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1 **Cross-taxonomic surrogates for biodiversity conservation in human-modified**
2 **landscapes - a multi-taxa approach**

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20 the manuscript.

21 **Abstract**

22 Cross-taxonomic surrogates are often used in conservation planning because inventorying large
23 suites of taxa is either not feasible or too costly. However, cross-taxonomic surrogates are
24 seldom tested rigorously using both correlational and representation-based approaches at the
25 spatial scales at which conservation management occurs. Here, we evaluated the effectiveness of
26 five ecologically contrasting taxa (birds, herpetofauna, wild bees, beetles, trees) as cross-
27 taxonomic surrogates in native woodland patches within a heavily modified, farming and
28 plantation-dominated landscape. We first compared species richness and compositional
29 heterogeneity across taxa before testing for cross-taxonomic congruence using a correlative
30 approach. We then quantified how well each taxon incidentally represented other taxa in their
31 best patch sets, and the costs of doing so using a complementarity-based approach. We found
32 significant pairwise associations between some taxa (birds, bees), but no single taxon was
33 strongly correlated with all other taxa. Woodland patch sets prioritised for beetles represented
34 other taxa best, followed by birds, but were the costliest and required the largest amount of
35 woodland. This contrasted with patch sets prioritised for wild bees or herpetofauna, which
36 achieved higher representation of other taxa at lower costs. Our study highlighted the influence
37 of taxon-specific patterns of diversity and heterogeneity on how remnant vegetation patches
38 should be prioritised for conservation, a consideration not immediately obvious in correlative
39 analyses of surrogacy. Second, taxa that are not the most speciose (e.g. wild bees) can be
40 efficient surrogates for other taxa, achieving higher incidental representation at lower costs.
41 Thus, while species-rich taxa are ideal as surrogates for prioritising conservation, conservation
42 planners should not overlook the potential of less speciose taxa such as bees, while considering
43 the cost-effectiveness of surveying multiple different taxa.

44 **Keywords**

45 Complementarity, compositional heterogeneity, farmland biodiversity, incidental representation,
46 indicators, systematic conservation planning

47

48 **1. Introduction**

49 Land use change driven by agricultural expansion and intensification is among the leading
50 drivers of biodiversity loss worldwide (Foley et al. 2011; Alexander et al. 2015). Presently, a
51 large proportion of the world's agricultural land is already used for grazing livestock, with
52 permanent pastures covering nearly a quarter of the world's land surface (Wirsenius et al. 2010;
53 FAOSTAT 2014). Intensification of agricultural production in existing farming landscapes is
54 expected to exacerbate biodiversity declines (Benton et al. 2003; Donald et al. 2006;
55 Cunningham et al. 2013). Therefore, effective conservation of biodiversity will necessitate
56 conservation initiatives in agricultural systems that are underpinned by robust ecological
57 research (Norris 2008; Ranganathan et al. 2008; Kay et al. 2016).

58

59 Knowledge of biodiversity patterns is essential for understanding the consequences of land use
60 change and guiding subsequent conservation decisions (Margules & Pressey 2000; Ferrier 2002;
61 Phalan et al. 2011; Guisan et al. 2013). Given that it is neither cost-effective nor practical to
62 inventory large groups of taxa, there is a need to adopt surrogate approaches drawing on more
63 easily gathered data to guide biodiversity conservation (Rodrigues & Brooks 2007; Caro 2010;
64 Lindenmayer et al. 2015). Surrogate approaches are usually grounded on the presumption that a
65 measured subset of biodiversity components in the landscape can provide useful information on

66 broader biodiversity patterns, therefore allowing variation in other aspects of biodiversity to be
67 predicted (Heino 2010; Larsen et al. 2012; Barton et al. 2015). Many surrogate approaches
68 adopted in conservation management and monitoring employ species data (e.g. cross-taxonomic
69 surrogates), often in combination with vegetation and environmental data (e.g. Grantham et al.
70 2010; Lindenmayer et al. 2014). Over time, the interest in using surrogates to guide conservation
71 management has fuelled a large amount of research to evaluate their utility.

72

73 Because cross-taxonomic surrogates offer expedient means to evaluate biodiversity for
74 conservation planning, easily surveyed taxa such as birds have been widely proposed as
75 surrogates (e.g. Eglinton et al 2012; Carrascal et al. 2012; Di Minin & Moilanen 2014).
76 However, while some studies endorse the use of cross-taxonomic surrogates (e.g. Larsen et al.
77 2012), others have highlighted problems (e.g. Andelman & Fagan 2000; Paavola et al. 2006).
78 First, there is increasing evidence of how spatial scale, grain and resolution can shape the extent
79 of correlation between different taxa, thus compromising their effectiveness as surrogates for
80 other groups (e.g. Hess et al. 2006; Paavola et al. 2006; Westgate et al. 2014). Second,
81 differences in ecology and responses to environmental variables among taxa can be expected to
82 drive taxon-specific turnover patterns (e.g. Turtureanu et al. 2014), weakening the strong cross-
83 taxonomic congruence expected of a good surrogate (Yong et al. 2016). Third, the diversity of
84 criteria, concepts and approaches used to evaluate the effectiveness of biodiversity surrogates
85 across different studies has rendered it challenging to draw a consensus on what constitutes a
86 good surrogate (Favreau et al. 2006; Hunter et al. 2015). Put together, these problems highlight
87 the need to identify better biodiversity surrogates, and cross-validate their effectiveness through
88 different analytical approaches (e.g. Favreau et al. 2006; Grantham et al. 2010).

89

90 In this study, we tested the effectiveness of a cross-taxonomic surrogate approach to guide
91 conserving planning for woodland biodiversity in a human-modified landscape. The conceptual
92 framework for our study was guided by three questions, and grounded systematically on field
93 inventorying, initial identification of surrogate taxa, and cross-validation of these surrogate
94 groups in a systematic conservation planning approach. First, we asked: (1) Which pairs of taxa
95 show strong cross-taxonomic congruence? To do this, we inventoried two vertebrate groups
96 (birds, herpetofauna), two insect groups (wild bees, beetles) and one plant group (trees). We then
97 applied a correlative approach to assess the degree of pairwise cross-taxonomic association (i.e.
98 cross-taxonomic congruence) in species richness and composition (Sauberer et al. 2004; Su et al.
99 2004; Rooney & Azeria 2015). As with many studies, we hypothesized that taxa showing high
100 cross-taxonomic congruency could perform better as species surrogates for other taxa.

101

102 Second, we asked: (2) How effective are surrogate taxa in incidentally representing the
103 occurrences of other taxa in sets of woodland patches prioritised for the surrogate? This question
104 is important because it allows initially identified surrogate taxa to be validated in realistic
105 conservation planning scenarios. Ideally, an effective surrogate taxon should be expected to
106 capture a high proportion of the representation targets for other taxa (Larsen et al. 2012; Di
107 Minin & Moilanen 2014), without being excessively costly itself – i.e. requiring the conservation
108 of a large amount of woodland patches. To do this, we adopted a complementarity-based, site-
109 selection approach (see Table 1 for definitions of terms) to identify near-optimal sets of remnant
110 woodland patches in our landscape using *a priori* representation targets set for each taxon. We
111 then determined how well other taxa were incidentally represented in the patch sets selected for

112 the (surrogate) taxon (e.g. Sætersdal et al. 2004; Albuquerque & Beier 2016). Additionally,
113 determining the total area of woodland patches in patch sets selected for each taxon at a given
114 representation target provided a proxy of relative cost, and allowed us to compare the cost-
115 effectiveness of multiple scenarios using different focal taxa as surrogates.

