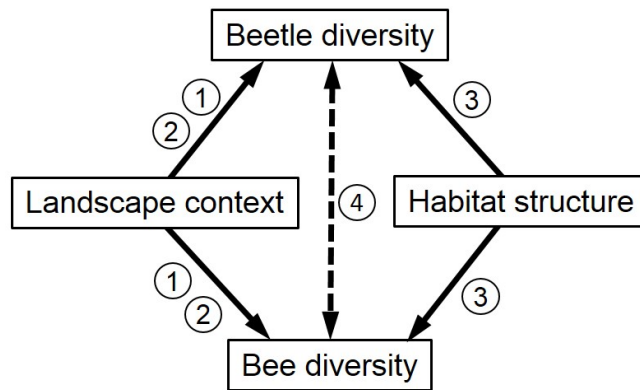
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820 **Figures**

821 Figure 1. Simplified conceptual framework showing the linkages between the different components of

822 our study landscape measured, and how this relates to habitat and cross-taxonomic surrogacy (see

823 inset).
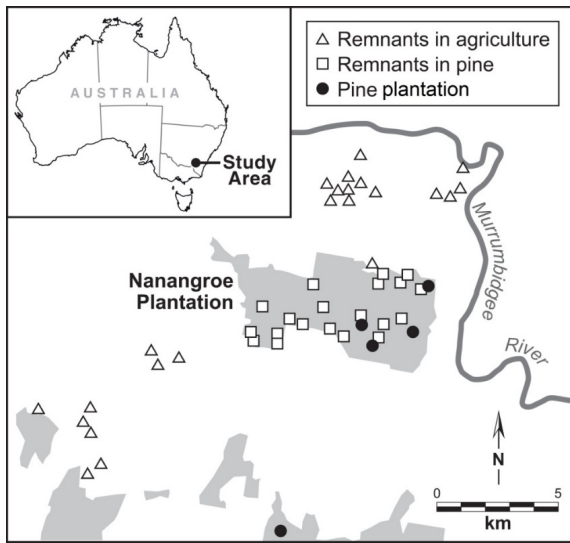
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836   Figure 2. Map of the Nanangroe experimental landscape, with inset map of Australia showing

837   locations of the woodland remnants studied and pine plantation sites.
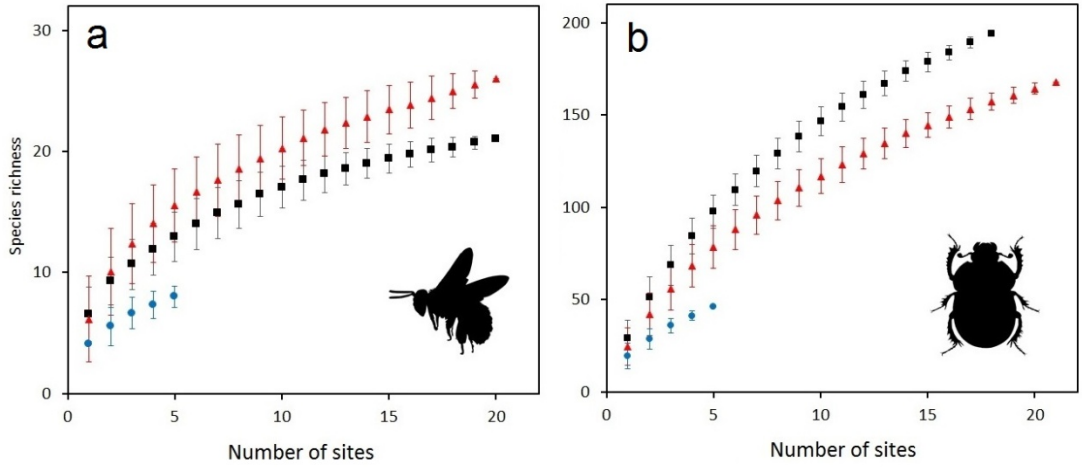

