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

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Abstract

Cross-taxonomic surrogates are often used in conservation planning because inventorying large

suites of taxa is either not feasible or too costly. However, cross-taxonomic surrogates are

seldom tested rigorously using both correlational and representation-based approaches at the

spatial scales at which conservation management occurs. Here, we evaluated the effectiveness of

five ecologically contrasting taxa (birds, herpetofauna, wild bees, beetles, trees) as cross-

taxonomic surrogates in native woodland patches within a heavily modified, farming and

plantation-dominated landscape. We first compared species richness and compositional

heterogeneity across taxa before testing for cross-taxonomic congruence using a correlative

approach. We then quantified how well each taxon incidentally represented other taxa in their

best patch sets, and the costs of doing so using a complementarity-based approach. We found

significant pairwise associations between some taxa (birds, bees), but no single taxon was

strongly correlated with all other taxa. Woodland patch sets prioritised for beetles represented

other taxa best, followed by birds, but were the costliest and required the largest amount of

woodland. This contrasted with patch sets prioritised for wild bees or herpetofauna, which

achieved higher representation of other taxa at lower costs. Our study highlighted the influence

of taxon-specific patterns of diversity and heterogeneity on how remnant vegetation patches

should be prioritised for conservation, a consideration not immediately obvious in correlative

analyses of surrogacy. Second, taxa that are not the most speciose (e.g. wild bees) can be

efficient surrogates for other taxa, achieving higher incidental representation at lower costs.

Thus, while species-rich taxa are ideal as surrogates for prioritising conservation, conservation

planners should not overlook the potential of less speciose taxa such as bees, while considering

the cost-effectiveness of surveying multiple different taxa.

47

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. 201; 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

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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. Eglington 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

In this study, we tested the effectiveness of a cross-taxonomic surrogate approach to guide

conserving planning for woodland biodiversity in a human-modified landscape. The conceptual

framework for our study was guided by three questions, and grounded systematically on field

inventorying, initial identification of surrogate taxa, and cross-validation of these surrogate

groups in a systematic conservation planning approach. First, we asked: (1) Which pairs of taxa

show strong cross-taxonomic congruence? To do this, we inventoried two vertebrate groups

(birds, herpetofauna), two insect groups (wild bees, beetles) and one plant group (trees). We then

applied a correlative approach to assess the degree of pairwise cross-taxonomic association (i.e.

cross-taxonomic congruence) in species richness and composition (Sauberer et al. 2004; Su et al.

2004; Rooney & Azeria 2015). As with many studies, we hypothesized that taxa showing high

cross-taxonomic congruency could perform better as species surrogates for other taxa.

101

Second, we asked: (2) How effective are surrogate taxa in incidentally representing the

occurrences of other taxa in sets of woodland patches prioritised for the surrogate? This question

is important because it allows initially identified surrogate taxa to be validated in realistic

conservation planning scenarios. Ideally, an effective surrogate taxon should be expected to

capture a high proportion of the representation targets for other taxa (Larsen et al. 2012; Di

Minin & Moilanen 2014), without being excessively costly itself – i.e. requiring the conservation

of a large amount of woodland patches. To do this, we adopted a complementarity-based, site-

selection approach (see Table 1 for definitions of terms) to identify near-optimal sets of remnant

woodland patches in our landscape using *a priori* representation targets set for each taxon. We

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.

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127   **2. Methods and materials**

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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

2.2.3. Wild bee sampling

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

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2.2.4. Ground-dwelling beetle sampling

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

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

To identify which pairs of taxa showed strong congruence patterns at the landscape level, we

used a combination of Spearman's rank correlations and partial Mantel tests. The correlation

strength in species richness between two taxa is frequently used as a metric of cross-taxonomic

congruence (e.g. Hess et al. 2006; Wolters et al. 2006; Duan et al. 2016). To assess the level of

correlation between site-level species richness for each pairwise combination of taxa, we

calculated the Spearman's correlation coefficient (e.g. Similä et al. 2006). Spearman's

correlation was used instead of Pearson's correlation as the sample size for number of sites was

small ($N = 42$) and does not fulfil parametric assumptions based on the Shapiro-Wilk test

(Royston 1983).

233

We used partial Mantel tests to assess the strength of cross-taxonomic congruence in

compositional dissimilarity between pairwise combinations of taxa (Landeiro et al. 2012). Partial

Mantel tests were used because they measure the correlation between two matrices (e.g. Su et al.