116

117 Finally, we asked: (3) How similar are these best sets of habitat patches selected for each taxa,
118 and at each defined representation target. We therefore compared the sets of woodland patches
119 selected for each taxon at each representation target by assessing the degree of overlap (as
120 measured with dissimilarity, distance metrics) in patch set solutions between taxa following Ikin
121 et al. (2016). Since many species in human-modified landscapes can be expected to be wide-
122 ranging generalists rather than habitat specialists given the effects of biotic homogenisation (e.g.
123 Ekroos et al. 2010), we expected differences between sets of woodland patches selected for each
124 taxon to be low because many of these taxa are likely occur in a large proportion of woodland
125 patches.

126

127 **2. Methods and materials**

128

129 2.1. Study area and design

130 The highly modified Nanangroe landscape (34°58'S, 148°28'E) consists of approximately 30,000
131 hectares of agricultural (i.e. grazing) land and exotic Monterey pine *Pinus radiata* plantations
132 (Figure 1). Much of the original cover of box-gum grassy woodlands, an ecological community

133 now listed as critically endangered (Rawlings et al. 2010), has been extensively cleared in the
134 past two centuries for agriculture. This has left numerous scattered remnant patches across the
135 landscape (Lindenmayer et al. 2008). In 1998, the landscape matrix surrounding many of these
136 remnants was transformed by the establishment of extensive plantations of pine (Lindenmayer et
137 al. 2008). As a result, these remnant woodland patches became embedded within either a matrix
138 of grassy pasture actively grazed by livestock or pine plantations. Permanent transects were
139 marked and established at all study patches prior to the commencement of the study. In
140 woodland patches exceeding one hectare, a 200-m long transect was established while 100-m
141 long transects were established for patches smaller than one hectare. For this study, a total of 42
142 remnant woodland patches in both kinds of matrix were identified to represent the full range of
143 patch area classes (See Supplementary Table 1 for full list of woodland patches and their
144 attributes) for biodiversity sampling.

145

146 2.2. Biodiversity sampling

147 We conducted field surveys of six animal taxa in our study landscape: birds, mammals, reptiles,
148 amphibians, wild bees and ground-dwelling beetles. However, the mammal dataset was
149 eventually excluded from our analyses due to its low diversity (< 10 species) at the landscape
150 and patch level. The species composition of the dominant trees (i.e. tree assemblage) in each of
151 our study woodland patches was identified and recorded as part of a detailed vegetation survey
152 last carried out in spring 2015.

153

154 2.2.1. Bird sampling

155 We sampled bird occurrence and diversity at each woodland patch using three 5-min point
156 counts along an established transect. Point counts were conducted between 0500–1000 hrs
157 during the Austral spring (October–November 2014). At each point, observers recorded the
158 numbers of individual bird species heard or seen within a 50 m radius. Birds observed in flight at
159 the sampling point were excluded from the survey. Each point was re-sampled by a different
160 observer on another day during the survey period to minimise detection biases resulting from
161 weather and the variation in identification skills between different observers.

162

163 *2.2.2. Herpetofauna sampling*

164 As amphibians and reptiles were surveyed using the same method, we pooled them as one group,
165 and defined them collectively as “herpetofauna”. To sample amphibian and reptiles, we
166 conducted standardised, time-constrained searches (c. 20 mins) at two points along each transect
167 once in early spring (October–November 2014) and covering an area of approximately one
168 hectare (see Michael et al. 2012). During the establishment of the transects, artificial substrates
169 consisting of a corrugated iron sheet (1.0 m × 1.0 m), wooden fence posts covered in mesh (4
170 pieces; 1.0 m long, 0.2 m thick) and roof tiles (4 pieces; 32 cm × 42 cm) were placed at each
171 sampling point to simulate microhabitats for small ground herpetofauna such as skinks and
172 geckos. Active searches for amphibians and reptiles were conducted by scanning the site for
173 basking animals, and turning over logs, rocks and the artificial substrates placed at each point
174 along a transect during a survey (Michael et al. 2012). Each point was re-sampled by a different
175 observer on another day during the survey period to minimise detection biases. Species
176 identification and nomenclature is based on Cogger (2000).

177

178 *2.2.3. Wild bee sampling*

179 To survey wild bees, we used blue vane traps (e.g. Lentini et al. 2012; Joshi et al. 2015). We
180 sampled all 42 woodland patches at the midpoint of each line transect with two traps at each site.
181 Traps were set in trees and placed approximately 20 m apart from where they were suspended at
182 about 1.5–2.0 m above ground. Bee sampling was conducted for 14 days from November to
183 December 2014 and in tandem with beetle sampling. At the end of the sampling period, the traps
184 were retrieved and all bees were preserved in 70% ethanol before species-level sorting. Bees that
185 were difficult to identify were: (1) carefully separated from other insects, (2) washed in detergent
186 and, (3) blown-dry before being prepared in a reference collection for subsequent species-level
187 identification based on the methodology recommended in Droeges (2015). Most bees were
188 identified to the species-level using the online database, Pest and Diseases Image Library (PaDIL
189 2016) and major bee identification keys (e.g. Walker 1995; Michener 2000). All bee
190 identifications were then rechecked by a bee taxonomist (Michael Batley, Australian Museum)
191 and the lead author to ensure accuracy.

192

193 *2.2.4. Ground-dwelling beetle sampling*

194 To survey ground-dwelling beetles, we used non-baited pitfall traps. Pitfall traps were placed in
195 pairs along four rows at the centre of the transect within each woodland patch (i.e. four equally
196 spaced pairs per site). Each pitfall trap consisted of a plastic container of 5.0 cm diameter and 7.5
197 cm depth. Traps were filled with 100 ml of ethylene glycol which functioned both as a killing
198 agent and a temporary preservative. To increase the invertebrate catch rate, we mounted plastic

199 drift fences (1.0 m × 0.2 m) along each pair of traps. Trapping was conducted from late
200 November to December 2014, with every trap opened for 14 days. Beetle specimens were
201 preserved in 70% ethanol before being sorted to family and morphospecies (hereafter referred to
202 as species) using a stereo microscope and relevant beetle identification keys (e.g. Matthews
203 1980; Hangay & Zborowski 2010). Vouchered specimens of each species were assembled into a
204 reference collection for identification. Highly similar species from species-rich families such as
205 Staphylinidae and Carabidae were re-checked by two of the co-authors for the accuracy of
206 identifications, leading to a substantial reduction of duplicate species and a higher robustness of
207 the dataset. The beetle dataset was then partitioned into two for analysis: (1) the full dataset with
208 all beetle species identified, and (2) a reduced dataset with rare species represented by singletons
209 excluded.

