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1 **Multi-criterion trade-offs and synergies for spatial conservation planning**

2  
3 **Running title: Multi-criterion trade-offs for conservation**

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43 **Summary**

44 1. Nature conservation policies need to deliver on multiple criteria, including genetic  
45 diversity, population viability and species richness as well as ecosystem services. The  
46 challenge of integrating these may be addressed by simulation modelling.

47 2. We used four models (MetaConnect, SPOMSIM, a community model and InVEST)  
48 to assess a variety of spatial habitat patterns with two levels of total habitat cover and  
49 realised at two spatial scales, exploring which landscape structures performed best  
50 according to five different criteria assessed for four functional types of organisms  
51 (approximately representing trees, butterflies, small mammals and birds).

52 3. The results display both synergies and trade-offs: population size and pollination  
53 services generally benefitted more from fragmentation than did genetic  
54 heterozygosity, and species richness more than allelic richness, although the latter two  
55 varied considerably among the functional types.

56 4. No single landscape performed best across all criteria, but averaging over criteria  
57 and functional types, overall performance improved with greater levels of habitat  
58 cover and intermediate fragmentation (or less fragmentation in cases with lower  
59 habitat cover).

60 5. *Synthesis and applications.* Different conservation objectives must be traded off,  
61 and considering only a single taxon or criterion may result in sub-optimal choices  
62 when planning reserve networks. Nevertheless, heterogeneous spatial patterns of  
63 habitat can provide reasonable compromises for multiple criteria.

64

65 **Keywords:** allelic richness, connectivity, fragmentation, genetic diversity, habitat  
66 area, heterozygosity, metapopulations, pollination, spatial scale, species richness

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67 **Introduction**

68 The success of nature conservation efforts may be assessed according to various  
69 criteria, and a good conservation strategy should perform well according to a range of  
70 criteria. These include preserving genetic diversity, maximising population viability,  
71 promoting species richness and enhancing various ecosystem functions – all of which  
72 may be implied by “biodiversity conservation” (Noss 1990). Many studies consider  
73 biodiversity as a single criterion or focus solely on one of its components (but see  
74 Tschamtkke *et al.* 2002). However, there is an open question about the extent to which  
75 different biodiversity and conservation criteria call for different strategies.

76

77 If the various conservation criteria reinforce each other hierarchically (Noss 1990), it  
78 should be straightforward to fulfil them simultaneously. For example, genetic  
79 diversity underpins population viability (Keller & Waller 2002; but see Tallmon,  
80 Luikart & Waples 2004), reducing local extinction rates and so promoting greater  
81 species richness, and diverse communities are thought to enhance ecosystem  
82 functioning (Klein *et al.* 2003; Zavaleta *et al.* 2010). However, spatial structure may  
83 introduce conflicts and trade-offs between conservation goals. For example, a widely-  
84 distributed habitat network might sample more environments and maximise species  
85 richness, but at the cost of protecting fewer individuals of each, increasing extinction  
86 rates (Mokany, Harwood & Ferrier 2013); or high connectivity may improve  
87 population persistence (Soulé & Simberloff 1986) but at the cost of reduced allelic  
88 richness owing to increased rates of gene-flow (Fenderson *et al.* 2014). Optimal  
89 solutions may also depend upon the taxa of concern (plants, birds, etc.), especially  
90 since differences in dispersal abilities can radically change the functional connectivity  
91 of a given landscape (Taylor *et al.* 1993). Considering ecosystem services as a

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92 conservation objective (de Groot, Wilson & Boumans 2002) adds new dimensions to  
93 the problem. For example, pollinator activity typically radiates from insect nesting  
94 habitat into croplands (Ricketts *et al.* 2008) such that crop pollination rates may  
95 increase with the habitat edge:area ratio. We can therefore imagine three situations. If  
96 all desirable criteria are linked by mutually-reinforcing effects, then for practical  
97 purposes the plurality of criteria is illusory (Fig. 1A). Otherwise, if there are certain  
98 kinds of conservation policies that fulfil all criteria (Fig. 1B), we should ask: what are  
99 the characteristics of these policies? Finally, if such win-win solutions are  
100 impractical, fragile or do not exist (e.g. Fig. 1C), then we should ask: how are the  
101 different criteria traded off so that policy-makers and conservationists may seek  
102 appropriate compromises?

103

104 These questions are especially pertinent when we consider the spatial arrangement of  
105 habitat patches. This is particularly the concern of the conservation planning literature  
106 (Miller, Bratton & White 1987). While habitat quality is of fundamental importance,  
107 in landscapes with many competing land-uses the spatial arrangement of habitat may  
108 be critical – particularly as regards the degree of fragmentation of a given area  
109 (Pardini *et al.* 2010; Doerr, Barrett & Doerr 2011). This question was previously  
110 addressed under the simplistic SLOSS framework (“single large or several small”  
111 Diamond 1975; Simberloff & Abele 1982), but contributions to that debate have  
112 rarely accounted for the full range of spatial scales at which conservation actions are  
113 undertaken, or the implications of mixed patch-sizes (but see Schwartz 1999). The  
114 diverse processes by which organisms interact with each other and with their habitat  
115 all have characteristic spatial scales (Levin 1992), so it is likely that the spatial  
116 arrangement of habitat patches will have different implications for different

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117 conservation criteria, depending on the sizes of patches, the distances between them  
118 and the characteristics of the taxa in question (With, Gardner & Turner 1997;  
119 Hodgson *et al.* 2011; Synes *et al.* accepted). The best spatial strategy for a regional  
120 scale may not simply be scaled up to give a global template for conservation planning,  
121 or scaled down for local recommendations.

122

123 There is therefore a need to investigate the value of a diverse range of spatial  
124 strategies at specific spatial scales and using a range of criteria simultaneously.  
125 Simulation models enable us to do this with some generality. Here we use four  
126 models to explore relationships among several ecological criteria as applied to  
127 configurations of habitat patches differing in their degree of fragmentation (number of  
128 fragments varying by two orders of magnitude). Considering four functional types of  
129 organism differing in population densities, dispersal distances and species richness,  
130 we explore how different landscapes perform according to the levels of genetic  
131 diversity (both heterozygosity and allelic richness), population size, species richness  
132 and pollination services that they are likely to sustain. On the basis of the reasoning  
133 given in the above examples of spatial scenarios, we predicted that (1) heterozygosity  
134 and (2) population viability would increase with decreasing fragmentation, while (3)  
135 allelic richness and (4) species richness would increase with some degree of patch  
136 separation, especially if there are any underlying habitat gradients, and subject to  
137 population viability being maintained – so these criteria would be maximized in  
138 moderately-fragmented landscapes. We expect all these benefits to be greatest for  
139 functional types with higher population densities and lower dispersal distances, but to  
140 be increasingly tempered by viability constraints when population densities are lower.  
141 Finally, (5) the export of pollination services to the matrix should benefit from higher

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142 fragmentation of landscapes. Functional connectivity – the degree to which a  
143 landscape facilitates movement for a given type of organism (Taylor *et al.* 1993; Pe'er  
144 *et al.* 2011) – must also be considered. Thus, while fragmentation is expected to cause  
145 problems under many criteria as assessed over local extents, over ranges approaching  
146 the dispersal limits of an organism we expect that landscapes with greater levels of  
147 fragmentation of a given overall habitat area will perform better, owing to reduced  
148 inter-patch distances pertaining between more-numerous fragments. Thus we expect  
149 no single habitat configuration to be optimal for all criteria (Fig. 1C).

150

151 Our study asks whether there are spatial patterns that are generally successful  
152 according to a range of conservation criteria, and how the best compromise solutions  
153 perform across criteria and functional types. Robust recommendations for the design  
154 and improvement of reserve networks can only be obtained once we can detect and  
155 negotiate any important trade-offs.

156

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157 **Materials and Methods**

158 **Landscape patterns**

159 We first generated a set of 25 gridded binary landscape patterns spanning a broad  
160 spectrum of fragmentation: from single isolated large patches to 500 small patches,  
161 and with a wide range of patch shapes so as to vary connectivity and edge–area ratios  
162 (Fig. 2). As habitat cover is a major constraint on  $\alpha$ - and  $\gamma$ - diversity in fragmented  
163 landscapes (Hodgson et al. 2011), we considered 15 patterns with 10% cover and 10  
164 with 2%. These are comparable to the levels so far attained in densely-populated  
165 regions, such as the UK’s 6% (Tier-1 protection) to 13% (Tiers 1+2) (Lawton *et al.*  
166 2010), especially because our patterns were considered to represent single habitat  
167 types. Seven of the patterns were derived from observed woodland landscapes and the  
168 remaining 18 from a simulation algorithm using patch-size distributions from the  
169 observed landscapes (Appendix S1). All the patterns were modelled on an arena of  
170  $100 \times 50$  cells. We considered the patches to represent wildlife-rich, semi-natural  
171 habitat within a wildlife-hostile matrix such as intensive agriculture or urbanisation.  
172 Such binary patterns are of course a greatly simplified model of real landscapes.

173

174 Each of these 25 patterns (“tiles”) was interpreted at two spatial scales that may be  
175 relevant to the scaling of both ecological processes and administrative regions: “local”  
176 meant a cell size of 50m, giving a tile size of  $5 \text{ km} \times 2.5 \text{ km}$ , while “regional” meant a  
177 cell size of 500m and tile size of  $50 \text{ km} \times 25 \text{ km}$ . The patterns were then tiled by  
178 transposition to add a ‘border’ of 50 cells (Fig. S1), to reduce edge effects; for  
179 analyses, we extracted results from only the focal tile ( $100 \times 50$  cells), referred to as  
180 the “landscape”. The scaling means that all local-scale landscapes are at least as  
181 fragmented as the most fragmented regional-scale landscapes. For example, tiled

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182 arrays of the most aggregated patterns (e.g. P) at the local scale have patches of a size  
183 (25 ha in this case) equivalent to the smallest patches in a highly-fragmented pattern  
184 taken at the regional scale (e.g. Y).

185

186 **Functional scenarios: species × scales**

187 The set of landscape patterns was considered with respect to four functional types  
188 represented by combinations of attributes for mean dispersal distance, potential  
189 population density (carrying capacity) and species richness, as shown in Table 1.  
190 These combinations are suggestive of four groups of conservation interest in Europe:  
191 forest trees, grassland butterflies, small mammals and passerine birds – and these  
192 names are used for simplicity hereafter. Since population densities tend to decrease  
193 (Gaston, Blackburn & Gregory 1999) while species richness increases (Arrhenius  
194 1921) with sampling extent, we scaled our values according to a power-law relation  
195 whereby species richness doubles for a 100-fold increase in area. Our estimates and  
196 calculations are fully explained in Appendix S1.

197

198 The trait values of the functional types were translated into per-cell carrying  
199 capacities and cell-based dispersal distances. Owing to computational limitations in  
200 some of the models, we did not run the scenarios for butterflies and trees at the  
201 regional scale, leaving a set of 6 functional scenarios (Table 1).

202

203 **Assessment of scenarios**

204 The scenarios were assessed using a different simulation model for each of the four  
205 main criteria: intraspecific genetic diversity, population size, species richness and  
206 pollination service. Each model was parameterised using the mean dispersal distance

---

207 and corresponding carrying capacity specified by each of the functional scenarios.  
208 Further details of all models and parameter choices are given in Appendix S1 (Table  
209 S5).

210

211 1) *Genetic diversity: heterozygosity and allelic richness*

212 The individual-based, patch-focused model MetaConnect (Baguette, Clobert &  
213 Moulherat 2012; Moulherat *et al.* submitted) was used to assess how conducive the  
214 landscapes are to the production and maintenance of neutral genetic diversity in each  
215 functional type. We considered two metrics, each for a set of 10 loci: allelic richness  
216 (overall number of alleles throughout the population; initially 10 per locus) and mean  
217 heterozygosity (proportion of heterozygotes). MetaConnect simulates population  
218 dynamics, dispersal among patches and mutation, with sexed individuals and panmixy  
219 within each patch. We calculated mean allelic richness in a landscape over the final  
220 75 time steps (generations) in each of 10 simulations with 100 time-steps, imputing  
221 zero if the population was extinct. Since heterozygosity is undefined in cases of  
222 extinction, we analysed its rate of change (slope of square-root transformed  
223 heterozygosity against time: Appendix S1, 3.1.2) rather than actual values.  
224 Landscapes with more negative change were deemed worse at maintaining  
225 heterozygosity.

226

227 2) *Population size*

228 The stochastic patch-occupancy simulator SPOMSIM (Moilanen 2004) was used for  
229 predicting the proportion of habitat area occupied, to give a surrogate for total  
230 population size. SPOMSIM models local extinction and colonisation as functions of  
231 patch-specific carrying capacities. Extinction rates were modelled using an

---

232 exponential function of patch area and population carrying capacity; colonisation was  
233 modelled as a function of patch area and the species' dispersal distance and  
234 colonisation ability, using minimum edge-to-edge distances between all pairs of  
235 patches. For every combination of landscape and species, 100 replicates were  
236 simulated over 300 time steps, starting with all patches occupied, and the mean  
237 proportion of occupied area was calculated for time steps 51-300.

238

### 239 3) *Species richness*

240 A spatially-explicit community model (Bocedi 2010; Bocedi, Gunton & Kunin 2011)  
241 was used to assess what levels of species richness the landscapes might sustain. This  
242 niche-based model simulates individuals of multiple species competing for resources.  
243 For a given run, each of a specified number of species was randomly assigned values  
244 for dispersal ability, population density and fecundity, according to probability  
245 distributions generated with reference to literature and unpublished data, and for its  
246 niche optimum and niche width, from uniform distributions. Niches were simulated  
247 by overlaying the habitat maps with both a linear gradient (representing, for example,  
248 a latitudinal temperature gradient) and random quasi-fractal heterogeneity with an  
249 autocorrelation coefficient based on European topographical maps (representing, for  
250 example, microclimatic variation); the ratio between these two components increased  
251 with spatial scale. Each run lasted for 50 generations to allow for equilibrium, after  
252 which the number of surviving species was obtained, to be averaged across 100 runs.

253

### 254 4) *Pollination services*

255 The model InVEST 2.4.2 (Nelson *et al.* 2009; Natural Capital Project 2012) provided  
256 assessments of how the scenarios may affect pollination rates of an insect-dependent

---

257 (e.g. top fruit) crop grown in the surrounding matrix. Our four functional types were  
258 not relevant here, but taking habitat patches as providing both nest sites and foraging  
259 resources for pollinating insects and the matrix as a foraging resource, the model  
260 assigns an abundance of pollinators to every cell in the landscape and thence a rate of  
261 pollination to each crop cell. We parameterised it according to published  
262 recommendations (Tallis *et al.* 2011), specifying an exponential movement kernel for  
263 pollinators with a distance-decay constant of 1800 m. We also assumed a transition  
264 zone between crop and habitat equivalent to a 2-m band with zero yield around all  
265 habitat patches, reducing the cropped area of the landscape by 0.01% (least  
266 fragmented) – 2% (most fragmented), representing for example a conservation  
267 headland to protect the habitat patches, or the ecosystem disservice of reduced crop  
268 value in the vicinity of trees or other marginal habitat (Sparkes *et al.* 1998). Fruit-set  
269 values for each cell in the matrix were multiplied by potential crop cover, and the  
270 resulting values averaged to give landscape-wide relative yield.

271

## 272 *Analyses*

273 Results from the simulation models were grouped so that the landscapes could be  
274 compared for each conservation criterion, functional type and spatial scale. Within  
275 these groups, for basic multi-criterion assessments we scaled the model outputs across  
276 landscapes as proportions of the value for the best-performing landscape. Other  
277 standardisation techniques are of course available (z-scores gave similar results – see  
278 Tables S12–S16 and Fig. S5), and we do not consider methods of weighting the  
279 criteria; here we simply focus on how different criteria may favour different types of  
280 landscapes.