2004) after accounting for spatial variation associated with a third matrix of Euclidean distances,

thus addressing the potential issue of spatial autocorrelation. We first quantified compositional

dissimilarity for each taxon across the landscape using the Jaccard similarity index which is

based on absence-presence data (Magurran 2004). We then performed the partial Mantel test for

all pairwise combinations of taxa. The significance of each Mantel test was assessed using 999

permutations.

243

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

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

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

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

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

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

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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 km^2) 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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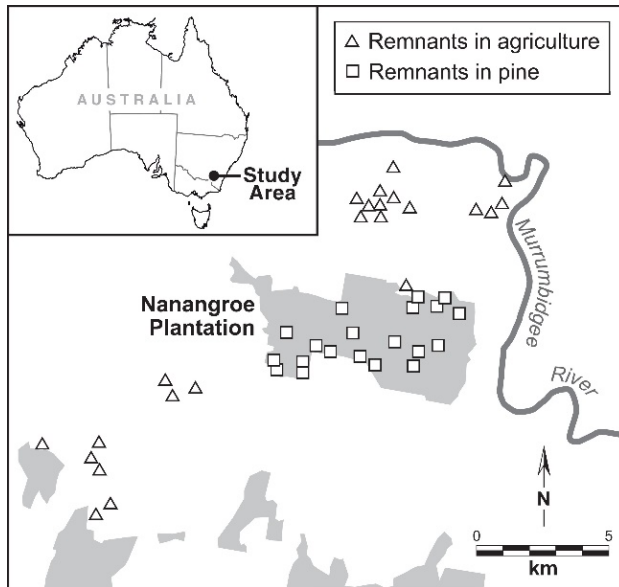
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Figure 1. Map of the Nanangroe study landscape showing the location and distribution of our 42

study sites in relation to the Murrumbidgee River. Grey-shaded areas are monoculture

plantations of *Pinus radiata* while unshaded areas are open grazing land.


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Figure 2 (a). Smoothed species accumulation curves for each taxon in the Nanangroe landscape

showing observed species richness and sampling effort for each taxon relative to other taxa. **(b).**

Bar plots (with error bars representing standard deviation) showing mean species richness at the

patch-level as a percentage of the total species pool in the landscape (gamma-diversity).
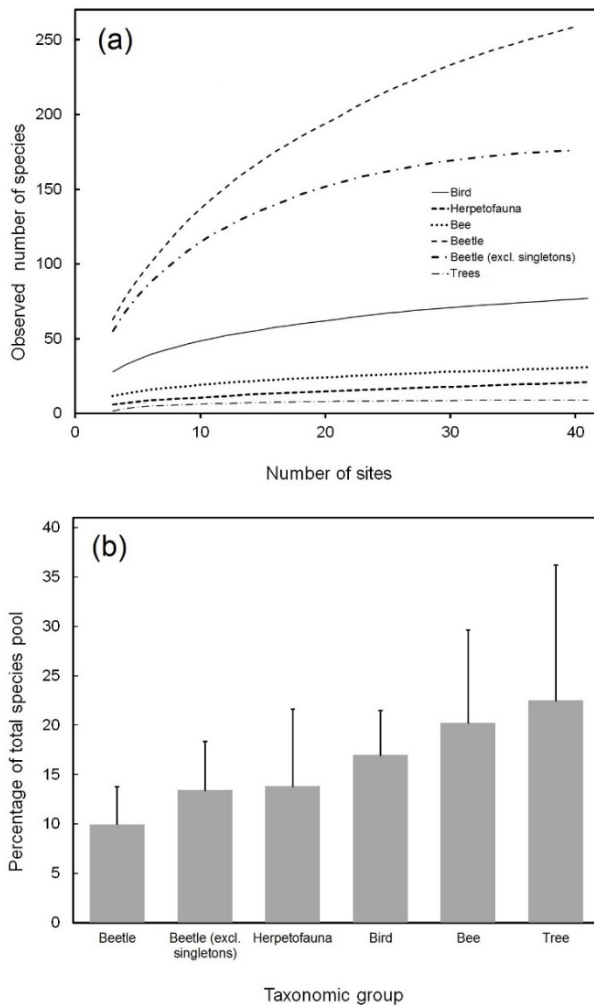
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813 **Figure 3 (a)**. Network diagram showing pairwise cross-taxonomic congruency in species