210

211 2.3. Statistical analysis

212 We explored the potential for each taxonomic group to be a surrogate for other groups by
213 comparing their diversity patterns across the study landscape. First, we pooled data for sampling
214 points within each woodland patch to calculate species richness at the site level (α -diversity). We
215 then pooled species richness from all patches across the landscape to estimate γ -diversity. To
216 determine sampling completeness, we calculated and plotted smoothed accumulation curves
217 based on observed species richness for each taxon. Observed species richness was then
218 calculated as a proportion of the average of four non-parametric estimators of species richness
219 (see Table S2). To estimate compositional heterogeneity, we calculated mean site species
220 richness (α -diversity) as a proportion of landscape-level species richness (γ -diversity) for each
221 taxon.

222

223 *2.3.1. Correlations of species richness and composition (Question 1)*

224 To identify which pairs of taxa showed strong congruence patterns at the landscape level, we
225 used a combination of Spearman's rank correlations and partial Mantel tests. The correlation
226 strength in species richness between two taxa is frequently used as a metric of cross-taxonomic
227 congruence (e.g. Hess et al. 2006; Wolters et al. 2006; Duan et al. 2016). To assess the level of
228 correlation between site-level species richness for each pairwise combination of taxa, we
229 calculated the Spearman's correlation coefficient (e.g. Similä et al. 2006). Spearman's
230 correlation was used instead of Pearson's correlation as the sample size for number of sites was
231 small ($N = 42$) and does not fulfil parametric assumptions based on the Shapiro-Wilk test
232 (Royston 1983).

233

234 We used partial Mantel tests to assess the strength of cross-taxonomic congruence in
235 compositional dissimilarity between pairwise combinations of taxa (Landeiro et al. 2012). Partial
236 Mantel tests were used because they measure the correlation between two matrices (e.g. Su et al.
237 2004) after accounting for spatial variation associated with a third matrix of Euclidean distances,
238 thus addressing the potential issue of spatial autocorrelation. We first quantified compositional
239 dissimilarity for each taxon across the landscape using the Jaccard similarity index which is
240 based on absence-presence data (Magurran 2004). We then performed the partial Mantel test for
241 all pairwise combinations of taxa. The significance of each Mantel test was assessed using 999
242 permutations.

243

244 *2.3.2. Analysis of incidental representation of taxa across patches (Question 2)*

245 We used a complementarity-based, site-selection approach to identify priority sets of woodland
246 patches that best represented the species richness and occurrence of each taxon. In such an
247 approach, woodland patches were iteratively added to a patch set in a step-wise manner based on
248 the degree of complementarity in species composition until the representation target of any given
249 taxon is met. To quantify incidental representation of other taxa in the patch set selected for the
250 surrogate, we calculated the total occurrences of other (target) taxa represented in these patch
251 sets as a proportion of their total occurrences across the whole landscape (Question 2). In
252 addition, we calculated the total area of woodland needed to conserve each taxon in their best
253 patch set as a proxy of cost for each representation target.

254

255 We defined the occurrence of each species in the study landscape as a ‘conservation feature’
256 (Game & Grantham 2008; Ardron et al. 2010) (See Table 1 for definitions). A total of 399
257 conservation features were established from the five taxa. We then set representation targets for
258 all taxa ranging from 10% to 80% and at 10% intervals. We chose not to include representation
259 targets of 90% and 100% as it is not practical to retain the majority of woodland patches for
260 conservation in active, production landscapes such as ours (Ikin et al. 2016). For each taxon and
261 at each representation target, we ran 100 iterations using the simulated annealing algorithm
262 implemented in Marxan to identify the best patch set (Game & Grantham 2008; Ball et al. 2009).
263 We did not set constraints on the number of patches (sites), therefore allowing as many patches
264 as required to be included in each Marxan solution to meet the representation target. The ‘species
265 penalty factor’, a Marxan parameter that measures the costs for failing to meet targets for each

266 conservation feature (Game & Grantham 2008) was kept constant for all conservation features,
267 thereby not giving higher weightage to any particular species.

268

269 To compare incidental representation of other taxa by the surrogate, we used the patch set from
270 the best of 100 solutions (hereafter as ‘best patch set’) identified by Marxan to meet
271 representation targets for the surrogate taxon. Using this solution, we calculated the total number
272 of conservation features for all other taxa represented therein, while recording if *a priori*
273 representation targets set for the surrogate had also been met for the target taxon. To quantify
274 representation of each taxon in the best patch set selected for the surrogate, we calculated species
275 occurrences captured in the patch set as a proportion of the total species occurrences. To
276 compare the relative cost needed to achieve each representation target, we calculated the sum of
277 woodland area (in hectares) of the best patch sets for each taxon as a proxy measure of cost
278 (Ardron et al. 2010).

279

280 2.3.3. Similarity in best patch sets across taxa (Question 3)

281 To compare the level of similarity or spatial correspondence among the best patch sets selected
282 for five taxa, we performed cluster analysis using an agglomerative hierarchical clustering
283 approach (Question 3). First, we created a distance matrix based on the Jaccard similarity index
284 for each taxon, and across four representation targets (20%, 40%, 60%, and 80%) using the
285 function ‘distance’. Jaccard similarity was calculated based on the presence or absence of a patch
286 (site) in the best solution for each representation target. We then implemented the function
287 ‘hclust’ using the complete-linkage clustering method. Pairs of clusters separated by the shortest

288 distances were thus combined in the cluster dendrogram, allowing the extent of similarity
289 between all patch sets for the five taxa to be visualised. Cluster analysis and partial Mantel
290 correlations were carried out using the ‘ecodist’ package (Goslee & Urban 2007), available on
291 the R platform (R Development Core Team 2013).

292

293 **3. Results**

294

295 3.1. Assemblage diversity for taxa sampled

296 We recorded a total of 77 bird, 21 herpetofauna, 31 bee, 258 beetle and nine tree species in
297 woodland patches in the Nanangroe landscape. Based on smoothed, species accumulation curves
298 (Figure 2a; Supplementary Table S2), our sampling effort was fairly complete for all taxa.
299 Average patch-level species richness (α -diversity) as a proportion of landscape-level species
300 richness (γ -diversity) was lowest for beetles at 9.98% (Figure 2b; Supplementary Table S2). For
301 beetles samples with singletons excluded, this rose to 13.43%. By comparison, each woodland
302 patch supported 16.98% of the total bird, 20.22% of the total bee, and 22.49% of the total tree
303 species pool (Supplementary Table S3).

304

305 3.2. Correlations of species richness and composition (Question 1)

306 We found that only bird species richness was correlated with wild bee species richness at the
307 patch level (Spearman’s $\rho = 0.309$, $P < 0.05$), but not with species richness of any other taxa.
308 Herpetofauna, beetle and tree species richness was not correlated with that of other taxa we

309 compared (Figure 3a). As with species richness correlations, we found that bird species
310 composition was correlated with bee species composition (partial Mantel $R = 0.207$, $P < 0.01$)
311 but not with any other taxa (Figure 3b). Similarly, herpetofauna species composition was
312 correlated only with that of beetles (partial Mantel $R = 0.137$, $P < 0.05$) and no other taxon.
313 Exclusion of rare beetles represented by singletons weakened this correlation (partial Mantel $R =$
314 0.127 , $P < 0.05$). Wild bee species composition was correlated with that of beetles (partial
315 Mantel $R = 0.128$, $P < 0.05$). This association was strengthened if rare beetles were excluded
316 (partial Mantel $R = 0.140$, $P < 0.05$). Compared with the four animal groups, tree species
317 composition at the patch level was not correlated with that of any taxa.