281

---

282 Two kinds of multi-criterion assessment were performed. First we averaged  
283 standardised results across multiple criteria and scenarios. The weighting of different  
284 criteria is a non-trivial decision (see ‘Outlook’); we simply used relative scores  
285 (scaled to  $\leq 1$ ), unweighted, for illustration. More sophisticated optimisation  
286 procedures, such as pareto optimisation, might be useful in realistic analyses for  
287 decision-making. Second, to visualise trade-offs among criteria and functional types  
288 we performed two principal components analyses (PCA) combining all assessments,  
289 one for each spatial scale. Each analysis was based on a correlation matrix of the  
290 response data for each criterion applied to each relevant functional type, with the 25  
291 landscapes as rows (cases). We then created biplots with landscape scores and criteria  
292 loadings scaled symmetrically by square roots of their eigenvalues, allowing a  
293 combined assessment of the different criteria.

294

295 In order to ascertain that differential patterns of assessments among the different  
296 criteria reflect differences in the biotic processes being assessed, rather than simply  
297 differences among the models, we made use of overlaps among the criteria that each  
298 model could assess. Two contrasting approaches were possible: (a) comparing  
299 predictions for the same criterion from several models, and (b) comparing predictions  
300 for multiple criteria from a single model. For (a) we cross-correlated population size  
301 assessments as available from each of the models except InVEST, and for (b) we  
302 analysed the three criteria available from MetaConnect using PCA, as above. The  
303 results of these validation checks are given in Appendix S2 (Table S6; Fig. S7).

---

304 **Results**

305 We found large differences between the landscapes according to the choice of  
306 conservation criteria. We present results for each criterion in turn, with reference to  
307 figures in Appendix S2 (where raw and z-transformed values are also given), before  
308 examining how far these assessments correlate with each other within and among  
309 functional types (Fig. 3).

310

311 Genetic diversity responded strongly to fragmentation. Allelic richness varied little  
312 across landscapes with 10% cover at both scales (Figs. S3a, S4a), except for birds in  
313 the local scale landscapes, where the low carrying capacity meant that even moderate  
314 fragmentation caused total extinction. By contrast, in the landscapes with 2% cover  
315 allelic richness generally declined with fragmentation. The rate of heterozygosity  
316 decline increased with fragmentation across all scenarios (Figs. S3b, S4b).

317

318 The population patch-occupancy model gave rather different predictions at the two  
319 scales. At the local scale (Fig. S3c), birds were unaffected by fragmentation but the  
320 other functional types generally increased their occupied area with increasing  
321 fragmentation – especially in landscapes with 2% cover, where occupancy was always  
322 low. At the regional scale (Fig. S4c), birds went extinct in some of the least-  
323 fragmented landscapes while occupancy by mammals generally declined with  
324 fragmentation, as judged from the cases with 10% cover. Overall, metapopulation  
325 'rescue effects' (Sutherland, Elston & Lambin 2012) seemed to favour a degree of  
326 fragmentation in most cases.

327

---

328 The community model was also very scale-sensitive. At the local scale (Fig. S3d),  
329 equilibrium species richness declined with increasing fragmentation, but this pattern  
330 was more pronounced for functional types with lower initial species richness, so that  
331 there were no large differences among the landscapes for butterflies or trees (Figs.  
332 3A, 3B). At the regional scale (Fig. S4d), the pattern was reversed, with species  
333 richness increasing with fragmentation – probably because of both broader sampling  
334 of a longer niche gradient and also greater viability of isolated populations. There was  
335 also a more pronounced effect of cover (10% > 2%), particularly in small mammals  
336 (Fig. 3C).

337

338 For pollination services, there were greater rates of fruit set and greater total crop  
339 yield for landscapes with 10% habitat coverage (90% crop) than those with 2% (98%  
340 crop). At the local scale there was minimal variation within these two levels of cover,  
341 and the yield deficit of the 2% landscapes eventually disappeared if baseline crop  
342 productivity in the absence of wild pollinators was increased from 20% to about 70%  
343 (data not shown). The small effect of the buffer strip may be seen in the slight decline  
344 for the most-fragmented landscapes (Fig. 3). At the regional scale, total yield  
345 increased with fragmentation, especially in the landscapes with 10% cover, and the  
346 most-fragmented 2% landscapes performed as well as the least-fragmented 10% ones.

347

#### 348 ***Multi-criterion assessments by functional type***

349 At the local scale most of the functional groups showed an interplay between low  
350 population sizes in landscapes with rather few, isolated patches vs. decreasing genetic  
351 diversities with increasing fragmentation. In trees and butterflies these factors tended  
352 to show opposite trends or none at all (Figs. 3A, 3B). In mammals and birds, severe

---

353 decreases in both allelic and species richness in the most fragmented landscapes  
354 resulted in overall performance peaking in landscapes with intermediate or low levels  
355 of fragmentation (Fig. 3C, 3D).

356

357 At the regional scale the fragmentation responses for birds and small mammals were  
358 largely reversed on all criteria (Figs. 3E, 3F). With 10% cover, performance on most  
359 criteria increased with fragmentation. Landscapes with 2% cover were more similar to  
360 each other, with genetic diversity decreasing and species richness and ecosystem  
361 services increasing with fragmentation.

362

### 363 ***Global multi-criterion assessment***

364 The ordination method is particularly revealing. The landscapes load in two swathes  
365 on the PCA biplot (Fig. 4), those with 10% cover having higher scores on the first  
366 principal component than those with 2% cover, and each set showing a progression  
367 from less-fragmented to more-fragmented patterns. At both scales the assessment  
368 criteria all load positively on the first axis, suggesting better performance of  
369 landscapes with 10%, but on the second axis they load rather differently for each  
370 functional type and scale. At the regional scale (Fig. 4B), the order for birds, from  
371 aggregated to more fragmented, runs: genetic criteria > population size > species  
372 richness > pollination services – which matches the conventional order of biological  
373 levels of organisation; for small mammals the allelic richness and species richness  
374 criteria appear further down this sequence, increasing more with fragmentation. At  
375 the local scale (Fig. 4A), the order is generally genetic criteria > species richness and  
376 pollination service > population size, although it differs somewhat among the  
377 functional types.

---

378

379 Combining all analyses for each scale, all three methods reveal the amount of habitat  
380 cover to be a major driver of the variables targeted by conservation criteria. At the  
381 local scale (Figs. 4A, 5A) less fragmentation is generally favoured: some of the  
382 landscapes with 10% cover and moderate fragmentation perform fairly well for most  
383 functional types, while the unfragmented one performs best among the 2%  
384 landscapes. At the regional scale (Figs. 4B, 5B) there is a shift towards more  
385 fragmented patterns, leaving no clear optimal habitat configuration and habitat cover  
386 as the most important driver.

387

---

388 **Discussion**

389 There is growing interest both in the significance of habitat configurations for  
390 conservation (Humphrey *et al.* 2015) and in the diversity of legitimate goals for  
391 conservation planning, thanks in part to the ecosystem services agenda (Cimon-  
392 Morin, Darveau & Poulin 2013) and changing conceptions of biodiversity (Gunton *et*  
393 *al.* 2016). The challenge of integrating across different components of biodiversity,  
394 however, remains little addressed. Combining studies that focus on a single aspect of  
395 biodiversity or consider only a single functional type may lead to conflicting advice  
396 for conservation practitioners and policy-makers, especially if recommendations come  
397 from studies conducted at differing spatial scales. For example, observational studies  
398 show how patch-connectivity may either increase (Martensen *et al.* 2012) or decrease  
399 population densities (Hopfenmüller, Steffan-Dewenter & Holzschuh 2014), and how  
400 this may depend upon levels of habitat cover (Pardini *et al.* 2010). A single  
401 publication may recommend contrasting geometries for different species (Henderson  
402 *et al.* 2012; Hopfenmüller, Steffan-Dewenter & Holzschuh 2014), or according to the  
403 value of a key modelled parameter (Bascompte *et al.* 2007). Our results confirm that  
404 the best solution for one conservation goal may not serve well in another case  
405 (Simberloff & Abele 1982). Such trade-offs have only occasionally been reported; for  
406 example, species richness of insects was increased by a more fragmentary pattern of  
407 grassland patches and overall metacommunity size by a more aggregated pattern  
408 (Tscharntke *et al.* 2002). Our approach allowed us to explore a wide range of  
409 possibility space by comparing results from several simulation models across a broad  
410 range of habitat patterns, exploring multiple taxa, criteria and scales simultaneously.

411

---

412 The importance of spatial configuration was clear. In line with our predictions, there  
413 was a contrast between the two genetic measures (in aggregated landscapes  
414 heterozygosity increased by more than allelic richness), reflecting the role of isolation  
415 in maintaining population-wide (beta-) diversity yet reducing outcrossing and hence  
416 heterozygosity. The relative importance of these two aspects of genetic diversity is an  
417 open question for conservation (Tallmon, Luikart & Waples 2004), and it should be  
418 noted that there is an expected correlation between allelic richness and overall  
419 population size. Also as predicted, taxa with low population densities tended to go  
420 extinct in highly fragmented landscapes (e.g. comparing mammals and butterflies,  
421 which differ in carrying capacity but not in dispersal distance). The effects of  
422 dispersal distance are less clear. We might expect fragmentation to matter less for  
423 strong dispersers, but impacts on genetic diversity were similar for trees and  
424 butterflies, which had equal carrying capacities but very different dispersal ranges.  
425 Contrasts between the two scales reflect shifts in both carrying capacity (100 times  
426 higher at the regional scale) and dispersal between cells (10 times lower), which may  
427 together explain why more-fragmented landscapes were favoured at the coarser scale.  
428 Overall, it seems that neither ‘few large’ (typical of coastal and upland habitats) nor a  
429 uniform ‘many small’ pattern (such as agri-environment schemes tend to foster) will  
430 generally be optimal; instead, non-uniform patterns of intermediate fragmentation  
431 (mixtures of patch sizes and inter-patch distances) appear to be the best compromise  
432 solutions (Rösch *et al.* 2015). Such patterns (e.g. J and K) are reminiscent of the  
433 patterns actually found in modern European landscapes, where habitat patches are  
434 often located haphazardly and opportunistically, and indeed some of the best-  
435 performing landscapes in the analyses for birds at the regional scale and for butterflies  
436 and trees at the local scale came from patterns I, J, M and N, which were taken from

---

437 U.K. forestry maps. Optimal spatial strategies for protecting and creating small  
438 amounts of habitat at fine scales are increasingly sought within the drive for green  
439 infrastructure around urban areas (Tzoulas *et al.* 2007).

440

441 Some of the simulation results are surprising. Landscapes A and B differ only in the  
442 shape of the large patch, so the contrasts that appear for allelic richness and  
443 metapopulation size in butterflies and birds may be due to differing functional  
444 connectivity for the trait values we used. For example, when patterns are tiled, more  
445 cells in the circular patch of landscape A are brought closer to those in neighbouring  
446 patches (Fig. S1) than happens in the case of the narrow patch in landscape B, and  
447 these distances will interact with organisms' dispersal ranges. There are also some  
448 contrasts between the population dynamics suggested by SPOMSIM and those of  
449 MetaConnect (Fig. S6) – thus, for example, for most of the landscapes with 10%  
450 cover, small mammals show almost zero patch occupancy (SPOMSIM) yet high  
451 allelic richness values (MetaConnect). More generally, our parameterisation of  
452 SPOMSIM seems to have produced rather high patch extinction and colonisation  
453 rates. The models we used are indeed diverse: patch-based and individual-based,  
454 stochastic and deterministic. Some divergence among assessments for the different  
455 criteria may therefore be attributed to differing model assumptions, a point which we  
456 explore further in Appendix S2 (Table S6, Fig. S7). The outputs are not meant as  
457 definitive predictions; rather our purpose was to explore the diversity of assessments  
458 that may be obtained for a common set of landscapes by using a range of parameter  
459 values (functional types) and conservation criteria, as well as various available  
460 models. The results suggest just some of the scale-specific trade-offs that will exist  
461 between functional types and criteria in real situations.

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462

463 Our findings validate the primary concern of conservationists with maximising overall  
464 habitat area (Fahrig 2013; Banks-Leite *et al.* 2014), particularly at the “regional”  
465 scale. However, two types of exceptions to this are important and may have profound  
466 economic implications in view of land prices, agricultural and other economic  
467 pressures, and in some contexts the direct costs of protecting habitat. First, according  
468 to most criteria there was overlap between landscapes with 2% and 10% cover such  
469 that some landscapes outperformed others containing five times as much habitat.  
470 Second, for both genetic criteria there are low-fragmentation landscapes that  
471 performed better with 2% than 10% cover. It is also notable that for realistic  
472 parameters, total production of a fruit crop should benefit from increased  
473 fragmentation, and also from taking land out of production to provide nesting habitat  
474 for pollinating insects. Policy-makers seeking to balance multiple pressures and costs  
475 judiciously can ill afford to ignore such exceptions as these.

476

477 The framework of ecosystem services is increasingly used to account for the value of  
478 all kinds of non-translatable landscape goods such as biodiversity, agricultural  
479 productivity and recreational opportunities (Nelson *et al.* 2009; Ekroos *et al.* 2014).  
480 Numerous studies have looked at effects of biodiversity on ecosystem services,  
481 suggesting generally positive relationships in some cases (Cardinale *et al.* 2012).  
482 However, few of these studies consider biodiversity criteria other than species  
483 richness. The present study shows that there may also be trade-offs among  
484 biodiversity criteria, reinforcing the message that conservation is a multi-criterion,  
485 multi-scale problem.

486

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487 **Outlook**

488 Our simulations were performed at two relatively fine spatial scales, and broader  
489 scales should be investigated as computing power permits. The dynamic natures of  
490 landscape change and biodiversity dynamics could also be considered more explicitly:  
491 the simulations began from fully-colonised landscapes and sought equilibrium, but  
492 real species distributions and habitat networks are in a state of flux (Hodgson *et al.*  
493 2011). Our simulations mostly ignored habitat-boundary effects, while only the  
494 community model considered varying habitat quality and multiple interacting species.  
495 Results and recommendations might differ for rarer species, which are often a focus  
496 of conservation efforts. This suggests two major challenges for generalising our  
497 results. First, how may the conservation value of habitat patterns be predicted from  
498 their geometric properties? Reliable correlations could reduce our dependence on  
499 computer-intensive simulation models. Second, how may particular traits of  
500 organisms of conservation concern be related to the types of habitat patterns that best  
501 protect them? Such functional relations will be important for improving the  
502 conservation of lesser-known taxa.

503

504 We conclude by returning to the question of correlation among different components  
505 of biodiversity. While the overall correlations that we found among landscape  
506 assessments by our five criteria were limited, the strengths of these correlations (as  
507 shown by the PCA) are generally consistent with the conceptual order of the criteria:  
508 from mean heterozygosity favouring the most aggregated patterns, through allelic  
509 richness, metapopulation size and community richness, to pollination service  
510 favouring the most fragmented patterns. Perhaps reasons for this will become clearer  
511 with the development of unified mechanistic community models (Evans, Norris &

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512 Benton 2012; Harfoot *et al.* 2014) – which should also help reduce elements of  
513 spurious divergence among models. Nevertheless, multi-criterion assessment methods  
514 will surely remain important. Ecologists and policy-makers alike need to explore and  
515 discuss trade-offs among the demands of different functional types and conservation  
516 criteria in order to improve the scientific underpinning of conservation policies  
517 (Wilson, Carwardine & Possingham 2009), and the trade-offs will need to be solved  
518 by justifiable schemes for weighting the different criteria (Roberts *et al.* 2003) within  
519 flexible multi-criterion methods (Smith & Theberge 1987). Our study shows how  
520 some of the most important decisions may lie in optimising the geometry of habitat  
521 networks in a scale-sensitive way and with the needs of particular types of organisms  
522 in view (Wiggering & Steinhardt 2015).  
523

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528 simulate heterogeneity, and Stephen Cornell and James Rosindell gave formative  
529 ideas. Jenny Hodgson and Jochen Krauß provided information on butterfly traits,  
530 Christopher Wright on small mammals and Riin Taam on trees. Data from the  
531 National Forest Inventory were provided by the U.K. Forestry Commission. Joseph  
532 Bennett and two anonymous reviewers helped us clarify a number of important  
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534

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535 **References**

- 536 Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95-99.
- 537 Baguette, M., Clobert, J. & Moulherat, S. (2012) Population viability across scales.  
538 *Securing the Conservation of biodiversity across Administrative Levels and*  
539 *spatial, temporal, and Ecological Scales.*
- 540 Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscin, G.,  
541 R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C. & Metzger, J.P.  
542 (2014) Using ecological thresholds to evaluate the costs and benefits of set-asides  
543 in a biodiversity hotspot. *Science*, **345**, 1041-1045.
- 544 Bascompte, J., Luque, B., Olarrea, J. & Lacasa, L. (2007) A probabilistic model of  
545 reserve design. *Journal of Theoretical Biology*, **247**, 205-211.
- 546 Bocedi, G. (2010) A general framework for modelling metacommunity dynamics  
547 under environmental changes. MSc, University of Aberdeen.
- 548 Bocedi, G., Gunton, R.M. & Kunin, W.E. (2011) Comparative analysis of putative  
549 drivers and parameterization of disturbance scaling simulation model *Securing*  
550 *the Conservation of biodiversity across Administrative Levels and spatial,*  
551 *temporal, and Ecological Scales.* School of Biology, University of Leeds.
- 552 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,  
553 Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C.,  
554 Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012)  
555 Biodiversity loss and its impact on humanity. *Nature*, **486**, 59-67.
- 556 Cimon-Morin, J., Darveau, M. & Poulin, M. (2013) Fostering synergies between  
557 ecosystem services and biodiversity in conservation planning: A review.  
558 *Biological Conservation*, **166**, 144-154.
- 559 de Groot, R.S., Wilson, M.A. & Boumans, R.M.J. (2002) A typology for the  
560 classification, description and valuation of ecosystem functions, goods and  
561 services. *Ecological Economics*, **41**, 393-408.