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.
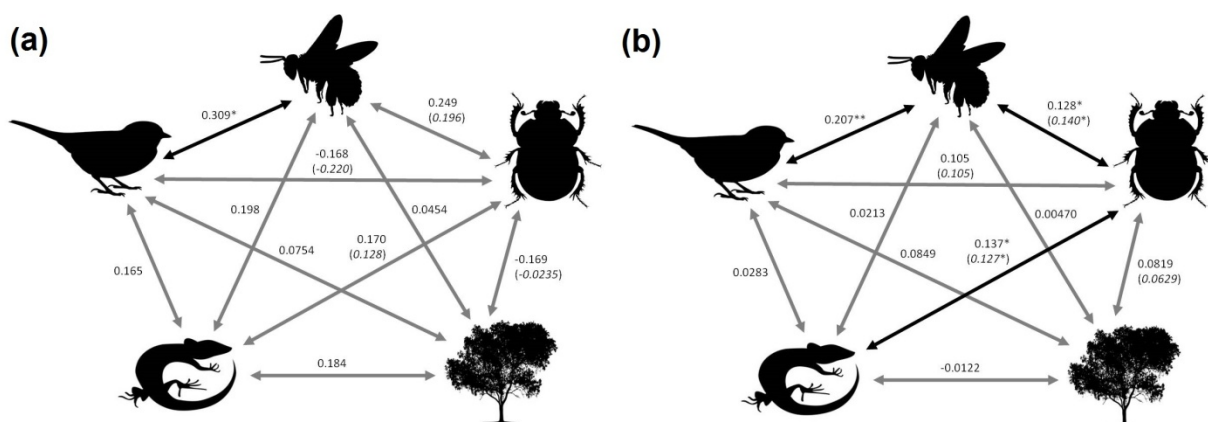

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829 **Figure 4**. Accumulation plots showing incidental representation of each taxon (indicated by

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.
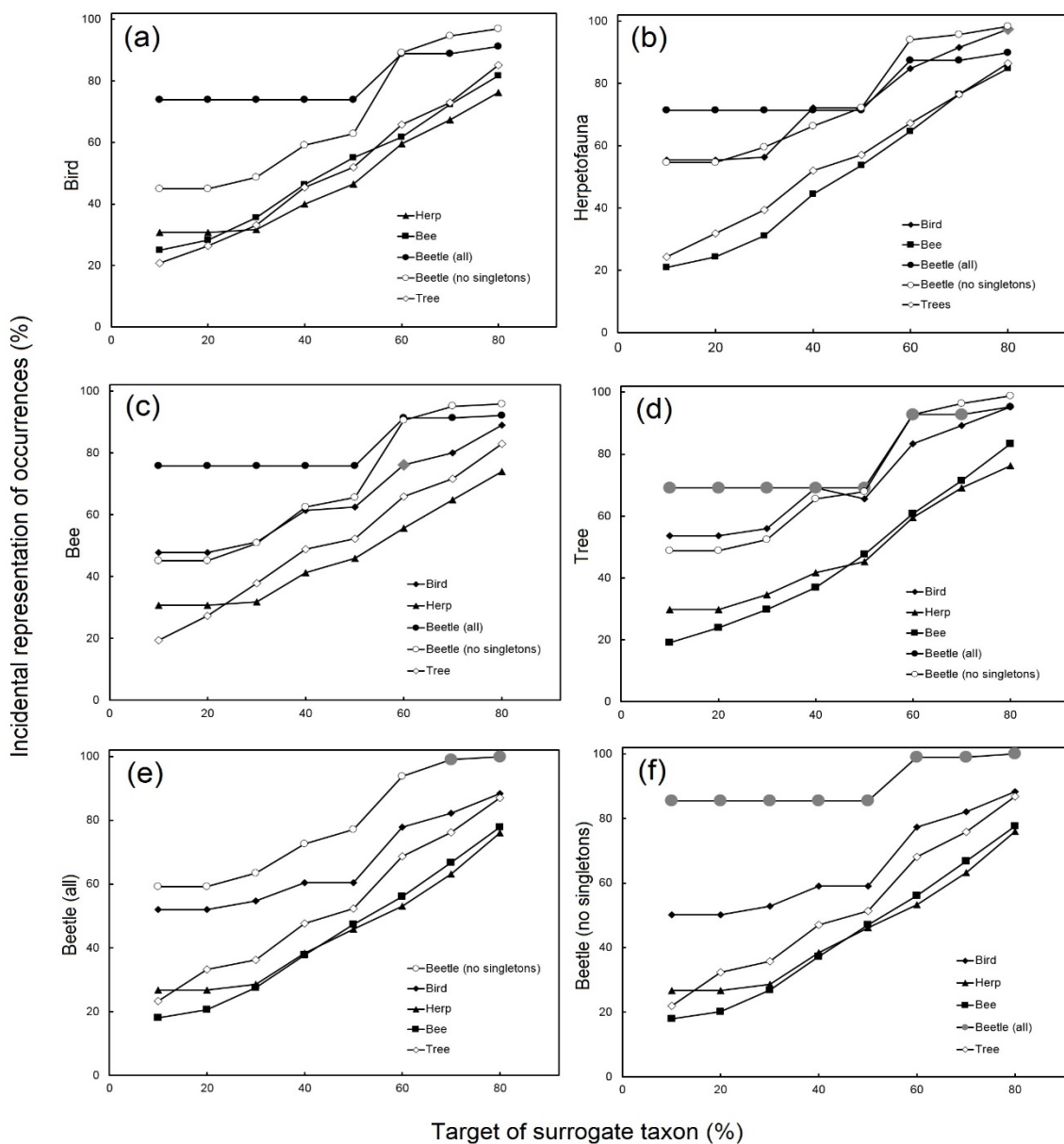
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835   **Figure 5**. Accumulation plots showing incidental representation of each taxon (indicated by