318

319 3.3. Incidental representation of target taxa by the surrogate taxon (Question 2)

320 We found that the best patch sets identified to meet representation targets for both sets of the
321 beetle data generally represented other taxa better than patch sets at equivalent targets for other
322 taxa, across the range of targets from 10-80% (Figure 4; Supplementary Table S4). For example,
323 the best patch sets selected for the full beetle assemblage were able to represent over 70% (73.9-
324 91.2%) of all bird occurrences across the landscape for the range of targets (Figure 4a).

325 However, patch sets selected to meet representation targets of the full beetle assemblage were
326 also consistently more costly than other taxa (Figure 5a-5d, 5f). For example, achieving a 10%
327 representation of beetle occurrences required the conservation of 31 woodland patches covering
328 86.1% of the total woodland area. Beetles were also the least cost-effective surrogate taxon in
329 representing other taxa, requiring more than 80% of the total area of woodland across the range
330 of representation targets (Figure 5a-5d). The beetle assemblage that excluded rare species was
331 less costly in representing other taxa if representation targets were low (Figure 5a-5e), but

332 became increasingly costly at the highest representation targets. Not unexpectedly, this subset of
333 the beetle assemblage consistently represented the full beetle assemblage better than other taxa at
334 equivalent costs (Figure 5e).

335

336 We found that some taxa (e.g. wild bees and herpetofauna) were able to achieve higher
337 incidental representation of other taxa at lower cost. Wild bees were relatively cost-effective
338 compared to other taxa, being able to achieve higher incidental representation of bird, beetle,
339 herpetofauna and tree targets at equivalent costs compared to other taxa across a range of its
340 representation targets (50-80%) (Figure 5a-5f). For example, the best patch set selected to meet a
341 representation target of 80.0% for wild bee occurrences could capture 81.7% of bird occurrences
342 in the landscape, while exceeding incidental representation of birds by other taxa at an equivalent
343 cost (Figure 4a, 5a). Similarly, at a representation target of 80.0%, wild bees captured a higher
344 proportion of herpetofauna occurrences (84.9%) than other taxa at an equivalent cost (Figure 5b).

345

346 The herpetofauna assemblage was comparatively species-poor and achieved lower incidental
347 representation of other taxa across a range of targets (Figure 4). However, patch sets selected for
348 herpetofauna occurrences were usually the least costly, and able to achieve higher incidental
349 representation of some taxa (e.g. trees, wild bees, birds) at lower costs (Figure 5a, 5c-5f). For
350 example, a patch set to represent 10-20% of herpetofauna targets could capture 30.8% of bird
351 occurrences in < 25.0 ha (23.7% of the total) woodland (Figure 5a). However, as representation
352 targets for herpetofauna increased, it became increasingly similar to birds and wild bees in its
353 cost-effectiveness in representing other taxa. Compared to other taxa, trees were generally less

354 efficient than wild bees, herpetofauna or birds in representing other taxa across the range of
355 representation targets (Figures 4, 5, Supplementary Table S5).

356

357 3.4. Similarity in patch sets for each taxon (Question 3)

358 We found that the best patch sets selected for each taxon were very dissimilar at low
359 representation targets ranging from 20-40%, but became increasingly similar at higher
360 representation targets (Figure 6). For instance, the best patch sets selected to meet representation
361 targets for wild bees from 20-60% were more similar to each other than with that of any other
362 taxon. Likewise, patch sets selected to meet representation targets for the herpetofauna from 20-
363 60% were more similar to each other than that for other taxa across different targets. At high
364 representation targets, the best patch sets for the five taxa become increasingly convergent. For
365 instance, the best patch sets selected to meet a range of representation targets from 60%–80% for
366 beetles were most similar to patch sets selected to meet similar targets for bird and tree
367 assemblages.

368

369 **4. Discussion**

370

371 4.1. Species richness and composition

372 Our study revealed the high species richness of vertebrate and insect assemblages persisting in
373 remnants of box-gum grassy woodland embedded in a wider matrix of grazing land and
374 monoculture plantations. The low proportion of total beetle species richness at the patch-level

375 suggests high compositional heterogeneity of the overall beetle assemblage relative to other taxa
376 (e.g. Soininen et al. 2007; Barton et al. 2010). By contrast, woodland patches supported lower
377 compositional heterogeneity of birds and wild bees. Such patterns of diversity can be explained
378 by differences in body size and dispersal ability among the taxa, as well as the different
379 ecological traits and habitat requirements specific to each group (Cadotte & Fukami 2005;
380 Cadotte 2006; Soininen 2010; Janssen et al. 2016). Vagile taxa such as birds can be expected to
381 show lower compositional heterogeneity at equivalent spatial scales compared to poor dispersers
382 like ground beetles (Baselga et al. 2012; Qian & Ricklefs 2012). Such differences in
383 compositional heterogeneity underscore the taxon-specific responses of different assemblages to
384 habitat structure and other abiotic gradients at the landscape scale (e.g. Benton et al. 2003; Lovell
385 et al. 2007).

386

387 Framed in the context of cross-taxonomic surrogacy, a consequence of such differences in
388 compositional heterogeneity and other beta-diversity measures is that groups of taxa with very
389 different spatial patterns of diversity will require dissimilar levels of comprehensiveness in
390 habitat patch sets or reserve networks to meet representation targets for their conservation (e.g.
391 Ferrier 2002; Si et al. 2015). Taxa with high species richness and compositional heterogeneity in
392 a landscape will require more sites in the reserve network to represent them comprehensively
393 (Ryti 1992; Lund & Rahbek 2002; Ikin et al. 2016). However using species-rich taxa to plan and
394 prioritise agricultural landscapes for biodiversity conservation, while ideal, would translate into
395 increased sparing of land to achieve conservation outcomes (e.g. Fischer et al. 2008). Ultimately,
396 it is necessary for conservation planners to recognise how differences in diversity patterns
397 specific to each taxon could compromise the effectiveness of some taxa as surrogates (e.g. Part

398 & Soderstrom 1999). Such a problem may arise because conservation planning for groups of
399 taxa with very dissimilar beta-diversity patterns could lead to moderate-good representation of
400 some taxa but poor representation of others in a reserve network.

401

402 4.2. Correlations of species richness and composition (Question 1)

403 Cross-taxonomic surrogates have an important role to play in guiding conservation planning
404 exercises, especially in identifying priority areas of high species diversity across spatial scales.
405 Species richness and composition correlations have been used widely as a first step to guide the
406 identification of cross-taxonomic surrogates (Sætersdal et al. 2004; Gardner et al. 2008; Landeiro
407 et al. 2012). Consistent with other studies using correlative approaches (e.g. Billeter et al. 2008),
408 we found that no single taxon was a good surrogate for all other taxa. Of five taxa, only birds
409 showed consistently strong congruence in both species richness and composition with wild bees,
410 underscoring the potential of either taxon as a surrogate for the other (e.g. Sauberer et al. 2004).
411 Such observed cross-taxonomic congruence may arise as a result of the similar (high) dispersal
412 ability of both groups. Alternatively, wild bee and bird assemblages may be responding to
413 similar biotic gradients such as shared food resources (e.g. flowers) (e.g. Lovell et al. 2007).
414 Similarly, significant congruence between species composition of the predominantly terrestrial
415 herpetofauna and ground-dwelling beetles allude to similarities in the responses of both groups
416 to habitat structure at the ground level.