- 
- 562 Doerr, V.A.J., Barrett, T. & Doerr, E.D. (2011) Connectivity, dispersal behaviour and  
563 conservation under climate change: a response to Hodgson et al. *Journal of*  
564 *Applied Ecology*, **48**, 143-147.
- 565 Ekroos, J., Olsson, O., Rundlof, M., Watzold, F. & Smith, H.G. (2014) Optimizing  
566 agri-environment schemes for biodiversity, ecosystem services or both?  
567 *Biological Conservation*, **172**, 65-71.
- 568 Evans, M.R., Norris, K.J. & Benton, T.G. (2012) Predictive ecology: systems  
569 approaches: introduction. *Philosophical Transactions of the Royal Society B-*  
570 *Biological Sciences*, **367**, 163-169.
- 571 Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount  
572 hypothesis. *Journal of Biogeography*, **40**, 1649-1663.
- 573 Fenderson, L.E., Kovach, A.I., Litvaitis, J.A., O'Brien, K.M., Boland, K.M. &  
574 Jakubas, W.J. (2014) A multiscale analysis of gene flow for the New England  
575 cottontail, an imperiled habitat specialist in a fragmented landscape. *Ecology and*  
576 *Evolution*, **4**, 1853-1875.
- 577 Gaston, K.J., Blackburn, T.M. & Gregory, R.D. (1999) Does variation in census area  
578 confound density comparisons? *Journal of Applied Ecology*, **36**, 191-204.
- 579 Gunton, R.M., Firbank, L.G., Inman, A. & Winter, D.M. (2016) How scalable is  
580 sustainable intensification? *Nature Plants*, **2**, 16065.
- 581 Harfoot, M., Newbold, T., Tittensor, D., Emmott, S., Hutton, J., Lyutsarev, V., Smith,  
582 M.J., Scharlemann, J.P. & Purves, D.W. (2014) Emergent global patterns of  
583 ecosystem structure and function from a mechanistic general ecosystem model.  
584 *PLoS Biology*, **12**, e1001841.
- 585 Henderson, I.G., Holland, J.M., Storkey, J., Lutman, P., Orson, J. & Simper, J. (2012)  
586 Effects of the proportion and spatial arrangement of un-cropped land on breeding  
587 bird abundance in arable rotations. *Journal of Applied Ecology*, **49**, 883-891.

- 
- 588 Henle, K., Kunin, W., Schweiger, O., Schmeller, D.S., Grobelnik, V., Matsinos, Y.,  
589 Pantis, J., Penev, L., Potts, S.G., Ring, I., Simila, J., Tzanopoulos, J., van den  
590 Hove, S., Baguette, M., Clobert, J., Excoffier, L., Framstad, E., Grodzinska-  
591 Jurczak, M., Lengyel, S., Marty, P., Moilanen, A., Porcher, E., Storch, D.,  
592 Steffan-Dewenter, I., Sykes, M.T., Zobel, M. & Settele, J. (2010) Securing the  
593 Conservation of Biodiversity across Administrative Levels and Spatial,  
594 Temporal, and Ecological Scales: Research needs and approaches of the  
595 SCALES project. *Gaia - Ecological Perspectives for Science and Society*, **19**,  
596 187-193.
- 597 Hodgson, J.A., Thomas, C.D., Cinderby, S., Cambridge, H., Evans, P. & Hill, J.K.  
598 (2011) Habitat re-creation strategies for promoting adaptation of species to  
599 climate change. *Conservation Letters*, **4**, 289-297.
- 600 Hopfenmüller, S., Steffan-Dewenter, I. & Holzschuh, A. (2014) Trait-specific  
601 responses of wild bee communities to landscape composition, configuration and  
602 local factors. *Plos One*, **9**.
- 603 Humphrey, J.W., Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peace, A.J.  
604 & Park, K.J. (2015) What can studies of woodland fragmentation and creation  
605 tell us about ecological networks? A literature review and synthesis. *Landscape*  
606 *Ecology*, **30**, 21-50.
- 607 Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in*  
608 *Ecology & Evolution*, **17**, 230-241.
- 609 Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J.,  
610 Haddow, R.W., Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P.,  
611 Sutherland, W.J., Tew, T.E., Varley, J. & Wynne, G.R. (2010) Making Space for  
612 Nature: a review of England's wildlife sites and ecological network. . pp. 107.  
613 DEFRA.
- 614 Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-  
615 1967.

- 
- 616 Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I. & Metzger, J.P. (2012)  
617 Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical  
618 Understory Bird Species Richness and Abundance. *Conservation Biology*, **26**,  
619 1100-1111.
- 620 Miller, R.I., Bratton, S.P. & White, P.S. (1987) A regional strategy for reserve design  
621 and placement based on an analysis of rare and endangered species distribution  
622 patterns. *Biological Conservation*, **39**, 255-268.
- 623 Moilanen, A. (2004) SPOMSIM: software for stochastic patch occupancy models of  
624 metapopulation dynamics. *Ecological Modelling*, **179**, 533-550.
- 625 Mokany, K., Harwood, T.D. & Ferrier, S. (2013) Comparing habitat configuration  
626 strategies for retaining biodiversity under climate change. *Journal of Applied  
627 Ecology*, **50**, 519-527.
- 628 Moulherat, S., Bestion, E., Baguette, M., Moulherat, M., Palmer, S.C.F., Travis,  
629 J.M.J. & Clobert, J. (submitted) MetaConnect, a new platform for population  
630 viability modeling to assist decision makers in conservation and urban planning.  
631 *Methods in Ecology and Evolution*.
- 632 Natural Capital Project, *InVEST*, <http://www.naturalcapitalproject.org/>, accessed 23  
633 Dec 2012.
- 634 Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan,  
635 K.M.A., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R.,  
636 Ricketts, T.H. & Shaw, M.R. (2009) Modeling multiple ecosystem services,  
637 biodiversity conservation, commodity production, and tradeoffs at landscape  
638 scales. *Frontiers in Ecology and the Environment*, **7**, 4-11.
- 639 Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach.  
640 *Conservation Biology*, **4**, 355-364.
- 641 Pardini, R., Bueno, A.D., Gardner, T.A., Prado, P.I. & Metzger, J.P. (2010) Beyond  
642 the fragmentation threshold hypothesis: Regime shifts in biodiversity across  
643 fragmented landscapes. *PloS one*, **5**.

- 
- 644 Pe'er, G., Henle, K., Dislich, C. & Frank, K. (2011) Breaking functional connectivity  
645 into components: a novel approach using an individual-based model, and first  
646 outcomes. *PloS one*, **6**, e22355.
- 647 Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C.,  
648 Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield,  
649 M.M., Morandin, L.A., Ochieng, A. & Viana, B.F. (2008) Landscape effects on  
650 crop pollination services: are there general patterns? *Ecology Letters*, **11**, 499-  
651 515.
- 652 Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J.,  
653 Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D.,  
654 Possingham, H.P., Ruckelshaus, M. & Warner, R.R. (2003) Ecological criteria  
655 for evaluating candidate sites for marine reserves. *Ecological Applications*, **13**,  
656 S199-S214.
- 657 Rösch, V., Tschardtke, T., Scherber, C. & Batáry, P. (2015) Biodiversity conservation  
658 across taxa and landscapes requires many small as well as single large habitat  
659 fragments. *Oecologia*, **179**, 209-222.
- 660 Schwartz, M.W. (1999) Choosing the appropriate scale of reserves for conservation.  
661 *Annual Review of Ecology and Systematics*, **30**, 83-108.
- 662 Smith, P.G.R. & Theberge, J.B. (1987) Evaluating natural areas using multiple  
663 criteria: theory and practice. *Environmental Management*, **11**, 447-460.
- 664 Soulé, M.E. & Simberloff, D. (1986) What do genetics and ecology tell us about the  
665 design of nature reserves? *Biological Conservation*, **35**, 19-40.
- 666 Sparkes, D.L., Jaggard, K.W., Ramsden, S.J. & Scott, R.K. (1998) The effect of field  
667 margins on the yield of sugar beet and cereal crops. *Annals of Applied Biology*,  
668 **132**, 129-142.
- 669 Sutherland, C., Elston, D.A. & Lambin, X. (2012) Multi-scale processes in  
670 metapopulations: Contributions of stage structure, rescue effect, and correlated  
671 extinctions. *Ecology*, **93**, 2465-2473.

- 
- 672 Synes, N.W., Watts, K., Palmer, S.C.F., Bocedi, G., Bartoń, K.A., Osborne, P.E. &  
673 Travis, J.M.J. (accepted) A multi-species modelling approach to examine the  
674 impact of alternative climate change adaptation strategies on range shifting  
675 ability in a fragmented landscape. *Ecological Informatics*.
- 676 Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Sharp, R., Nelson, E., Ennaanay,  
677 D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema,  
678 J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C.,  
679 Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J., Marsik, M. &  
680 Bernhardt, J. (2011) InVEST 2.4.3 User's Guide. Stanford.
- 681 Tallmon, D.A., Luikart, G. & Waples, R.S. (2004) The alluring simplicity and  
682 complex reality of genetic rescue. *Trends in Ecology & Evolution*, **19**, 489-496.
- 683 Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital  
684 element of landscape structure. *Oikos*, **68**, 571-573.
- 685 Tschamtkke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of  
686 small habitat fragments to conservation of insect communities of grassland-  
687 cropland landscapes. *Ecological Applications*, **12**, 354-363.
- 688 Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kazmierczak, A., Niemela, J. &  
689 James, P. (2007) Promoting ecosystem and human health in urban areas using  
690 Green Infrastructure: A literature review. *Landscape and Urban Planning*, **81**,  
691 167-178.
- 692 Wiggering, H. & Steinhardt, U. (2015) A conceptual model for site-specific  
693 agricultural land-use. *Ecological Modelling*, **295**, 42-46.
- 694 Wilson, K.A., Carwardine, J. & Possingham, H.P. (2009) Setting Conservation  
695 Priorities. *Year in Ecology and Conservation Biology 2009*, pp. 237-264.
- 696 With, K.A., Gardner, R.H. & Turner, M.G. (1997) Landscape connectivity and  
697 population distributions in heterogeneous environments. *Oikos*, **78**, 151-169.
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699 **Supporting Information**

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

701 **Appendix S1. Details of simulation modelling**

702 Table S1. Values used to parameterise the MetaConnect model for each functional  
703 type

704 Table S2. Correlations between heterozygosity slopes and final estimates.

705 Table S3. Values used to parameterise the SPOMSIM model for each functional type.

706 Table S4. Sampling distributions of the species-specific traits used to parameterise the  
707 community model, with data sets used for fitting.

708 Table S5. Comparison of settings and parameter values across all models.

709 Fig. S1. Tiling of patterns for local-scale bird simulations.

710 Fig. S2. Generic life cycle simulated in MetaConnect

711 **Appendix S2. Additional results and validation**

712 Table S6. Rank correlations for population size between 3 pairs of models

713 Tables S7–S11: Raw output data for Allelic richness, Heterozygosity, Metapopulation  
714 size, Species richness, Pollination services

715 Tables S12–S16: Standardised z-scores of output data for Allelic richness,  
716 Heterozygosity, Metapopulation size, Species richness, Pollination services

717 Figs. S3–S4. Results for each conservation criterion at local and regional scales

718 Fig. S4. Between-criteria trade-offs – mean standardised z-score values

719 Fig. S5. Population sizes from MetaConnect

720 Fig. S6. Biplots of principle components analyses from MetaConnect results

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721 **Tables**

722 Table 1. Basic attributes used for functional types in the simulation models. Carrying  
723 capacity and species richness vary inversely between the two scales such that  
724 population densities were doubled and species richness values halved at the 5 km  
725 (local) scale compared to the 50 km (regional) scale. Cells are left blank for scenarios  
726 that were not assessed.

727

<b>Functional type</b>	<b>Mean dispersal distance (m)</b>	<b>Carrying capacity at 5-km scale (inds /ha)</b>	<b>Carrying capacity at 50-km scale (inds /ha)</b>	<b>Community carrying capacity (inds /ha)</b>	<b>Species richness at 5-km scale</b>	<b>Species richness at 50-km scale</b>
Trees	50	400	-	1600	8	-
Butterflies	200	400	-	6400	16	-
Mammals	200	16	8	64	8	16
Birds	5000	1	0.5	16	16	32

728

729

---

730 **Figure legends**

731

732 Figure 1. Possible scenarios for the relationship between a pair of conservation  
733 criteria across the possibility space of landscape geometries: (A) positive association;  
734 (B) independence; (C) negative association. The stars indicate optimal geometries; in  
735 (C) there is an indefinite number of these and just three are shown.

736

737 Figure 2. The 25 landscape tiles used, grouped by percentage of area covered and  
738 annotated with number of patches and source (either simulated or extracted from  
739 observed patterns of British woodland at either 50 m or 500 m resolutions).

740 Landscapes are ordered first by decreasing habitat amount, then by increasing  
741 fragmentation, then by increasing edge:area ratio (Fahrig 2003).

742

743 Figure 3. Results for each functional scenario (for landscape codes see Fig. 2). Points  
744 show the scaled mean values ( $\pm 1$  standard error) at the 5-km scale (A-D) and the 50-  
745 km scale (E, F), for birds (D, F), butterflies (B), small mammals (C, E) and trees (A),  
746 as assessed according to five conservation criteria: allelic richness (red),  
747 heterozygosity (orange), metapopulation size (yellow), species richness (blue) and  
748 pollination service (green). Pollination service was assessed for a single functional  
749 type (wild pollinators) so is included in each of the plots. For each criterion, scores  
750 are expressed as a proportion of the maximum attained, and the shaded profile shows  
751 the unweighted mean over all five criteria.