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Figure 3. Sample-based rarefaction curves for (a) wild bees and (b) ground-active beetles based on 999 random permutations. Black squares represent woodland remnants in the pine plantation matrix; red triangles represent woodland remnants in the agricultural matrix; blue circles represent pine plantation sites.
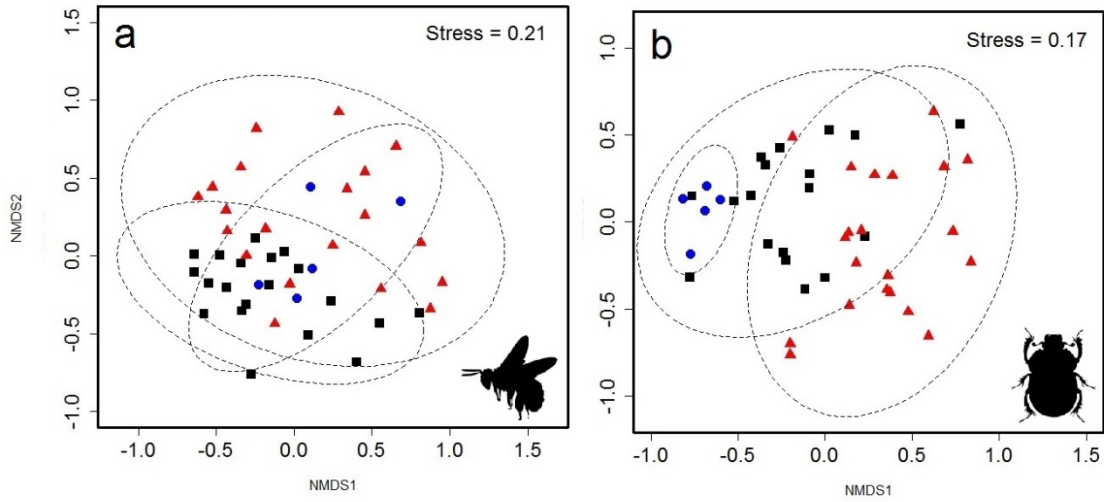
867   Figure 4. NMDS ordination plots of (a) wild bee and (b) ground-active beetle species composition

868   across the different landscape contexts. (Black square – woodland remnants in pine, red triangle –

869   woodland remnants in agriculture, blue circle – pine plantation)
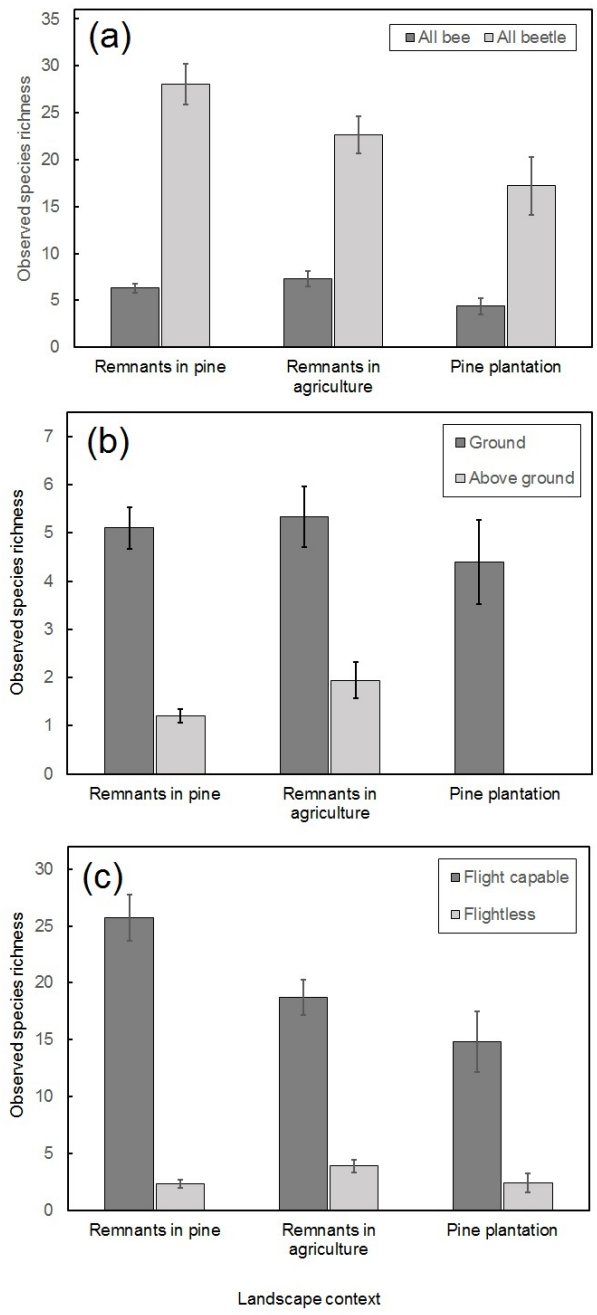

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Figure 5. (a) Mean site species richness (with standard errors) for all bees and beetles, (b) for functionally-defined bee groups classified by nesting requirement across different landscape contexts, and, (c) Mean site morphospecies richness for functionally-defined beetle groups.