417

418 Generally, species-rich groups such as beetles and birds exhibited stronger cross-taxonomic
419 associations with other taxa, while pairs of species-poor groups tend to be weakly correlated. A

420 similar response in compositional turnover of taxa to habitat and environmental gradients (Lovell
421 et al. 2007; Duan et al. 2016) at the landscape scale offers one explanation to account for such
422 patterns. Additionally, despite differences in compositional heterogeneity across the groups, it is
423 recognised that species-rich groups can capture a greater range of environmental conditions and
424 habitat types (Larsen et al. 2009; Larsen et al. 2012; Ikin et al. 2016). Such a prediction was
425 broadly consistent with our complementarity-based, patch-selection analysis, which revealed that
426 patch sets prioritised for groups like beetles were able to achieve high representation of other
427 taxa. Because woodland patches selected for species-rich surrogate groups in systematic
428 conservation planning scenarios can be expected to achieve a higher representation of other taxa
429 (Larsen et al. 2009), a first step in the selection of surrogate taxa should be the species richness
430 within a taxonomic group of interest.

431

432 4.3. Representation of targets in patch sets selected for different taxa (Question 2)

433 We found that sets of woodland patches selected to meet representation targets for the species-
434 rich beetle and bird assemblages were often able to capture a high proportion of most other taxa,
435 but came at a very high cost. By comparison, wild bee and herpetofauna assemblages achieved
436 higher representation of other taxa when costs were low and thus could be efficient surrogates to
437 prioritise landscapes for conserving other taxa in scenarios where little natural vegetation can be
438 spared (i.e. intensively farmed landscapes). Our findings reiterates the practical issues (e.g. Caro
439 2010) which are easily overlooked in the use of biodiversity surrogates when surrogate taxa are
440 determined alone from correlative analyses, and in relation to the costs of land allocation/sparing
441 to meet conservation targets. In practice, prioritising woodland patches in production landscapes
442 to maximise the representation of beetles or other taxa showing high species richness and

443 compositional heterogeneity could become costly because more sites and effectively a larger area
444 of woodland has to be set aside to meet conservation targets. For instance, the costs to conserve
445 certain taxa in planning scenarios could be inflated due to the inclusion of a small number of
446 disproportionately large woodland patches which support a larger suite of taxa.

447

448 Our analyses demonstrated that wild bee and herpetofauna assemblages on their own could act as
449 efficient cross-taxonomic surrogates in conservation planning scenarios if cost/land allocation for
450 conservation becomes a major limitation. Despite low bee or herpetofauna species richness and
451 limited congruence with other taxa (Figures 2, 3), woodland patches prioritised to represent bee
452 diversity achieved higher incidental representation of other taxa at lower costs. Given the
453 sensitivity of bee assemblages to landscape change and fine-scale habitat structure (Holzschuh et
454 al. 2006; Carré et al. 2009) and their roles as providers of pollination services (Kremen et al
455 2004; Mallinger & Gratton 2015), bee assemblages not only have an overlooked potential as
456 broad indicators of landscape change, but also as cross-taxonomic surrogates to prioritise
457 remnant woodland/forest patches to optimise biodiversity conservation. Further studies are
458 needed to better understand the use of wild bee assemblages as surrogates to plan conservation
459 for other elements of biodiversity and across different types of farming landscapes.

460

461 4.4. Similarity in patch sets for different taxa (Question 3)

462 Although the best patch sets selected for each taxon were generally dissimilar to other taxa, they
463 became increasingly similar at high representation (> 40%) targets. Increasing similarity of patch
464 sets at high representation targets across taxa is expected to result because a larger proportion

465 (and number) of woodland patches with high species richness of each taxon increasingly overlap
466 in these patch sets. One clear conservation implication is that for cross-taxonomic surrogates of
467 biodiversity to be most effective, representation targets set for the surrogate taxon of interest in
468 conservation planning scenarios will need to be reasonably high. However, this correspondingly
469 raises the costs of using any one taxon as a surrogate to prioritise for other taxa, and may not be
470 feasible in intensive production landscapes. Additionally, the limited overlap in woodland patch
471 sets prioritised for different taxa, particularly at low representation targets ($\leq 40\%$) showed that
472 cross-taxonomic congruence of species richness is overly simplistic an approach in identifying
473 what makes a good surrogate taxon. For instance, while correlations of species richness indicated
474 congruence of bird and bee assemblages (and thus the potential of either as a good surrogate)
475 (Figure 3), they fail to account for compositional heterogeneity, the complexity of different
476 planning/prioritisation scenarios, as well as the poor overlap in woodland patches important to
477 either taxa. Thus, strong correlations of species diversity does not necessarily translate to better
478 representation of other taxa in woodland patches prioritised for the surrogate.

479

480 4.5. Costs of sampling different (surrogate) taxa

481 Conducting field surveys of multiple taxa adds the practical dimension of increased cost, on top
482 of the costs of land sparing for biodiversity. This is because the effort needed to sample different
483 taxa in biodiversity assessments can vary widely due to differences in monetary cost, time
484 investment and the availability of specialist expertise for particular taxa (e.g. Gardner et al. 2008;
485 Yu et al. 2012). Gardner et al. (2008) showed that standardised costs of biodiversity surveys
486 could vary by nearly three orders of magnitude across different taxa. In the context of this study
487 on cross-taxonomic surrogacy, birds are relatively cost-effective to survey as little specialised

488 equipment is needed, and expertise is more easily available (e.g. Bibby et al. 2000). Conversely,
489 using highly species-rich groups such as beetles as surrogates not only demand considerable land
490 allocations for conservation to capture the high diversity and compositional heterogeneity, but
491 also high investment in field and laboratory equipment and time, as well as technical expertise
492 (New 2007). Given scarce resources in many conservation projects, it is necessary and strategic
493 to consider the cost-effectiveness of different sampling efforts to assess biodiversity, even while
494 recognising the fact (as demonstrated in our study) that specific, species-rich taxa may perform
495 better as surrogates.

496

497 4.6. Conclusions

498 The use of surrogate taxa to prioritise landscapes for biodiversity conservation is a well-
499 established idea in conservation biology (Ryti 1992; Margules & Pressey 2000; Larsen et al.
500 2009). While many studies of cross-taxonomic surrogates have been completed at very large
501 spatial scales (e.g. Howard et al. 2006; Billeter et al. 2008; Westgate et al. 2014), our study
502 provides one of few examples where cross-taxonomic surrogacy is down-scaled to a complex,
503 production landscape (c. 300 km²) and based on simultaneous sampling of five important and
504 ecologically distinct taxa. Our study offers three key insights on the use of surrogates for
505 biodiversity conservation in farming landscapes.