752

753 Figure 4. Biplots of principle components analyses of conservation assessments of (A)  
754 local-scale landscapes and (B) regional-scale landscapes. For each scale a single

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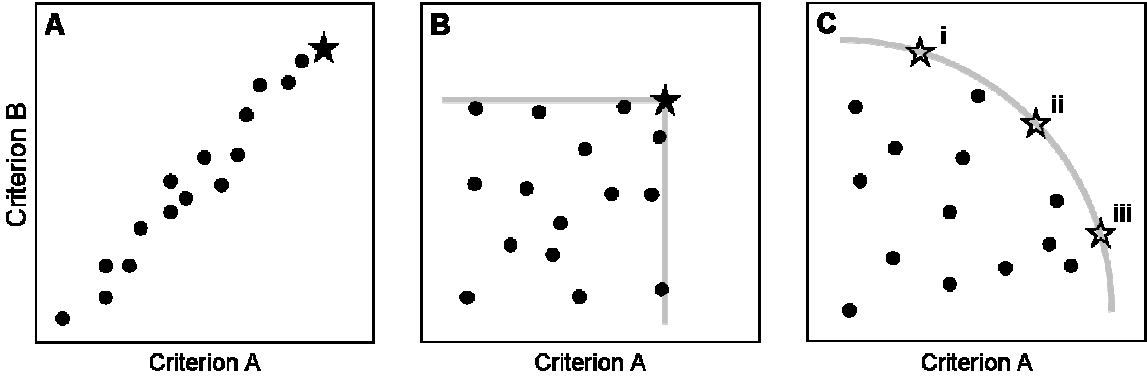
755 biplot was produced, and each plot here is a layer of that biplot for one of the  
756 functional types, showing how the assessments for that type (arrows) load onto the  
757 first two axes (PC1, PC2). The pollination services assessment (unrelated to these  
758 functional types) is shown by a red arrow in the plots for butterflies (in A) and birds  
759 (in B). The loadings of landscapes (identical in each plot) are indicated by the codes  
760 A–Y; the inset plots group landscapes by percentage cover (blue region = 2%; green  
761 region = 10%), with arrows showing the directions of increasing fragmentation. The  
762 axes for the regional-scale plots have been reversed to aid comparison.

763

764 Figure 5. Mean overall landscape conservation values (for landscape codes see Fig.  
765 2). Values are averages of all the mean scaled values for criteria and functional types,  
766 which are overlain as lines for allelic richness (red), heterozygosity (orange),  
767 population size (yellow), species richness (blue) and pollination service (green).  
768 Vertical bars indicate standard errors.

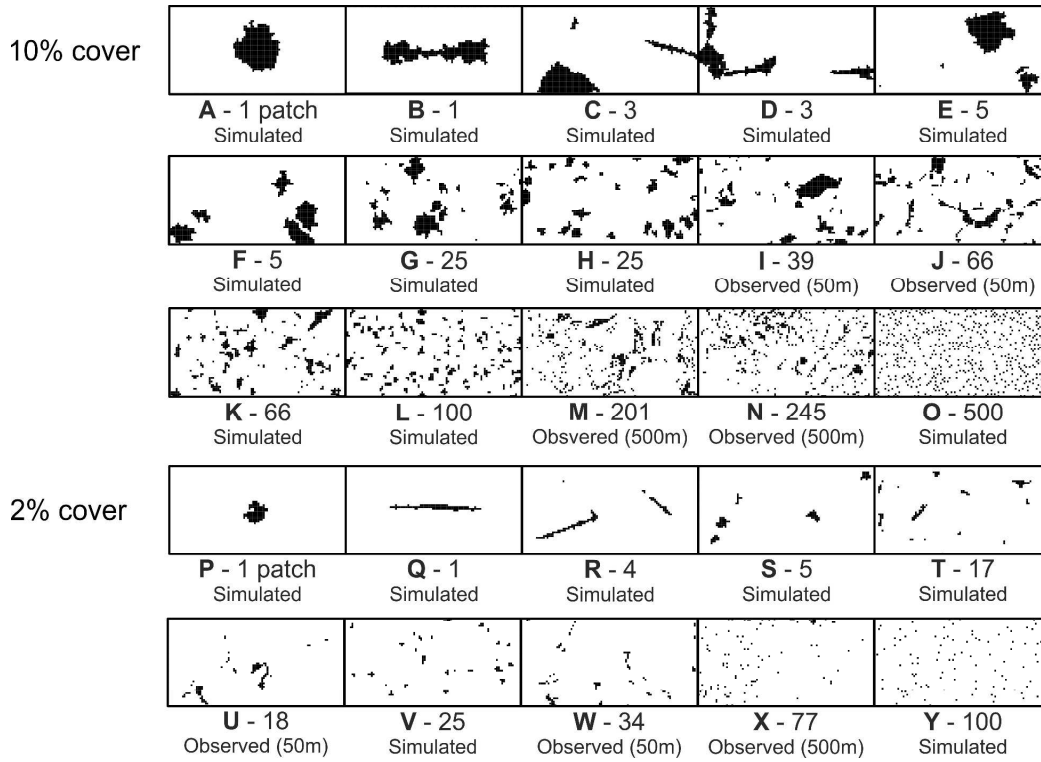
769

770 Fig. 1

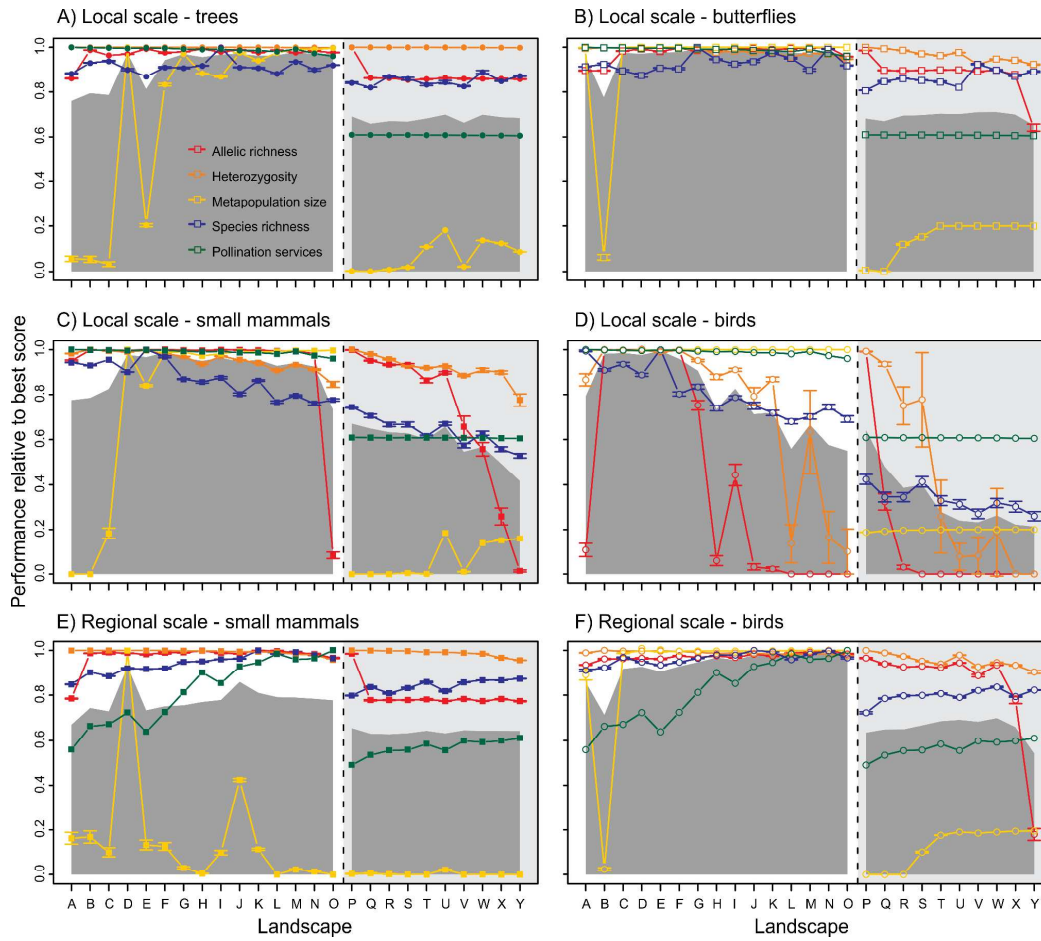


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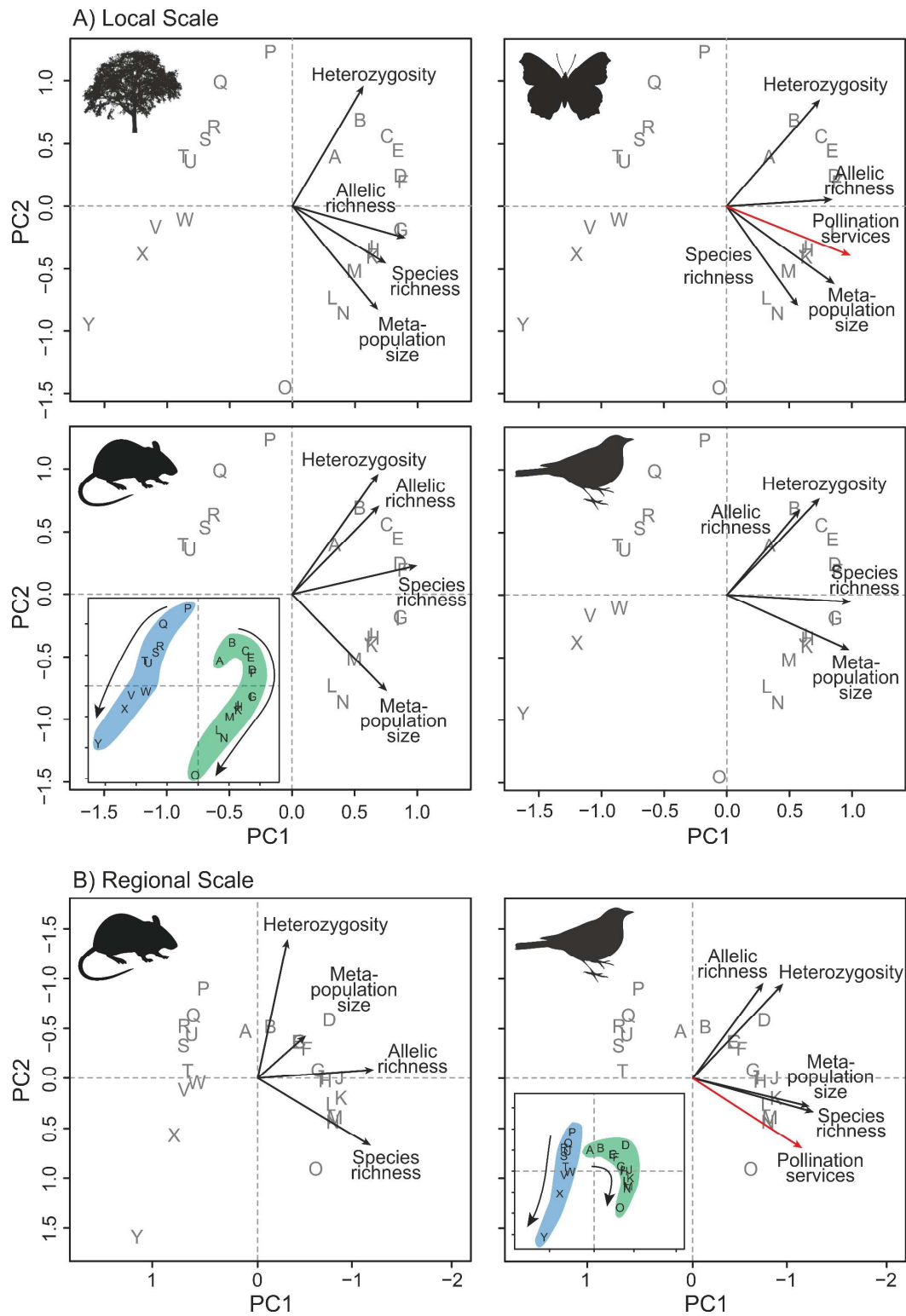
775 Fig. 3



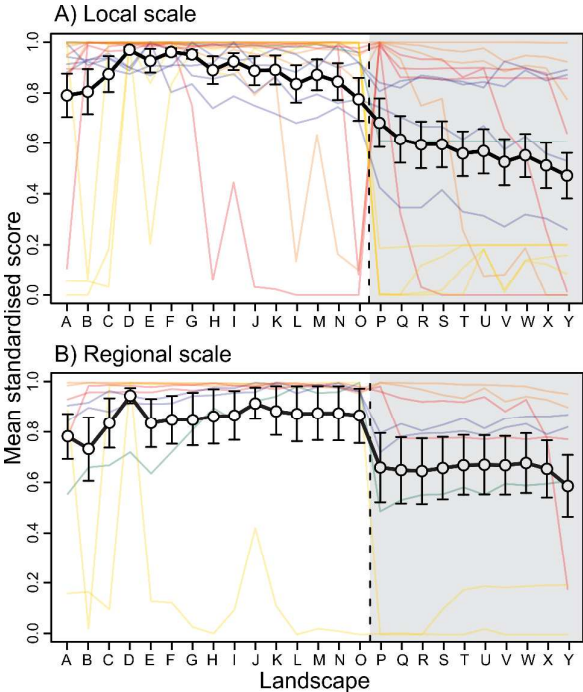
776

777

778



781 Fig. 5



782

783

## **Multi-criterion trade-offs and synergies for spatial conservation planning**

Richard M. Gunton, Charles J. Marsh, Sylvain Moulherat, Anne-Kathleen Malchow,  
Greta Bocedi, Reinhard A. Klenke, William E. Kunin

## **Appendix S1: Details of simulation modelling**

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## **1. Generation of landscape patterns**

### ***1.1 Observed landscape patterns***

Some of the landscape patterns were obtained from maps of overall woodland cover in Great Britain from the National Forest Inventory NFI; Forestry Commission (2010). Raster maps were generated at resolutions of 500 m and 50 m, covering the whole of Great Britain in the first case, and taking four regional samples for the finer resolution. At each resolution, quadrats of 50 × 100 cells were selected that had either 2% or 10% (±0.5%) coverage and for which patches spanned at least 75% of their length. From these we selected three quadrats at the coarser scale (one with 2% cover and two with 10%) and four at the finer scale (two with each level of cover).

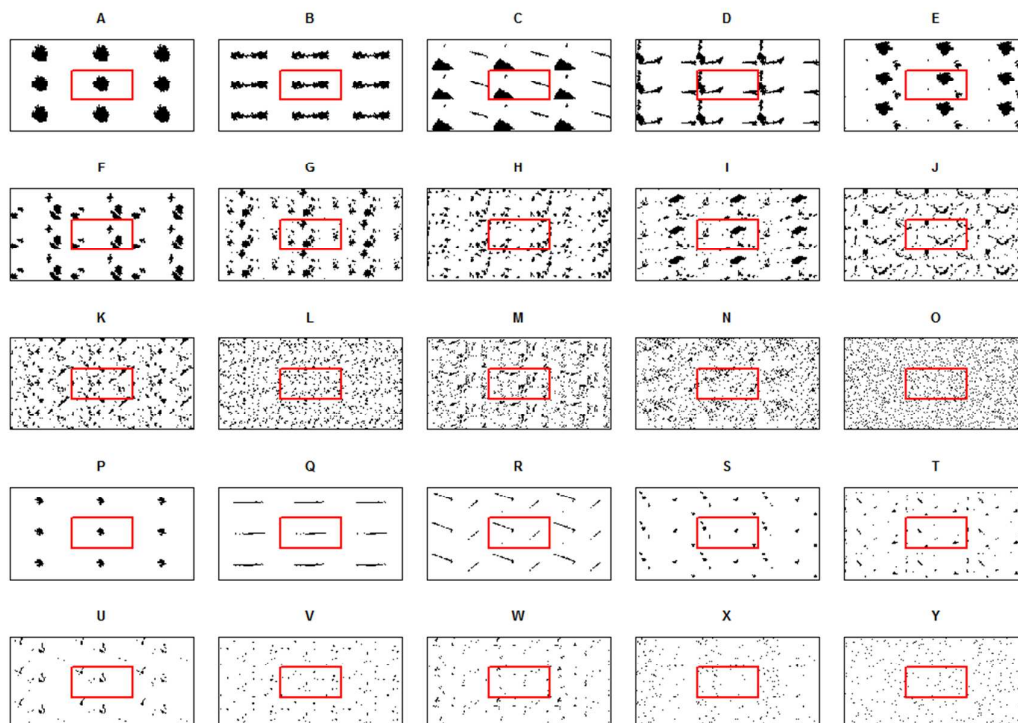
## 1.2 Simulated landscape patterns

We found that histograms of patch size distributions for both scales and for both coverage rates had a continuously-decreasing form which became approximately linear on log–log axes, suggesting power-law distributions with exponents between  $-0.8$  and  $-1.5$ . We therefore used an iterative algorithm to generate spatial patterns on the  $50 \times 100$ -cell arena with specified total area of either 2% or 10% and with patch-size distributions drawn from gamma distributions with shape parameters of either 0.01 (for a power-law distribution) or 2.5 (for a symmetrical distribution). We repeated the method as necessary to obtain patterns that met our criterion for a 75% span of the arena and where any merging of patches did not reduce the total number below 50% of the number seeded.