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.
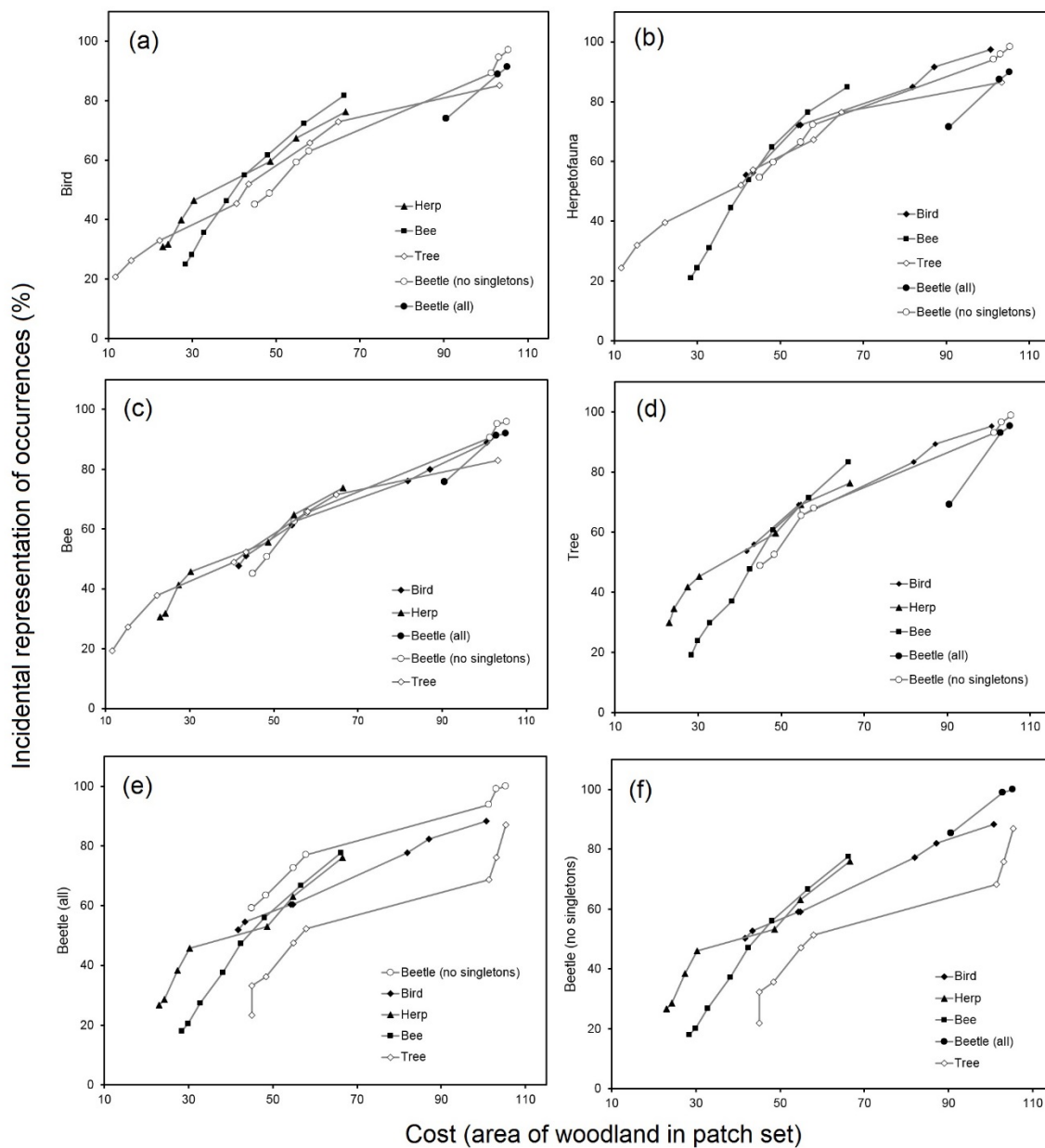
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840 **Figure 6**. Dendrogram of clusters for best patch sets selected for every taxa at four target threshold