506 **First**, patterns in compositional heterogeneity tend to be taxon-specific, being highest for
507 species-rich taxa such as beetles. Less speciose groups that contain good dispersers such as bees
508 tend to show lower spatial turnover. Therefore, conservation planning in heterogeneous
509 agricultural landscapes based on a limited set of surrogate taxa will need to consider taxon-

510 specific turnover patterns (e.g. Ferrier 2002; Si et al. 2015). On the one hand, conservation
511 planning and prioritisation determined by assessments of species-poor and/or non-vagile groups
512 may result in a smaller number and total area of habitat patches conserved, to the detriment of
513 species-rich taxa. On the other, prioritising woodland conservation with taxa that are speciose
514 and show high compositional heterogeneity such as beetles could become exceedingly costly as
515 it necessitates the sparing of more land for conservation.

516 **Second**, sets of woodland remnant patches selected to prioritise conservation of different taxa
517 become increasingly similar at higher representation targets. This means that conservation
518 planning in landscapes based on low representation targets of one or few surrogate taxa would be
519 inefficient and uneven in representing broad suites of other biota. While it is ideal to spare as
520 much remnant natural woodland as possible for biodiversity conservation, trade-offs will need to
521 be better defined to meet biodiversity conservation targets (e.g. Cunningham et al. 2013) without
522 unrealistically compromising on agricultural production and vice versa.

523 **Third**, species-rich taxa like beetles and birds were able to achieve high incidental representation
524 of other taxa in systematic conservation planning scenarios. While species-rich groups have been
525 recognised as being more effective surrogates (e.g. Larsen et al. 2012; Ikin et al. 2016) and
526 ideally should be the focus of how remnant woodland are prioritised for conservation, the issue
527 of cost cannot be overlooked. Costs may come from increased investment in land spared for
528 conservation, or the direct costs of implementing biodiversity surveys and laboratory sorting. In
529 scenarios where limited land can be allocated for conservation, taxa with less species such as
530 bees may in fact be more efficient surrogates in representing the broader biota. Moreover, since
531 birds are already well known surrogates in agricultural landscapes (e.g. Part & Soderstrom 1999;
532 Eglington et al. 2012; Ikin et al. 2016), biodiversity assessments based on bird data could be

533 complemented with that of wild bee assemblages to identify remnant habitat important to a broad
534 suite of taxonomic groups, especially where achieving high representation of every taxa is not
535 possible.

536

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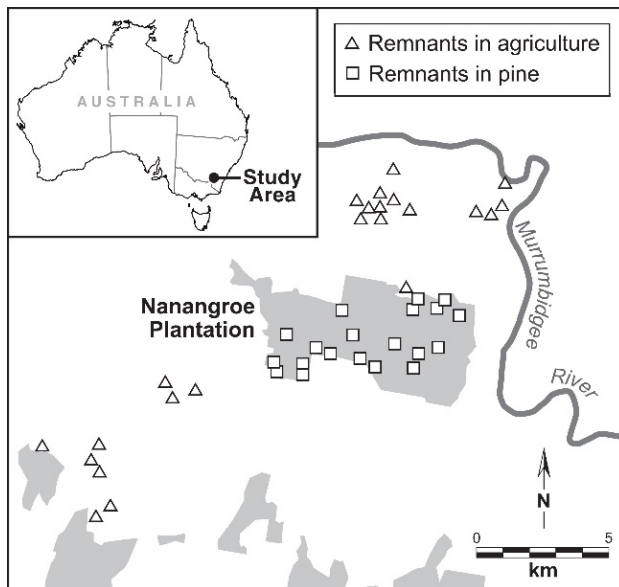
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793 **Figure 1.** Map of the Nanangroe study landscape showing the location and distribution of our 42
794 study sites in relation to the Murrumbidgee River. Grey-shaded areas are monoculture
795 plantations of *Pinus radiata* while unshaded areas are open grazing land.



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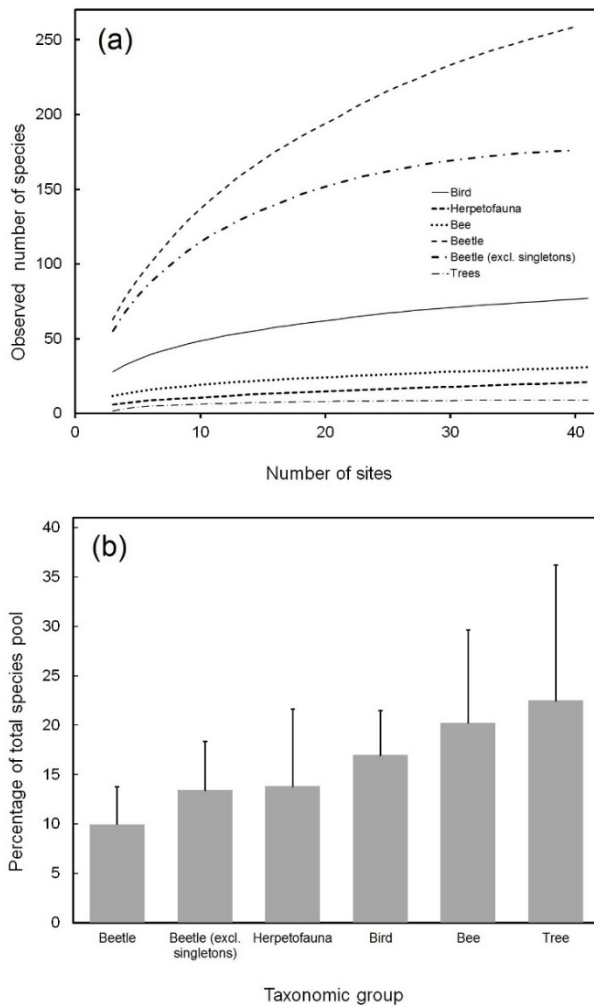
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806 **Figure 2 (a).** Smoothed species accumulation curves for each taxon in the Nanangroe landscape
807 showing observed species richness and sampling effort for each taxon relative to other taxa. **(b).**
808 Bar plots (with error bars representing standard deviation) showing mean species richness at the
809 patch-level as a percentage of the total species pool in the landscape (gamma-diversity).