## 1.3 Partial tiling

The patterns were tiled by transposition to add a ‘border’ of 50 cells (2.5 km at the local scale and 25 km at the regional scale). For birds at the local scale a border of 100 cells (5 km) was used, because of their higher dispersal distances. Figure S1 illustrates these kinds of tiling.

A)



B)

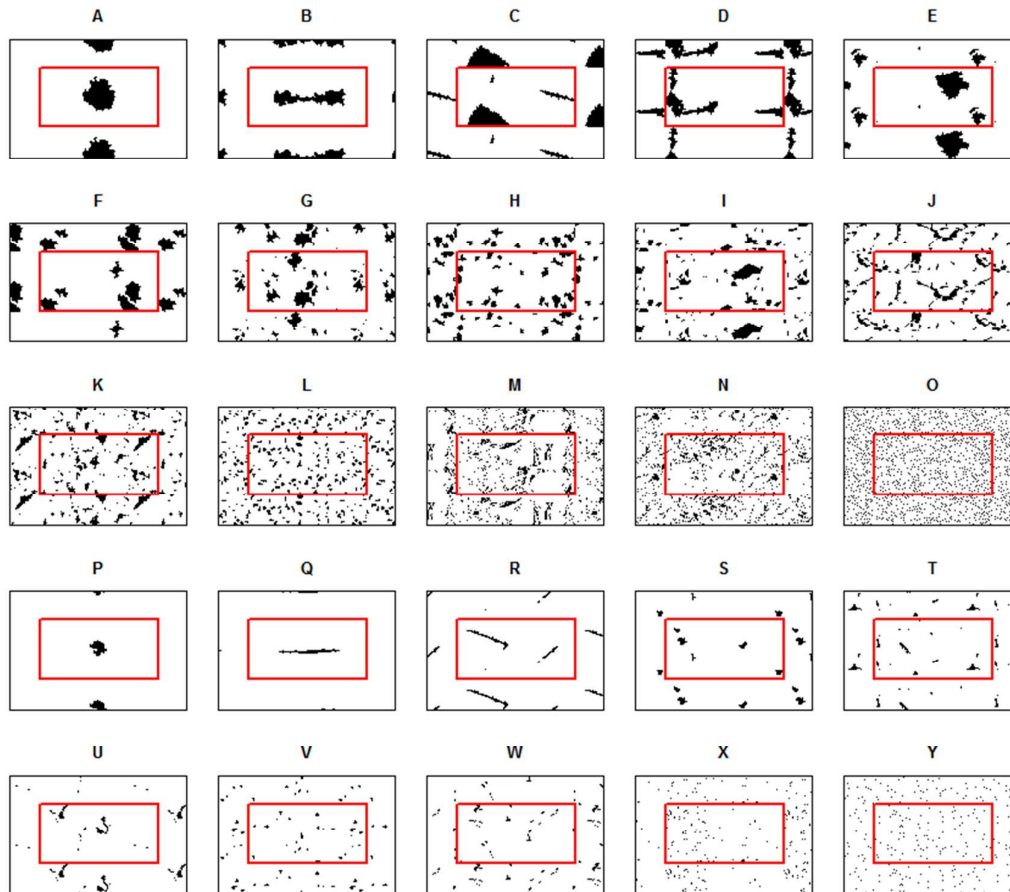


Figure S1. Tiling of patterns for (A) local-scale bird simulations and (B) all other simulations.

## 2. Functional scenarios: species and scales

Four combinations of dispersal distance, carrying capacity and species richness values were used, which for illustrative purposes are called “forest trees”, “grassland butterflies”, “small mammals” and “passerine birds”; they may be considered “ecological species profiles” (Vos et al. 2001). The dispersal distances were attributed with reference to a dispersal trait database (Götzenberger et al. 2011) by taking medians from appropriate subsets of taxa. Population densities tend to decrease (Gaston et al. 1999) while species richness increases (Arrhenius 1921) with sampling extent, so for each functional type we chose plausible species richness

values for an area of 1250 km<sup>2</sup> (our regional-scale tile area). For the two vertebrate groups we then specified population carrying capacities for this scale with reference to a population-density database (Tsianou et al. 2011), while for butterflies and trees we specified realistic community carrying capacities with reference to expert advice (Josef Settele, Jenny Hodgson, pers. comm.) and forest plot data (Center for Tropical Forest Science 2010) respectively. These four values were then multiplied or divided by the species richness values to obtain, respectively, corresponding community or population carrying capacities. Finally we obtained values for the local-scale tiles by keeping the community carrying capacities constant while allowing population capacities to vary inversely with species richness according to a power-law relation whereby the latter doubles for a 100-fold increase in area. This implies an exponent ( $z$ -value) of 0.15, which is broadly realistic at the scales in question for plants in the UK (Crawley and Harral 2001) and more generally for small organisms at high latitudes (Drakare et al. 2006). Although this is lower than values often quoted elsewhere, we might also expect inflated diversities at finer scales because of a ‘nature-reserve effect’ whereby (i) protected areas are often selected for their high diversity, with greater possibilities of selection for smaller areas, and (ii) smaller areas can be more rigorously protected and/or intensively managed for biodiversity.

It should be emphasised that the trait values we chose are intended to elicit contrasts among the functional and spatial scenarios examined. They are not intended to be accurate representations of any particular region or system. The population densities and dispersal distances are intended to reflect a “typical” species within the functional type considered. Since species rank–abundance curves normally decrease with an upward-concave shape, modelling species that are especially rare or common within the habitat in question might require an alternative set of parameters.

### 3. Simulation models

#### 3.1 MetaConnect

##### 3.1.1 Modelling

MetaConnect is an individual-based, process-based modelling platform (Moulherat et al., submitted), meaning that individuals behave independently. It is patch-based and reproduction is assumed to occur by random mating (panmixy) within each patch.

Within a patch, population dynamics follow a simple scheme (Fig. S2). The population is composed of reproductive (R) and non-reproductive (NR) individuals, with a 1:1 sex-ratio. At each time-step a proportion  $d$  of NR individuals disperses from the patch, and a fraction  $g$  of the NR individuals is transferred to the pool of R individuals depending on the total patch population size ( $N_T$ ):

$$g = \frac{1}{1 + k \cdot N_T}$$

The constant  $k$  in this equation relates to the intensity of competition. Reproduction then takes place by adding a multiple  $F \cdot s_0$  of the number of R individuals to the population of NR individuals.  $F$  represents fecundity and was adjusted so as to obtain an asymptotic population growth rate around 1.1 (see Table S1 for values). The factor  $s_0$  represents the survival of juvenile (yearling) individuals, while NR and R individuals survive to the next time-step with respective probabilities of  $s_1$  and  $s_2$ .

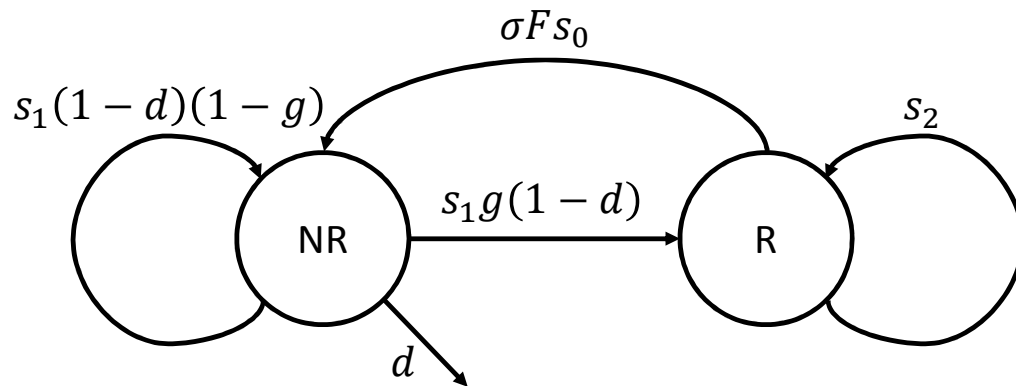


Figure S2. Generic life cycle simulated in MetaConnect, indicating how the parameters defined in the text relate to the pools of reproductive (R) and non-reproductive (NR) individuals in a single patch. Immigration from other patches is not shown since it depends upon the emergent behaviour of the whole system.

Dispersal occurs by random walk. To obtain the required mean dispersal distance, the maximum number of steps moved at each dispersal event was made equal to the square of the specified mean dispersal distance measured in step-lengths (and this was verified empirically). Individuals stop as soon as they reach a new habitat patch; those that do not reach a new habitat patch during the random walk are considered dead.

Table S1. Values used to parameterise the MetaConnect model for each functional type. Values were harvested from the literature (Habel *et al.* 2007, Legendre *et al.* 1999, Stevens *et al.* 2012, Stevens *et al.* 2013)

Functional type	Fecundity ( $F$ )	Mortality of juveniles ( $s_0$ )	Mortality of non-reproductives ( $s_1$ )	Mortality of reproductives ( $s_2$ )	Dispersal rate ( $d$ )	Competition coefficient ( $k$ )*
Trees	1000	0.9985	0.80	0.03	0.2	0.05
Butterflies	250	0.938	0.85	1	0.3	0.0028
Mammals	6	0.7	0.50	0.3	0.1	0.325
Birds	4.5	0	0.65	0.6	0.3	2.385

\*These values are for the regional-scale scenarios. For the landscape-scale, mammals were attributed a  $k$  value of 0.0065 and birds 0.0477.

### 3.1.2 Measuring heterozygosity

All habitat patches were initially occupied at the population carrying capacity and individuals dispersed by random walk, with path lengths drawn from a negative exponential distribution with mean specified according to the functional scenario (Table 1). 10 loci were simulated, each starting with 10 alleles in the population. Simulations were run for 100 time steps (sufficient for a stable equilibrium) and averages were taken over 10 replicates for each landscape, functional type and scale combination.

As heterozygosity is undefined in cases where populations went extinct, we calculated heterozygosity as the rate of decline. We first checked that the slope of heterozygosity was a good indicator of final heterozygosity. For each functional type and for all scenarios for which populations remained viable, we estimated the slope of square-

root-transformed heterozygosity against time for five time periods after an initial period for the model to settle: from time steps 6 to 10, time steps 6 to 20, time steps 6 to 30, time steps 6 to 40 and time steps 6 to 50. Calculating slopes from time steps 6 to 50 had the highest average correlations with final heterozygosity for four of the scenarios (Table S2). In two landscapes with 2% cover for birds, populations went extinct before time-step 10, such that slope estimates would be unreliable; here a slope of -0.1 was attributed (equivalent to a reduction in heterozygosity from 1 to 0 in 10 time-steps).

In landscapes where heterozygosity could be calculated at time step 100, slopes were also highly correlated with this final heterozygosity (data not shown).

Table S2. Correlations between final estimate of heterozygosity at time-step 100 (where available) and slope of square-root transformed heterozygosity for time-steps 6 to 10, 20, 30, 40 and 50. For each functional type, the greatest correlation is indicated in bold.

Functional type	Scale	6–10	6–20	6–30	6–40	6–50
Trees	50 km	-0.464	-0.838	-0.934	-0.984	<b>-0.990</b>
Butterflies	50 km	-0.921	-0.958	-0.982	<b>-0.992</b>	-0.989
Mammals	50 km	-0.868	-0.900	-0.947	-0.973	<b>-0.983</b>
Birds	50 km	-0.161	<b>-0.958</b>	-0.865	-0.816	-0.927
Trees	500 km	-0.940	-0.996	-0.998	<b>-0.999</b>	<b>-0.999</b>
Birds	500 km	-0.821	-0.949	-0.968	-0.979	<b>-0.983</b>
	<b>Mean</b>	-0.696	-0.933	-0.949	-0.957	<b>-0.979</b>

For two of the 2% landscapes for birds at the 5-km scale populations went extinct in under 10 time steps, and so estimating slope was inaccurate or impossible. These two cases were assigned heterozygosity slopes of -0.1, equivalent to extinction within 10 time steps.

## **3.2 SPOMSIM**

SPOMSIM (Moilanen 2004) is a patch-based simulator for the stochastic patch-occupancy model of Hanski (1994). It considers a single species in a set of habitat patches, each of which can be either occupied or empty at each time-step. The simulation is shaped by two basic processes: extinction and colonisation, which are determined by functions parameterised for each of our functional types.

### **3.2.1 Preparation of landscape files**

SPOMSIM is spatially implicit. To encode the information from the landscape maps, we calculated the area of each patch and its shortest edge-to-edge distances from all other patches.

### **3.2.2 Extinction rate**

The probability  $E_i$  that an occupied patch  $i$  becomes unoccupied (excluding the effect of immigration) at a given time step is a function of its area  $A_i$ :

$$E_i = 1 - \exp(-uA_i^{-b}) \quad (1)$$

where  $b$  is set to 0.5. The parameter  $u$  is species-specific; we determined it by specifying that, for any species, a patch holding one individual has an extinction risk per generation of 0.99, a patch holding 40 has a risk of 0.1 and a patch holding 400 has a risk of 0.01. The latter two values came from combining results of two observational (Pimm et al. 1988, Woodroffe and Ginsberg 1998) and three simulation studies (Grimm and Storch 2000, Reed et al. 2003, Reed 2004). These three points were used to calculate  $u$  by interpolation in a rearranged version of equation (1):

$$u = -\ln(1 - E_i) / A_i^{-b}$$

in which  $A_i$  values for 1, 40 and 400 individuals were determined from the carrying capacity of each functional type.

### **3.2.3 Colonisation rate**

Colonisation rates are modelled with three functions. First, the dispersal rate  $D$  is specified by a dispersal kernel. We chose the exponential kernel implemented as

$$D(d_{ij}, \alpha) = \exp(-\alpha d_{ij}) \quad (2)$$

This is dependent on the distance  $d_{ij}$  between patches  $i$  and  $j$ , as well as on the parameter  $\alpha$ , which is defined as the reciprocal of the average dispersal distance, so can be calculated from Table 1 (main article). To account for the shape of the habitat patches, and assuming that individuals can move freely within each patch, we used patch edge-to-edge distances for  $d_{ij}$ .

Next, the overall connectivity  $S_i$  of patch  $i$  at time  $t$  is conceived as an effective source area from which that patch can be colonised: i.e. a function of the areas of all other patches that are occupied at that time, weighted by their dispersal rates:

$$S_i(t) = \sum_{j \neq i} O_j(t) D_{ij} A_j^b \quad (3)$$

where  $b = 0.5$  as before and  $O_j(t)$  indicates the occupancy status of patch  $j$  at time  $t$ :

$$O_j(t) = \begin{cases} 1 & \text{if patch } j \text{ is occupied} \\ 0 & \text{if patch } j \text{ is empty} \end{cases}$$

Finally, the colonisation probability  $C_i$  of an empty habitat patch  $i$  at time  $t$  is calculated from its connectivity  $S_i$  with an Allee effect (Hanski 1994):

$$C_i(t) = \frac{S_i^2(t)}{S_i^2(t) + y^2} \quad (4)$$

The parameter  $y$  determines the colonisation ability of the functional type at low connectivity values. We determined it by assuming that the colonisation probability when a given number of individuals arrives at an unoccupied patch is simply one minus the extinction probability when the same number of individuals remains:

$$C_i(n) = 1 - E_i(n)$$

where  $\rho_{pop}$  is the carrying capacity for a given functional type (Table 1).

Table S3. Values used to parameterise the SPOMSIM model for each functional type.