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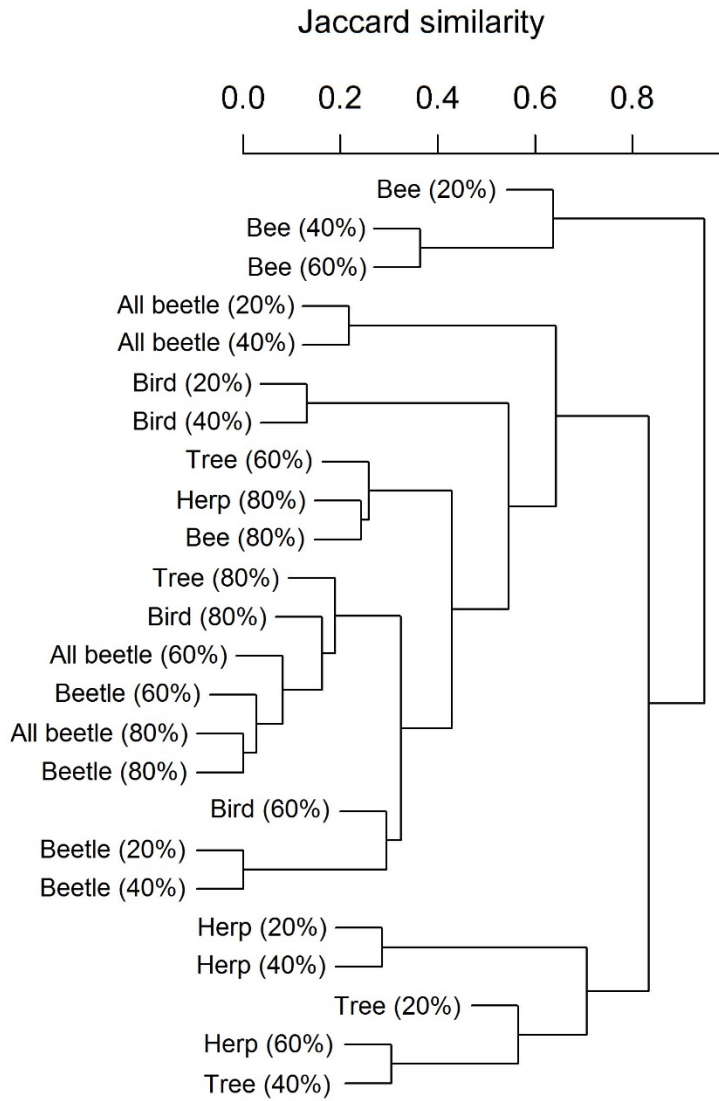
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847   **Table 1**. Glossary of key terms (in text) and definitions

Term	Definition
Biodiversity surrogate	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.
Cross-taxonomic congruence	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*.
Compositional turnover	Variation in the composition of species across space; an approach to quantify beta diversity in a landscape.
Conservation feature	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.
Incidental representation	Representation of a species in a set of identified sites/reserves that was not targeted *a priori*, usually in a systematic conservation planning scenario.
Representation target	Defined numerical thresholds in the representation of selected conservation features (e.g. occurrence and distribution of a surrogate) in a systematic conservation planning context.
Complementarity	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).
Simulated annealing	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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