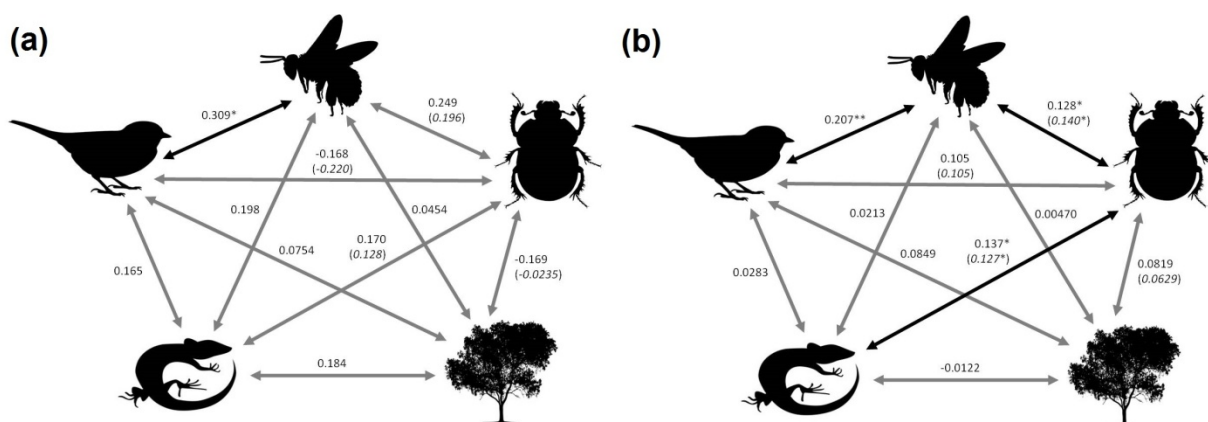


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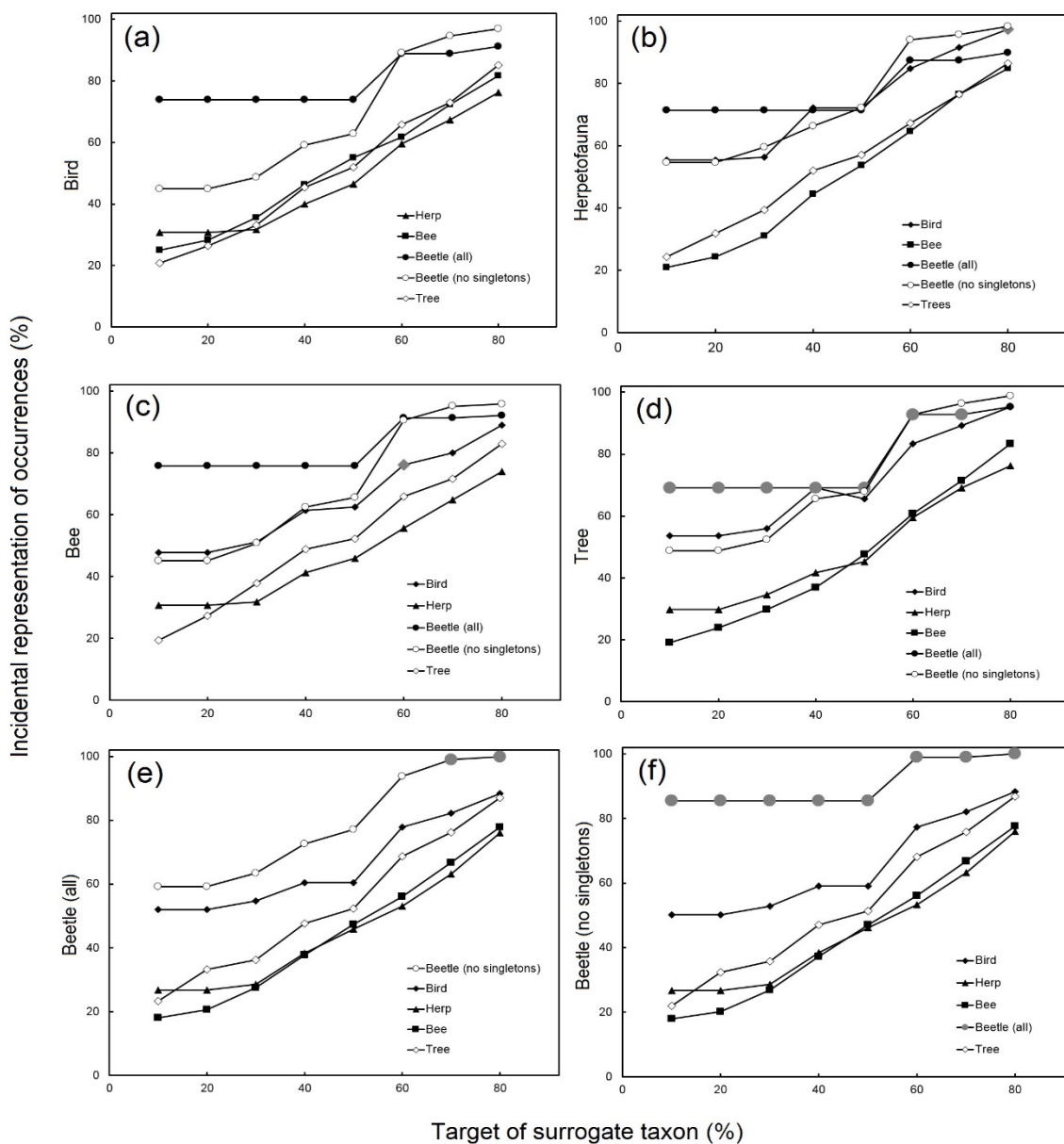
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813 **Figure 3 (a)**. Network diagram showing pairwise cross-taxonomic congruency in species
 814 richness between five taxa based on the Spearman's rho. Significant correlations are presented as
 815 black arrows while non-significant correlations are presented as grey arrows. **(b)**. Network
 816 diagram showing pairwise cross-taxonomic congruency in species composition between five taxa
 817 conditioned on geographic space, based on the partial Mantel *R*. Significant correlations are
 818 represented as black arrows while non-significant correlations are presented as grey arrows.
 819 Correlations using the beetle dataset excluded singletons is presented in parenthesis.