	<b>Extinction coefficient</b>	<b>1/dispersal distance</b>	<b>Colonisation ability</b>
<b>Functional type</b>	$u$	$\alpha$ (km <sup>-1</sup> )	$y$
Trees	0.025	20	0.00132

Butterflies	0.025	5	0.00132
Mammals	0.126	5	0.03292
Birds	0.503	0.2	0.52667

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### ***3.2.4 Simulations***

For every scenario (combination of landscape and functional type), 100 replicates were simulated with identical random initial conditions over 300 time steps. At each time step we obtained a list of the occupied patches, from which could be calculated the proportion of total area occupied. This was averaged over time steps 51-300 and then over the 100 replicates for each scenario.

## ***3.3 Community model***

Details of the community model are given by Bocedi (2010) and its application is further explained in Bocedi et al. (2011).

### ***3.3.1 Creation of environmental gradients and heterogeneity***

The maps of reserve networks were overlaid with environmental values that then define the niche space occupied by each species. The range and structure of environmental values were calibrated with reference to topographic maps of five regions of Europe, as used by a microclimate model (Gunton et al. 2015) showing how topography affects surface soil temperature. This model allowed a partitioning of the total variation in predicted soil temperature at each of our spatial scales into estimates for a latitudinal variation component and a topographic component. Total variation was found roughly to double from the local to the regional scale, with a constant autocorrelation (Moran's  $I = 0.93$ ). Meanwhile the relative contribution of the latitudinal gradient increased from around 5% to 25% of total variation. For the simulated maps we therefore set the environmental variation to range from 0 to 25 and from 0 to 50 for the local and regional scales respectively, with linear trends of 1 and 10 running along the long axes of the local-scale and regional-scale arenas

respectively. Heterogeneity was then simulated for our niche maps using a diamond-square algorithm (Richard German, unpublished R code) to create the specified range of values and level of spatial autocorrelation (Moran's *I* of 0.912 to 0.923: mean of 100 runs).

### ***3.3.2 Specifying niches***

On the niche maps, the model then causes individuals' resource acquisition rates to decay according to a Gaussian kernel with increasing distance from their niche optimum (note that this niche parameter is taken to be orthogonal to the definition of habitat patches; it may represent, for example, a soil moisture or temperature gradient). We drew niche optima and widths from the same uniform distributions for all taxonomic and scale scenarios, on the assumption of fractal heterogeneity in habitat quality. (It should be remembered that our increased species richness at coarser scales may be attributed in part to fine-scale heterogeneity of the habitat with respect to unmodelled niche axes.) In order to achieve approximately our specified initial numbers of species throughout the landscapes, we (i) allowed niche optima to fall outside the range of values actually found in the landscape, within a buffer of 90% of the total range, and (ii) specified a minimum niche width of 10 units. This pair of constraints minimised both the inflation of species richness towards the middle of the arena, and the proportion of species that would fail to establish anywhere at all within the arena. The niches were thus characterised by optima and widths as shown in Table S5, randomly allocated to an initial number of species as specified in Table 1.

### ***3.3.3 Parameterisation***

The model requires reproductive rate, carrying capacity and mean dispersal distance for each species. These were drawn from distributions fit to data from a range of sources (Table S4). The "fitdistr" function in the library "MASS" (Venables and Ripley 2002) for R (R Development Core Team 2014) allowed comparison of gamma, Weibull, normal, logistic, lognormal, exponential and Cauchy distributions, for selection of that with the lowest AIC value. The overall community carrying capacity was specified as in Table 1, causing species-specific carrying capacities to be scaled with respect to this value. Dispersal mortality was set between 0 and 0.2, taken from a uniform distribution, emigration probability at 0.5, and lottery competition for

resources and establishment space was characterised by random pairwise species interaction coefficients drawn from a triangular distribution.

Table S4. Sampling distributions of the species-specific traits used to parameterise the community model, with data sets used for fitting. For each functional type, distributions were fitted for mean dispersal distance, population density and potential reproductive rate. The final column shows sample median values obtained from the distributions. Note that the model only requires relative population densities, so values drawn from the distributions were always scaled with respect to the community density values shown in Table 1 (main article).

Functional type	Trait	Unit	Species in data	Details of data set	Selected distribution	Parameter 1 (location)	Parameter 2 (dispersion)	Data source	Median value
Trees	Dispersal	m	15	European trees	Normal	51.786	24.251	Götzenberger et al. (2011)	52
	Density	indiv/ha	34	5 European forest transects	Lognormal	4.082	1.304	Phillips (2002)	59
	Reproduction	fecundity	20	European trees, based on $344 \times \text{seed weight}(\text{mg})^{-0.56}$	Negative exponential	0.000496		Seed weights from Götzenberger et al (2011); formula from Greene and Johnson (1994)	1399
Butterflies	Dispersal	m	23	European butterflies	Lognormal	4.839	0.689	Tsianou et al. (2011)	126
	Density	indiv/ha	34	European butterflies	Weibull	0.147	1320.483	Jochen Krauß (unpublished data)	2.3
	Reproduction	fecundity	52	European butterflies	Lognormal	5.514	0.742	Garcia-Barros (2000)	248
Mammals	Dispersal	m		Used same distribution as for butterflies	Lognormal	4.839	0.689		126
	Density	indiv/ha	28	All European Erinaceomorpha, Rodentia and Soricomorpha < 300g	Weibull	0.668	33.480	PanTHERIA (Jones et al. 2009)	19

	Reproduction	litter size	70	All European Erinaceomorpha, Rodentia and Soricomorpha < 300g	Gamma	10.381	2.147	PanTHERIA (Jones et al. 2009)	4.7
Birds	Dispersal	m	16	European passerines and near-passerines; 2 American near-passerines	Lognormal	8.855	1.357	Tsianou et al. (2011)	7013
	Density	indiv/ha	20	European passerines and near-passerines	Negative exponential	0.173		Tsianou et al. (2011)	4.0
	Reproduction	clutch size	233	European passerines	Logistic	4.387	0.611	Jetz et al. (2008)	4.4

### 3.4 InVEST

InVEST is a deterministic simulator of spatial patterns across a landscape for assessing the delivery of ecosystem services. Its pollination module assigns an abundance of pollinators to every cell in the landscape and thence a rate of pollination to each crop cell. We took a single characteristic pollinator foraging range (distance-decay constant) of 1800 m, such that the rate of pollinator movements between cells  $d$  metres apart declines as  $\exp(-d/1800)$ . This was based on the visitation decay rate of 0.00053 reported for insect pollinators, excluding the honeybee *Apis mellifera*, in temperate crops from a recent meta-analysis (Ricketts et al. 2008).

The model was used to convert our landscapes to maps of relative pollinator activity density and thence maps of pollination service density ( $0 \leq p < 1$ ) for the cropped part of each landscape (the matrix). These maps were then converted into maps of relative pollination service by assuming a hyperbolic function for crop yield:

$$Y = 1 - y_0 + y_0(p/(p+k))$$

where  $y_0$  is proportional yield loss when no pollinators are provided by the habitat, and  $k$  is a scaling constant, the pollination rate required to achieve 50% yield (Tallis et al. 2011). We set  $k$  at 0.125 (Tallis et al. 2011), and  $y_0$  at 0.8, representing a crop that achieves a 20% pollination rate by ubiquitous pollinators such as the honeybee *Apis mellifera* (Free 1993, Holzschuh et al. 2012, Garibaldi et al. 2013).

Results output by the model were then processed as described in the main text to obtain a mean fruit-set value and a total crop yield value for each landscape.

A comparative summary of the settings and parameter values used in all four models is given in Table S5 below.

Table S5. Comparison of settings and parameter values across all models. The code “~Table S4” means that values were randomly allocated to multiple simulated species according to the distribution specified in Table S4. For stochastic processes, ~B means the result of a single binomial (Bernoulli) trial with specified probability, ~P means a

random integer from a Poisson distribution with specified mean and  $\sim U$  means a random value from a uniform distribution with specified minimum and maximum.

	MetaConnect	SPOM-SIM	Community	InVEST
Number of runs per scenario	10	100	100	1
Time-steps per run	100	300	50	n/a
Individual-based?	yes	no	yes	no
Stochastic?	yes	yes	yes	no
Carrying capacity = Initial density	Table 1	Table 1	Table 1 ~Table S4	Table 1
Dispersal function	Random walk	Exponential	Exponential	Exponential
Mean dispersal distance	Table 1	Table 1	Table 1 ~Table S4	Table 1
Emigration rate/Patch colonisation ability	$\sim B(\text{Table S1})$	Table S3	$\sim B(0.5)$	n/a
Dispersal mortality (besides failure to reach any patch)	0	n/a	0	n/a
Mortality of juveniles	$\sim B(\text{Table S1})$	n/a	n/a	n/a
Mortality of non-reproductives	$\sim B(\text{Table S1})$	n/a	n/a	n/a
Mortality of adults /Patch extinction rate	$\sim B(\text{Table S1})$	Table S3	n/a	n/a
Reproduction rate (offspring per adult)	Table S1	n/a	$\sim P(\text{Table S4} \sim \text{Table S4})$	n/a
Reproductive allocation*(=1 - Establishment allocation)	n/a	n/a	$\sim U(0.5,0.9)$	n/a
Intra-specific interaction affecting reproduction	n/a	n/a	1 = compensatory density-dependence	n/a
Inter-specific interaction affecting reproduction	n/a	n/a	$\sim U(-1,1)$ = under-compensatory**	n/a
Intra-specific interaction affecting establishment	compensatory density-dependence	n/a	1 = compensatory density-dependence	n/a
Inter-specific interaction affecting establishment	n/a	n/a	$\sim U(-1,1)$ = under-compensatory**	n/a

Number of genetic loci	10	n/a	n/a	n/a
Initial number of alleles per locus	10	n/a	n/a	n/a
Mutation rate	0.00001	n/a	n/a	n/a
Number of species per run	1	1	Table 1	1
Niche optimum***:	n/a	n/a		n/a
- local scale			~U(-22.5,47.5)	
- regional scale			~U(-45,95)	
Niche breadth (standard deviation)	n/a	n/a	~U(10,100)	n/a

\* The Reproductive and Establishment allocation values are used, in the Community model, to weight the respective inter-specific interactions.

\*\* ranging from symmetric depensation (facilitation) to symmetric compensation (competition)

\*\*\* Niche values are given in units on the environmental scale; where values from 0 to 25 (0 to 50 for regional scale) were present in the landscapes.

## 4. Literature cited

- Arrhenius, O. 1921. Species and area. *Journal of Ecology* **9**:95-99.
- Bocedi, G. 2010. A general framework for modelling metacommunity dynamics under environmental changes. University of Aberdeen, Aberdeen.
- Bocedi, G., R. M. Gunton, and W. E. Kunin. 2011. Comparative analysis of putative drivers and parameterization of disturbance scaling simulation model School of Biology, University of Leeds.
- Center for Tropical Forest Science. 2010. Plots Summary. Smithsonian Tropical Research Institute,, Panamá. <http://www.ctfs.si.edu/plots/summary/>.
- Crawley, M. J. and J. E. Hurrell. 2001. Scale dependence in plant biodiversity. *Science* **291**:864-868.
- Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters* **9**:215-227.
- Forestry Commission. 2010. National Forest Inventory Shapefiles. Forestry Commission. <http://www.forestry.gov.uk/website/forestry.nsf/byunique/INFD-8EYJWF>.
- Free, J. B. 1993. *Insect Pollination of Crops*. 2nd edition. Academic Press, London.
- Garcia-Barros, E. 2000. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biological Journal of the Linnean Society* **70**:251-284.
- Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N. P. Chacoff, J. H.

- Dudenhöffer, B. M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipólito, A. Holzschuh, B. Howlett, R. Isaacs, S. K. Javorek, C. M. Kennedy, K. Krewenka, S. Krishnan, Y. Mandelik, M. M. Mayfield, I. Motzke, T. Munyuli, B. A. Nault, M. Otieno, J. Petersen, G. Pisanty, S. G. Potts, R. Rader, T. H. Ricketts, M. Rundlöf, C. L. Seymour, C. Schüepp, H. Szentgyörgyi, H. Taki, T. Tschardtke, C. H. Vergara, B. F. Viana, T. C. Wanger, C. Westphal, N. Williams, and A. M. Klein. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*.
- Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1999. Does variation in census area confound density comparisons? *Journal of Applied Ecology* **36**:191-204.
- Götzenberger, L., M. Zobel, R. Tamme, M. Pärtel, R. Lange, G. Pe'er, A. Trochet, V. Stevens, and D. S. Schmeller. 2011. Review manuscript on dispersal traits and distances, including the underlying trait database (preliminary version).
- Greene, D. F. and E. A. Johnson. 1994. Estimating the mean annual seed production of trees. *Ecology* **75**:642-647.
- Grimm, V. and I. Storch. 2000. Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. *Wildlife Biology* **6**:219-225.
- Gunton, R. M., C. Polce, and W. E. Kunin. 2015. Predicting ground temperatures across European landscapes. *Methods in Ecology and Evolution* **6**:532-542.
- Habel, J. C., T. Schmitt, W. Hardtle, M. Lutkepohl, and T. Assmann. 2007. Dynamics in a butterfly-plant-ant system: influence of habitat characteristics on turnover rates of the endangered lycaenid *Maculineaalcon*. *Ecological Entomology* **32**:536-543.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151-162.
- Holzschuh, A., J.-H. Dudenhoeffer, and T. Tschardtke. 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation* **153**:101-107.
- Jetz, W., C. H. Sekercioglu, and K. Boehning-Gaese. 2008. The Worldwide Variation in Avian Clutch Size across Species and Space. *Plos Biology* **6**:2650-2657.
- Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, G. M. Mace, A. Purvis, and W. K. Michener. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**:2648-2648.
- Legendre, S., J. Clobert, A. P. Moller, and G. Sorci. 1999. Demographic Stochasticity and Social Mating System in the Process of Extinction of Small Populations: The Case of Passerines Introduced to New Zealand. *The American Naturalist* **153**:449-463.
- Moilanen, A. 2004. SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. *Ecological Modelling* **179**:533-550.
- Phillips, O. 2002. Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set. Missouri Botanical Garden Press.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* **132**:757-785.
- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.  
<http://www.R-project.org>.

- Reed, D. H. 2004. Extinction risk in fragmented habitats. *Animal Conservation* **7**:181-191.
- Reed, D. H., J. J. O'Grady, B. W. Brook, J. D. Ballou, and R. Frankham. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* **113**:23-34.
- Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, L. A. Morandin, A. Ochieng, and B. F. Viana. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* **11**:499-515.
- Stevens, V. M., A. Trochet, H. Van Dyck, J. Clobert, and M. Baguette. 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecology letters* **15**:74-86.
- Stevens, V. M., A. Trochet, S. Blanchet, S. Moulherat, J. Clobert, and M. Baguette. 2013. Dispersal syndromes and the use of life-histories to predict dispersal. *Evolutionary Applications* **6**:630-642.
- Tallis, H. T., T. Ricketts, A. D. Guerry, S. A. Wood, R. Sharp, E. Nelson, D. Ennaanay, S. Wolny, N. Olwero, K. Vigerstol, D. Pennington, G. Mendoza, J. Aukema, J. Foster, J. Forrest, D. Cameron, K. Arkema, E. Lonsdorf, C. Kennedy, G. Verutes, C. K. Kim, G. Guannel, M. Papenfus, J. Toft, M. Marsik, and J. Bernhardt. 2011. InVEST 2.4.3 User's Guide. Stanford.  
<http://www.naturalcapitalproject.org/>.
- Tsianou, M., K. Franz, G. Pe'er, and Y. G. Matsinos. 2011. Report on area requirements of viable populations.
- Venables, W. N. and B. D. Ripley. 2002. *Modern Applied Statistics with S*. 4th edition. Springer, New York.
- Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Toward ecologically scaled landscape indices. *American Naturalist* **157**:24-41.
- Woodroffe, R. and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**:2126-2128.