889 **Tables**

890 Table 1. Summary information on study site attributes, and mean site-level species richness for bee

891 and beetle in each landscape context

Landscape context	N	Mean area (hectares) (± se)	Mean perimeter (km) (± se)	Mean bee richness (± se)	Mean beetle richness (± se)
Woodland remnant in pine	20	3.880 ± 1.165	0.976 ± 0.117	6.30 ± 0.493	28.06 ± 2.17
Woodland remnant in agriculture	23	2.097 ± 0.234	0.809 ± 0.0446	7.28 ± 0.795	22.62 ± 1.98
Pine plantation	5	-	-	4.40 ± 0.872	17.20 ± 3.10

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905 Table 2. Pairwise MRPP values denoting differences between site-level bee and beetle species

906 composition in the different landscape contexts. The A statistic is the measure of effect size for each

907 MRPP analysis.

Landscape context comparison		All bees		All beetles		Ground-nesting bees ($N = 23$)		Above-ground-nesting bees ($N = 10$)		Flightless beetles ($N = 43$)		Flight-capable beetles ($N = 231$)	
		A	P	A	P	A	P	A	P	A	P	A	P
All landscape contexts		0.0590	0.001	0.0610	0.001	0.0451	0.003	-	-	0.0533	0.001	0.0486	0.001
Pine plantation	Remnants in pine	0.0406	0.010	0.0511	0.001	0.0207	0.070	-	-	0.0079	0.205	0.0419	0.001
Pine plantation	Remnants in agriculture	0.0430	0.010	0.0794	0.001	0.0224	0.100	-	-	0.0431	0.002	0.0691	0.001
Remnants in pine	Remnants in agriculture	0.0442	0.002	0.0266	0.001	0.0411	0.001	0.0677	0.002	0.0463	0.001	0.0179	0.003

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919 Table 3. Model parameters for the best five candidate models relating bee (57 models) and ground-

920 active beetle (25 models) site species richness to a set of landscape variables. Models were selected

921 and ranked by Bayesian Model Averaging (BMA) and their posterior probability.

Predictor	P!=0[a]	EV[b]	Top ranked candidate models				
			1	2	3	4	5
Bee species richness							
Intercept	1.000	1.754	1.911	1.721	1.985	1.986	1.797
Native tree cover	0.452	0.0173	-	0.0365	-	-	0.0392
Landscape context: Pine	0.255	-0.0479	-	-	-0.1443	-	-
Topography: slope	0.267	-0.0553	-	-	-	-0.1205	-0.1451
BIC value	-	-	-89.38	-88.96	-87.07	-86.62	-86.58
Posterior probability	-	-	0.159	0.129	0.050	0.040	0.039
Beetle species richness							
Intercept	1.000	2.490	2.479	2.462	2.477	2.528	2.513
Native tree cover	0.166	-0.00154	-	-	-	-	-0.00804
Elevation	1.000	0.00171	0.00173	0.00182	0.00159	0.00165	0.00174
Distance to water	0.588	0.000224	0.000382	-	-	0.000442	0.000366
Topography: slope	0.852	-0.185	-0.245	-0.153	-	-0.275	-0.244
Topography: ridge	0.142	-0.0112	-	-	-	-0.137	-
BIC value	-	-	-18.65	-17.22	-15.73	-15.67	-15.48
Posterior probability (model)	-	-	0.293	0.143	0.068	0.066	0.060

[a] Probability that the coefficient for a given predictor is not zero
[b] BMA posterior distribution mean for each coefficient

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932   Table 4. Significant habitat structure variables for bee and beetle assemblages across the study

933   landscape, identified by fitted vectors on NMDS ordination axes.

Habitat structure variable	Bee			Beetle		
	*NMDS*1	*NMDS*2	R^2	*NMDS*1	*NMDS*2	R^2
Basal count	0.266	0.964	0.130·	-0.989	0.149	0.473***
Canopy depth	0.298	0.955	0.189**	-0.409	-0.913	0.0286
% Crown affected	-0.525	-0.851	0.253**	0.961	-0.277	0.137*
% Blackberry cover	-0.249	0.968	0.160*	-0.720	-0.694	0.0802
% Exposed rock	0.0507	-0.999	0.279**	0.404	0.915	0.184*
Litter layer	0.387	0.922	0.128·	-0.998	0.0683	0.144*
Weed cover	-0.0633	0.998	0.0343	-0.992	0.126	0.143*
P ≤ 0.001 ***, *P* ≤ 0.01**, P ≤ 0.05* , P ≤ 0.1·						

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