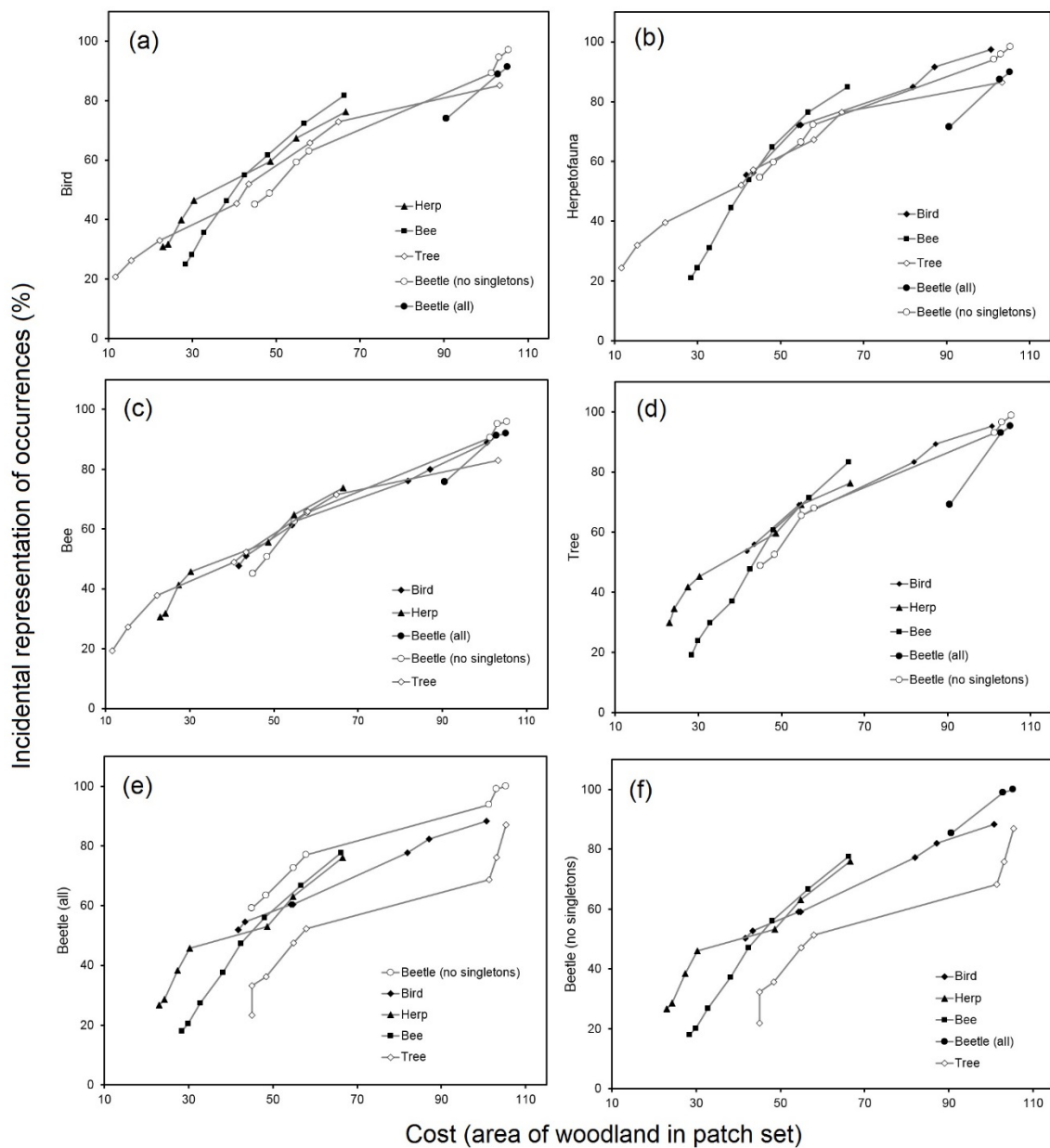
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829 **Figure 4.** Accumulation plots showing incidental representation of each taxon (indicated by
 830 taxon name on the vertical axis: (a) bird, (b) herpetofauna, (c) bee, (d) tree, (e) all beetle, (f)
 831 beetle excluding species represented by singletons) in the best patch sets prioritised for the
 832 surrogate taxa (see inset legend). Enlarged points in grey indicate that that representational target
 833 for that taxon has been met. See also Supplementary Table S4 for details.



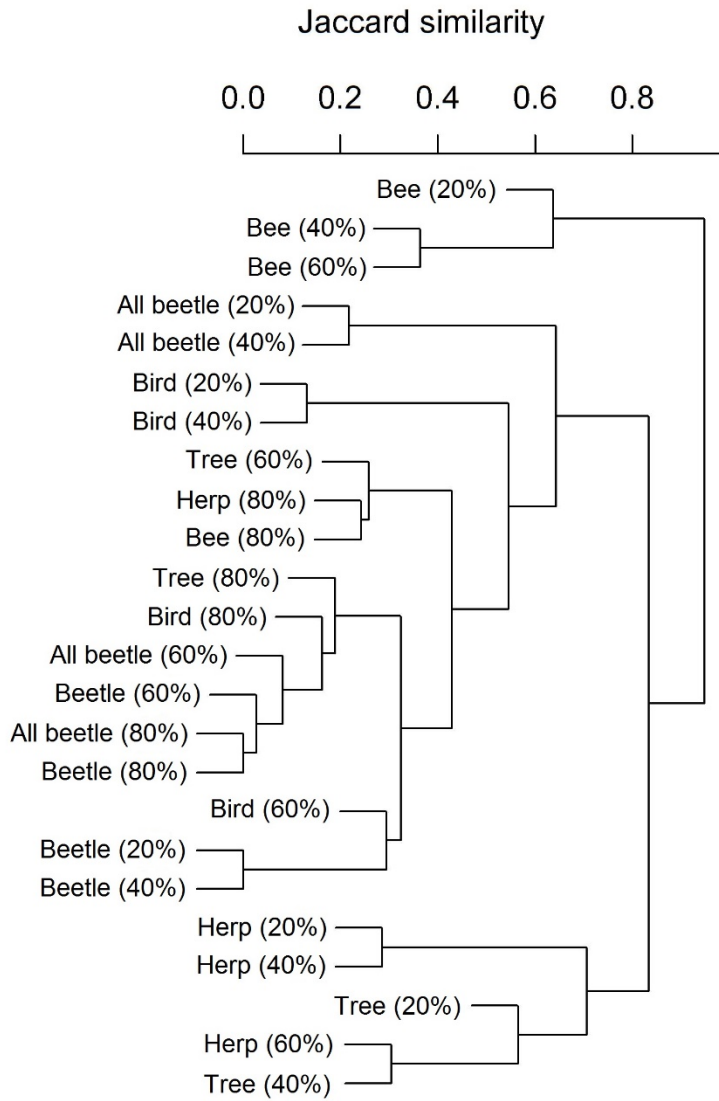
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835 **Figure 5.** Accumulation plots showing incidental representation of each taxon (indicated by
 836 taxon name in the vertical axis): (a) bird, (b) herpetofauna, (c) bee, (d) tree, (e) all beetle, (f)
 837 beetle excluding species represented by singletons, in relation to the cost of the best patch sets
 838 selected for the surrogate taxa (see inset legend). See also Supplementary Table S5 for details.



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840 **Figure 6.** Dendrogram of clusters for best patch sets selected for every taxa at four target threshold
 841 (20%, 40%, 60%, 80%) based on the complete linkage method. The taxon and its corresponding
 842 representation target is shown at each node of the dendrogram.



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847 **Table 1.** Glossary of key terms (in text) and definitions

Term	Definition
<i>Biodiversity surrogate</i>	A defined taxonomic group (e.g. birds) or group of species whose occurrence or diversity predicts that of another, usually less well-known group of species.
<i>Cross-taxonomic congruence</i>	Degree of association or co-variation in the diversity pattern of a defined group of species with respect to another group. Common metrics include measures of correlation strength such as Spearman's ρ and Pearson's r .
<i>Compositional turnover</i>	Variation in the composition of species across space; an approach to quantify beta diversity in a landscape.
<i>Conservation feature</i>	A unit to be represented in a solution of reserve sites in systematic conservation planning scenarios. Usually quantified as the absence of a species in a defined site.
<i>Incidental representation</i>	Representation of a species in a set of identified sites/reserves that was not targeted <i>a priori</i> , usually in a systematic conservation planning scenario.
<i>Representation target</i>	Defined numerical thresholds in the representation of selected conservation features (e.g. occurrence and distribution of a surrogate) in a systematic conservation planning context.
<i>Complementarity</i>	A principle in designing networks of reserve sites in conservation whereby the selection of sites iteratively adds sites that complement those already selected (Vane-Wright et al. 1991; Justus & Sarkar 2002).
<i>Simulated annealing</i>	An algorithm implemented in Marxan to identify near-optimal solutions in selecting networks of reserve sites in conservation (Game & Grantham 2008).

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