# Multi-criterion trade-offs and synergies for spatial conservation planning

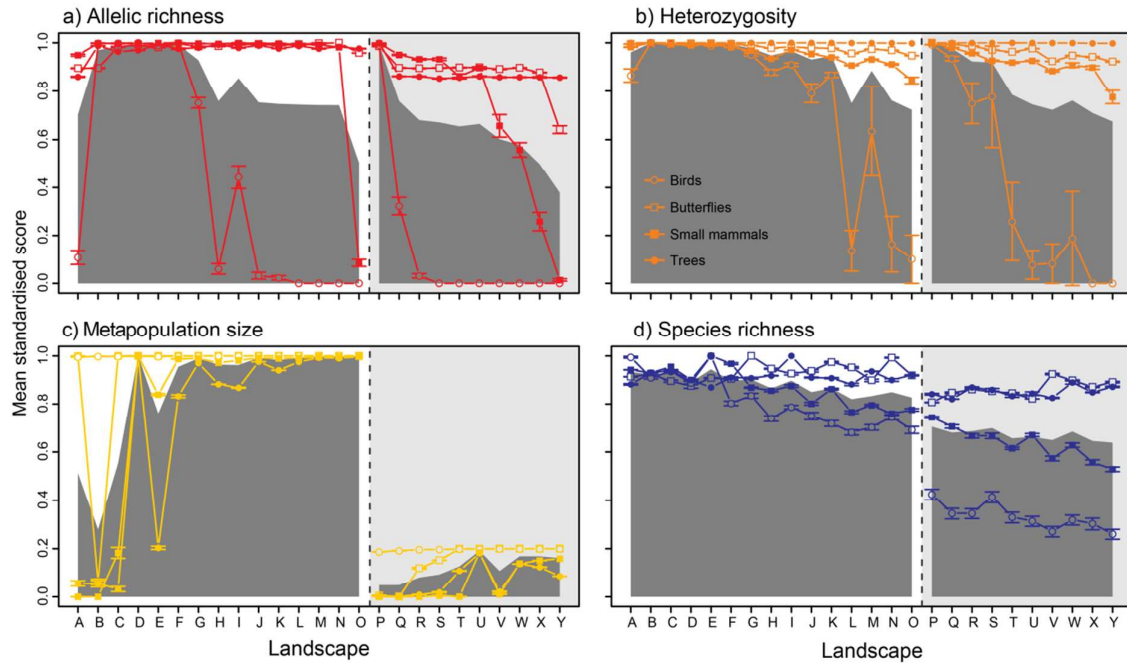
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## Appendix S2: Additional results and validation

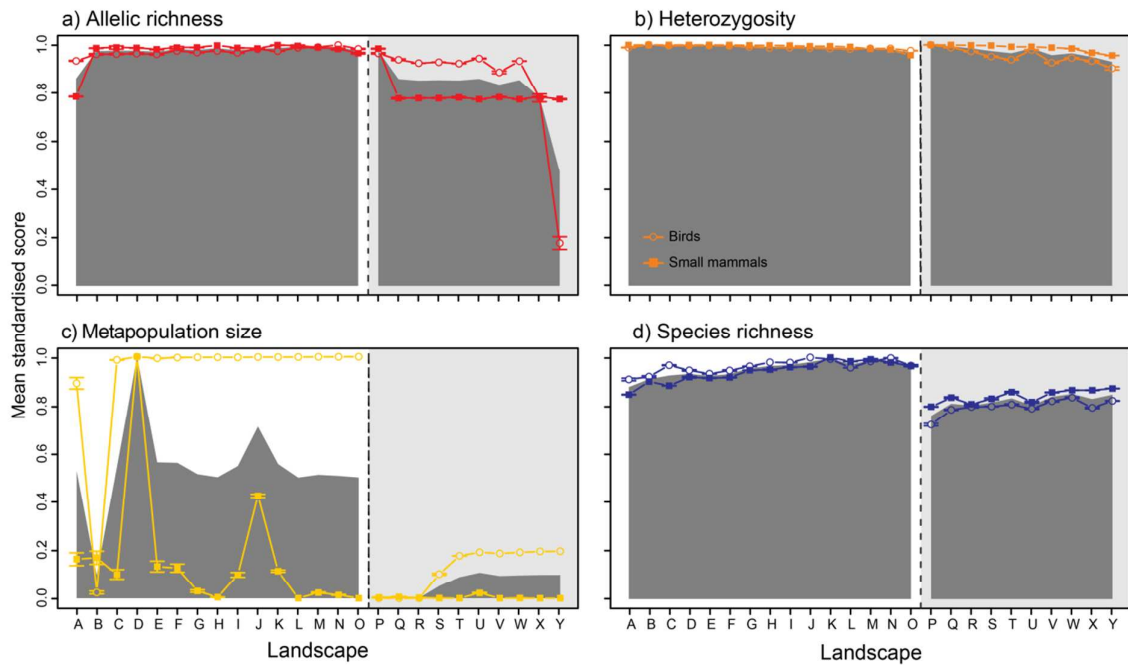
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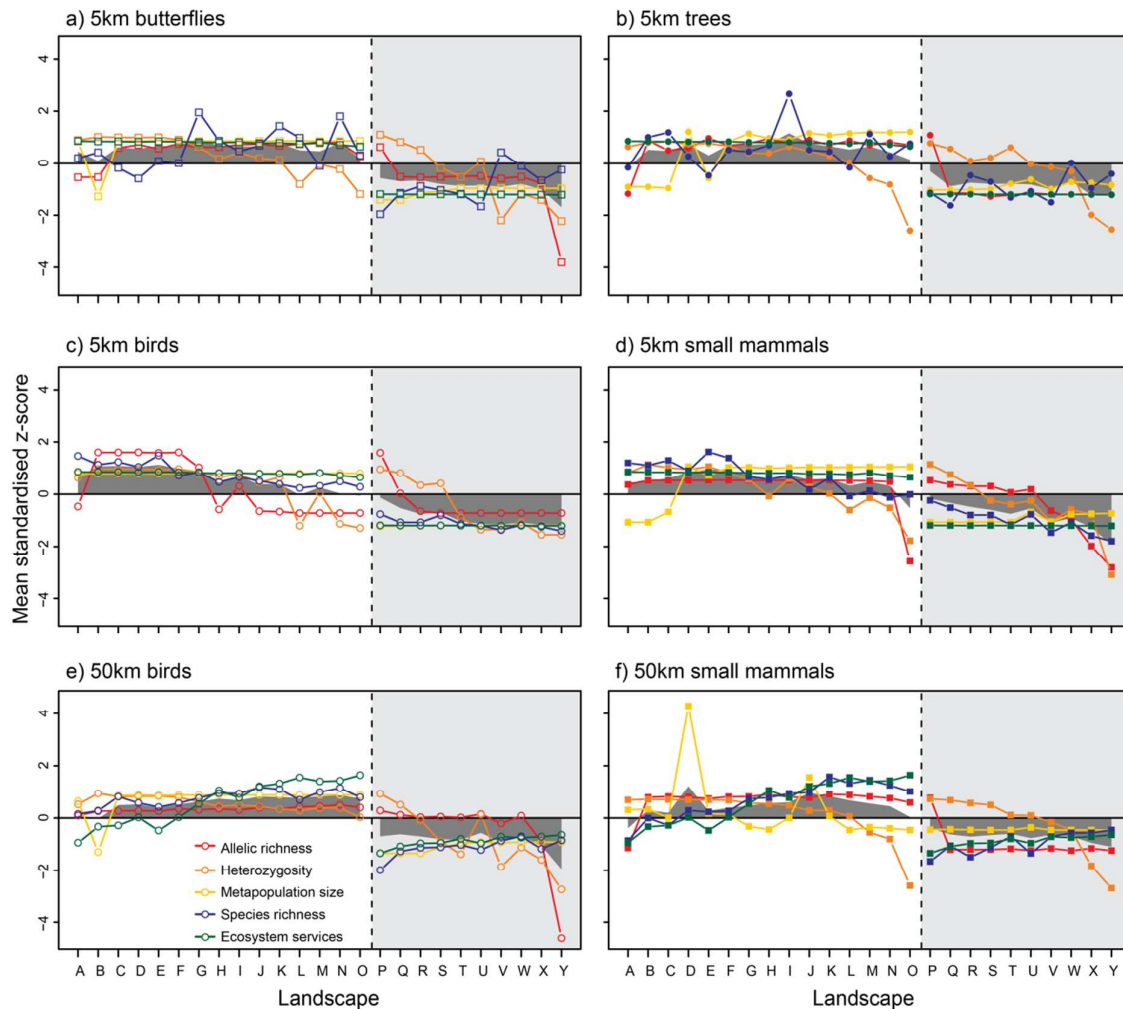
## 1. Additional results



**Figure S3.** Results for each conservation criterion at the 5-km scale. Points are the scaled mean values ( $\pm 1$  standard error) for the 25 landscapes (see Fig. 2 in main article for codes) from multiple runs of simulation models for four conservation criteria: (a) allelic richness (red), (b) heterozygosity (orange), (c) metapopulation size (yellow) and (d) species richness (blue) for four functional types: birds (open circles), butterflies (open squares), trees (closed circles), and small mammals (closed squares). For each criterion, scores are expressed as a proportion of the maximum score attained. The grey polygon represents the unweighted mean of relative scores over all four functional types for each criterion.



**Figure S4.** Results for each conservation criterion at the 50-km scale. Points are the scaled mean values ( $\pm 1$  standard error) for the 25 landscapes (see Fig. 2 in main article for codes) from multiple runs of simulation models for four conservation criteria: (a) allelic richness (red), (b) heterozygosity (orange), (c) metapopulation size (yellow) and (d) species richness (blue) for four functional types: birds (open circles), butterflies (open squares), trees (closed circles), and small mammals (closed squares). For each criterion, scores are expressed as a proportion of the maximum score attained. The grey polygon represents the unweighted mean of relative scores over all four functional types for each criterion.



**Figure S5.** Standardised results for each functional scenario. Points indicate z-scores at the 5-km scale (a-d) and the 50-km scale (e, f), for birds (c, e), butterflies (a), small mammals (d, f) and trees (b), as assessed according to five conservation criteria evaluated by our simulation models: allelic richness (red), heterozygosity (orange), metapopulation size (yellow), species richness (blue) and pollination services (green). Simulations for pollination services were carried out for a single functional type (wild pollinators) at each scale and these values used for each of the plots above. The grey polygon represents the unweighted mean of relative scores over all five criteria, for each functional scenario.

### Effects of process versus model differences

Of necessity, we use different models to assess the different conservation criteria. This raises a potential concern: can we be sure that the contrasting patterns we describe reflect real differences in the biotic processes interacting with our conservation criteria, or could they be simply due to intrinsic differences among the models? Of course, it is not possible to decouple processes from models entirely – our pollination service model, for instance, makes no genetic predictions. There is, however, a degree of overlap in the criteria that each of our models can assess, which allows us to undertake a partial investigation of the relative

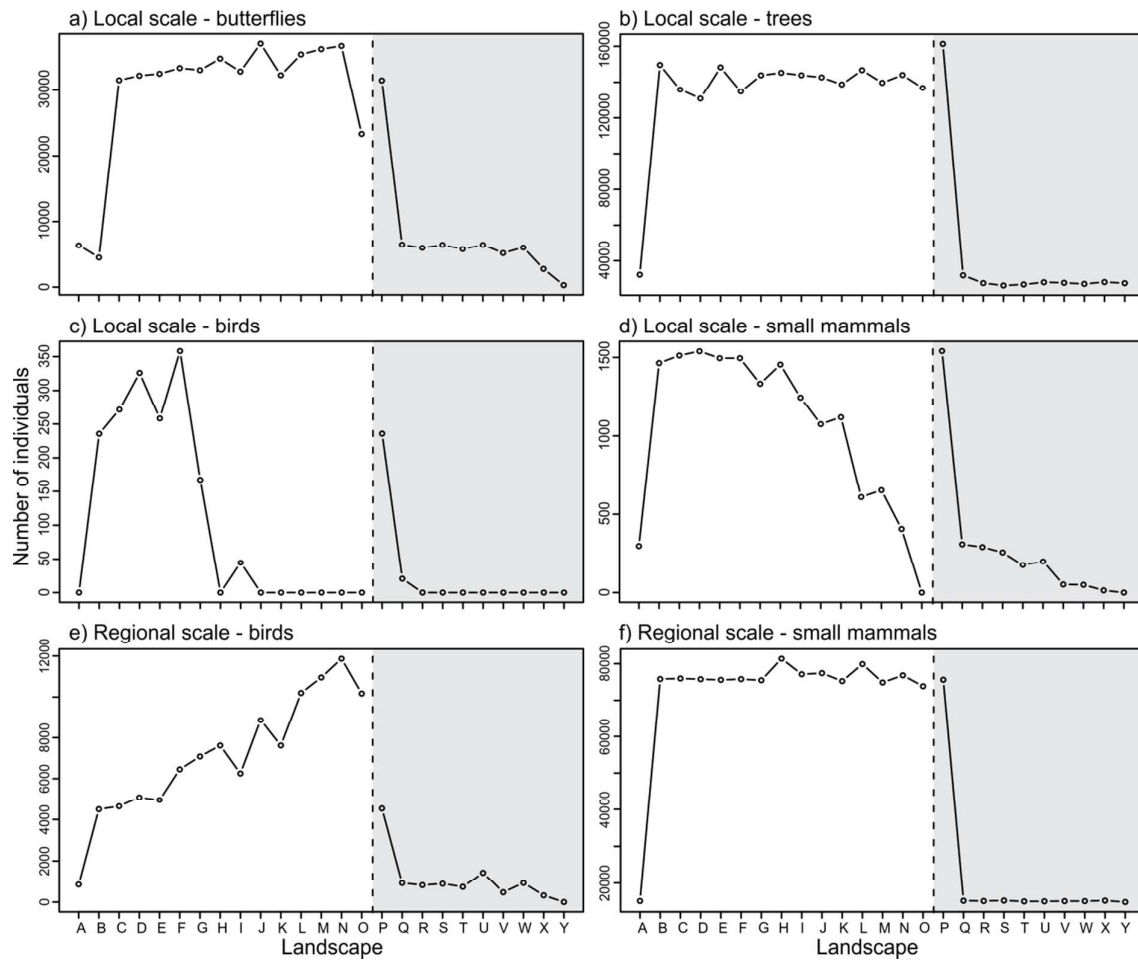
importance of model differences. Two contrasting approaches are possible: (a) compare predictions for a single criterion from multiple models; and (b) compare predictions for multiple criteria from a single model.

First, we have three models that involve some proxy for population size: as well as the metapopulation viability model SPOMSIM that we used to assess metapopulation capacity, MetaConnect and the community model also simulate population size. This gives us the opportunity to compare their population predictions to see if they would give broadly consistent assessments for the criterion of landscape population capacity. Some compromise is entailed: SPOMSIM actually models occupancy of patches in a landscape rather than population size and so can only give an estimate of mean habitat occupancy rates, while the community model simulates a number of coexisting species and so must be taken to yield average population sizes (here we use the median amongst surviving species in each scenario). Table S6 below shows the correlations among these three models in population predictions. Given the differences of metrics as well as model structures, it is not surprising that the results are not in close agreement – but there is nevertheless an appreciable degree of mutual correlation in most cases (birds in fine-scale landscapes being the obvious exception).

**Table S6.** Rank correlations between landscape scores for population size between 3 pairs of models (MetaC = MetaConnect, Comm = community model, SPOM = SPOMSIM) across landscape patterns for each functional scenario.

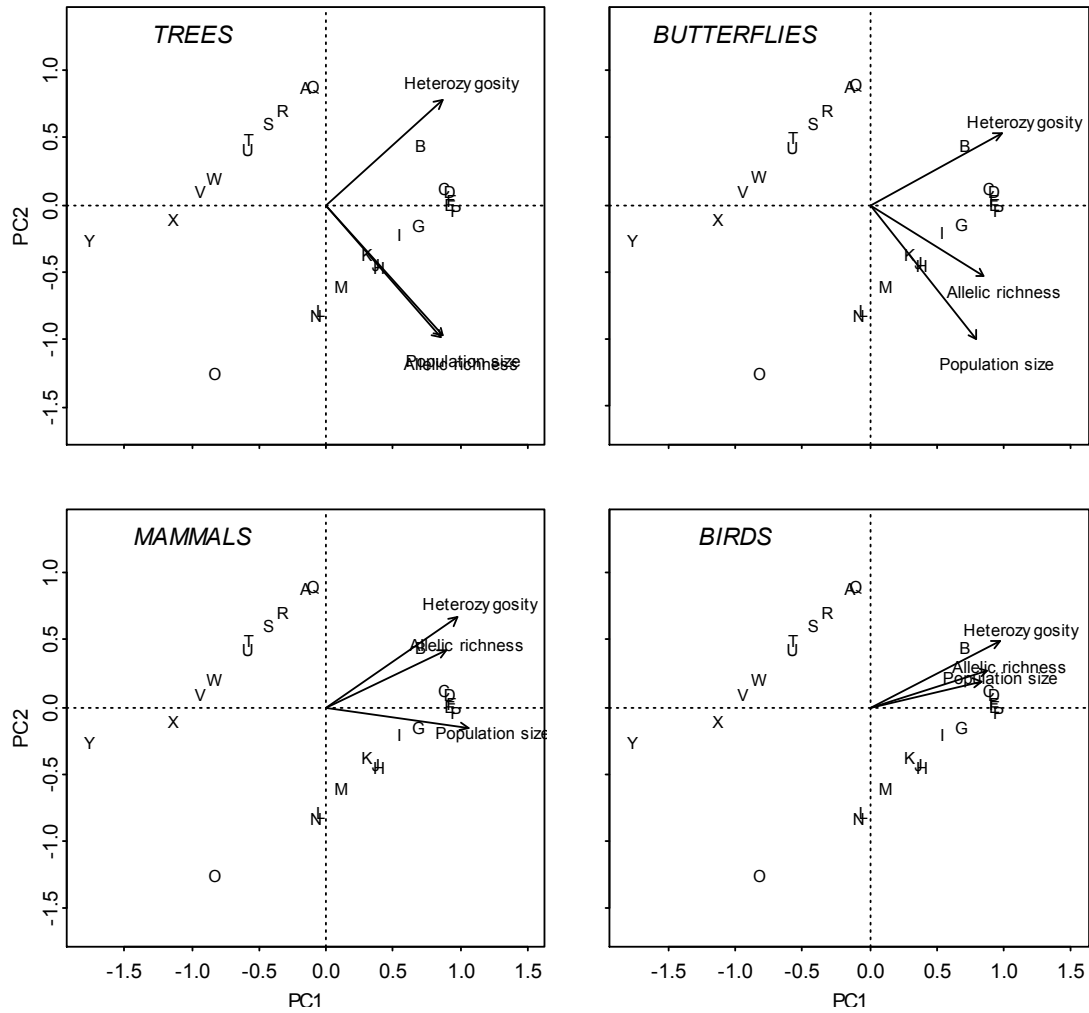
	MetaC:Comm	MetaC:SPOM	Comm:SPOM
Tree – fine scale	0.66	0.50	0.49
Butterfly – fine scale	0.52	0.80	0.59
Mammal – fine scale	0.76	0.16	0.24
Bird – fine scale	0.68	–0.07	0.53
Mammal – regional scale	0.62	0.49	0.77
Bird – regional scale	0.50	0.78	0.39

Second, MetaConnect not only produced data for genetic heterozygosity and allelic richness but also simulates population size (Fig. S6). We can therefore analyse the scores for landscapes on all three of these variables simultaneously to see if a multi-criterion assessment based on this single model supports our general claim that different criteria call for different landscape structures. Figure S7 below shows biplots from principle components analyses, which indicate that while two or three of these criteria do coincide in some functional scenarios (especially birds in fine-scale landscapes), overall there is no redundancy in criteria among the scenarios. Indeed, in most cases the loading of population size onto PC2 appears in the same relative position with respect to the genetic criteria as it did in the main analyses using SPOMSIM (i.e. the arrows appear in the same order as in Fig. 5 of the main text).

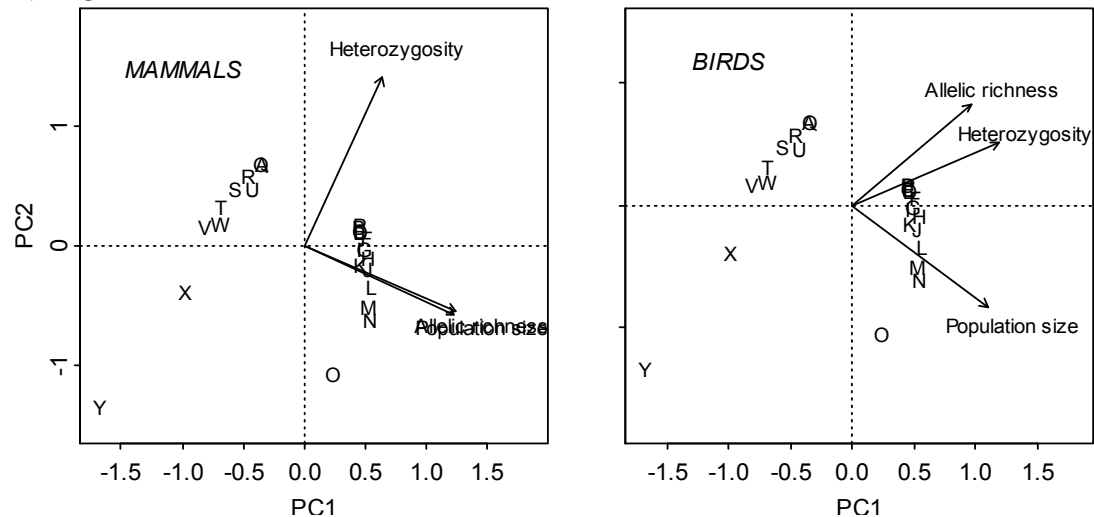


**Figure S6.** Mean total population sizes (number of individuals) estimated from 10 MetaConnect simulations parameterised for local scale butterflies (a), trees (b), birds (c) and small mammals (d) and regional scale birds (e) and small mammals (f).

A) Local Scale



B) Regional Scale



**Figure S7** – Biplots of principle components analyses (PCA) from MetaConnect results for (A) local-scale landscapes and (B) regional-scale landscapes. For each scale a single biplot was produced, and each plot here is a layer of that biplot for one of the functional types, showing how the assessments for that type (arrows) load onto the first two axes (PC1, PC2). The loadings of landscapes (identical in each plot) are indicated by the codes A–Y.

## 2. Raw output data

**Table S7.** Allelic richness: mean (standard error) allelic richness across the landscape.

<b>Landscape</b>	<b>Birds 5 km</b>	<b>Butterflies 5 km</b>	<b>Mammals 5 km</b>	<b>Trees 5 km</b>	<b>Birds 50 km</b>	<b>Mammals 50 km</b>
<b>A</b>	1.08 (0.23)	10.22 (0.02)	9.57 (0.06)	10.40 (0.04)	9.94 (0.03)	10.79 (0.05)
<b>B</b>	10.01 (0.01)	10.23 (0.02)	10.06 (0.01)	11.94 (0.07)	10.23 (0.02)	13.57 (0.10)
<b>C</b>	10.01 (0.01)	11.23 (0.06)	10.04 (0.01)	11.66 (0.07)	10.24 (0.02)	13.61 (0.18)
<b>D</b>	10.03 (0.02)	11.33 (0.09)	10.05 (0.02)	11.72 (0.07)	10.26 (0.02)	13.58 (0.10)
<b>E</b>	9.93 (0.02)	11.20 (0.05)	10.07 (0.02)	12.00 (0.10)	10.23 (0.02)	13.50 (0.10)
<b>F</b>	10.02 (0.01)	11.37 (0.06)	10.08 (0.02)	11.80 (0.10)	10.38 (0.04)	13.60 (0.15)
<b>G</b>	7.54 (0.23)	11.25 (0.03)	10.05 (0.01)	11.85 (0.07)	10.31 (0.03)	13.61 (0.08)
<b>H</b>	0.60 (0.22)	11.26 (0.05)	10.04 (0.01)	12.00 (0.06)	10.38 (0.03)	13.72 (0.09)
<b>I</b>	4.45 (0.49)	11.34 (0.06)	10.07 (0.01)	11.84 (0.09)	10.30 (0.03)	13.58 (0.10)
<b>J</b>	0.32 (0.14)	11.35 (0.05)	10.06 (0.01)	11.95 (0.08)	10.46 (0.03)	13.55 (0.07)
<b>K</b>	0.23 (0.09)	11.30 (0.05)	10.05 (0.01)	11.81 (0.07)	10.37 (0.04)	13.74 (0.08)
<b>L</b>	0	11.35 (0.08)	10.01 (0.02)	11.94 (0.08)	10.52 (0.04)	13.70 (0.14)
<b>M</b>	0	11.39 (0.06)	10.00 (0.01)	11.81 (0.09)	10.55 (0.04)	13.61 (0.12)
<b>N</b>	0	11.42 (0.04)	9.90 (0.02)	11.89 (0.08)	10.64 (0.05)	13.52 (0.14)
<b>O</b>	0	10.94 (0.03)	0.85 (0.15)	11.80 (0.08)	10.47 (0.03)	13.28 (0.13)
<b>P</b>	9.95 (0.01)	11.25 (0.02)	10.06 (0.02)	12.09 (0.07)	10.27 (0.02)	13.54 (0.07)
<b>Q</b>	3.24 (0.37)	10.24 (0.02)	9.58 (0.04)	10.42 (0.05)	9.99 (0.01)	10.69 (0.03)
<b>R</b>	0.31 (0.09)	10.22 (0.02)	9.40 (0.05)	10.41 (0.04)	9.84 (0.04)	10.70 (0.05)
<b>S</b>	0	10.24 (0.02)	9.40 (0.07)	10.32 (0.04)	9.88 (0.04)	10.70 (0.05)
<b>T</b>	0.002 (0.002)	10.26 (0.02)	8.69 (0.12)	10.36 (0.04)	9.82 (0.04)	10.74 (0.03)
<b>U</b>	0	10.27 (0.03)	9.04 (0.07)	10.42 (0.04)	10.04 (0.03)	10.64 (0.06)
<b>V</b>	0	10.18 (0.01)	6.62 (0.48)	10.38 (0.03)	9.43 (0.10)	10.76 (0.04)
<b>W</b>	0	10.24 (0.02)	5.62 (0.31)	10.38 (0.04)	9.93 (0.04)	10.64 (0.06)
<b>X</b>	0	10.02 (0.02)	2.60 (0.39)	10.38 (0.03)	8.29 (0.21)	10.76 (0.04)
<b>Y</b>	0	7.32 (0.21)	0.14 (0.05)	10.36 (0.04)	1.91 (0.29)	10.64 (0.04)

**Table S8.** Heterozygosity: slope (standard error) of square-root transformed heterozygosity against time.

<b>Landscape</b>	<b>Birds 5 km</b>	<b>Birds 50 km</b>	<b>Butterflies 5 km</b>	<b>Mammals 5 km</b>	<b>Mammals 50 km</b>	<b>Trees 5 km</b>
<b>A</b>	-0.0142 (0.0029)	-0.00144 (0.00013)	-0.00061 (0.00005)	-0.0021 (0.0002)	-0.0021 (0.0002)	-0.000003 (0.000015)
<b>B</b>	-0.0009 (0.0002)	-0.00033 (0.00003)	-0.00033 (0.00003)	-0.0004 (0.0001)	-0.0004 (0.0001)	0.000008 (0.000005)
<b>C</b>	-0.0014 (0.0003)	-0.00067 (0.00007)	-0.00036 (0.00003)	-0.0010 (0.0001)	-0.0010 (0.0001)	0.000010 (0.000012)
<b>D</b>	-0.0011 (0.0002)	-0.00062 (0.00005)	-0.00038 (0.00002)	-0.0014 (0.0001)	-0.0014 (0.0001)	0.000004 (0.000007)
<b>E</b>	-0.0020 (0.0003)	-0.00060 (0.00004)	-0.00035 (0.00002)	-0.0008 (0.0001)	-0.0008 (0.0001)	0.000006 (0.000008)
<b>F</b>	-0.0012 (0.0003)	-0.00073 (0.00004)	-0.00057 (0.00003)	-0.0022 (0.0001)	-0.0022 (0.0001)	-0.000001 (0.000010)
<b>G</b>	-0.0057 (0.0007)	-0.00119 (0.00005)	-0.00122 (0.00003)	-0.0035 (0.0001)	-0.0035 (0.0001)	-0.000018 (0.000005)
<b>H</b>	-0.0129 (0.0014)	-0.00165 (0.00004)	-0.00228 (0.00005)	-0.0068 (0.0002)	-0.0068 (0.0002)	-0.000018 (0.000009)
<b>I</b>	-0.0098 (0.0009)	-0.00151 (0.00010)	-0.00173 (0.00003)	-0.0033 (0.0001)	-0.0033 (0.0001)	-0.000003 (0.000010)
<b>J</b>	-0.0215 (0.0041)	-0.00167 (0.00004)	-0.00221 (0.00005)	-0.0050 (0.0001)	-0.0050 (0.0001)	-0.000013 (0.000005)
<b>K</b>	-0.0140 (0.0012)	-0.00192 (0.00006)	-0.00236 (0.00004)	-0.0063 (0.0002)	-0.0063 (0.0002)	-0.000025 (0.000007)
<b>L</b>	-0.0865 (0.0085)	-0.00207 (0.00006)	-0.00452 (0.00005)	-0.0096 (0.0002)	-0.0096 (0.0002)	-0.000041 (0.000008)
<b>M</b>	-0.0371 (0.0185)	-0.00181 (0.00003)	-0.00275 (0.00005)	-0.0072 (0.0002)	-0.0072 (0.0002)	-0.000080 (0.000008)
<b>N</b>	-0.0838 (0.0115)	-0.00182 (0.00004)	-0.00319 (0.00006)	-0.0092 (0.0004)	-0.0092 (0.0004)	-0.000095 (0.000005)
<b>O</b>	-0.0900 (0.0100)	-0.00275 (0.00009)	-0.00541 (0.00006)	-0.0158 (0.0014)	-0.0158 (0.0014)	-0.000209 (0.000009)
<b>P</b>	-0.0016 (0.0002)	-0.00036 (0.00005)	-0.00013 (0.00002)	-0.0004 (0.0001)	-0.0004 (0.0001)	0.000006 (0.000008)
<b>Q</b>	-0.0073 (0.0011)	-0.00148 (0.00008)	-0.00078 (0.00006)	-0.0024 (0.0002)	-0.0024 (0.0002)	-0.000008 (0.000009)
<b>R</b>	-0.0256 (0.0085)	-0.00304 (0.00017)	-0.00147 (0.00009)	-0.0046 (0.0004)	-0.0046 (0.0004)	-0.000037 (0.000019)
<b>S</b>	-0.0229 (0.0210)	-0.00518 (0.00021)	-0.00307 (0.00009)	-0.0077 (0.0003)	-0.0077 (0.0003)	-0.000030 (0.000018)
<b>T</b>	-0.0744 (0.0162)	-0.00647 (0.00018)	-0.00386 (0.00012)	-0.0085 (0.0004)	-0.0085 (0.0004)	-0.000004 (0.000031)
<b>U</b>	-0.0923 (0.0060)	-0.00247 (0.00019)	-0.00251 (0.00008)	-0.0077 (0.0002)	-0.0077 (0.0002)	-0.000044 (0.000017)
<b>V</b>	-0.0918 (0.0082)	-0.00774 (0.00025)	-0.00776 (0.00010)	-0.0119 (0.0004)	-0.0119 (0.0004)	-0.000052 (0.000015)
<b>W</b>	-0.0814 (0.0195)	-0.00579 (0.00021)	-0.00538 (0.00013)	-0.0095 (0.0010)	-0.0095 (0.0010)	-0.000063 (0.000013)
<b>X</b>	-0.1000 (0.0000)	-0.00704 (0.00028)	-0.00594 (0.00022)	-0.0105 (0.0007)	-0.0105 (0.0007)	-0.000170 (0.000025)
<b>Y</b>	-0.1000 (0.0000)	-0.01005 (0.00069)	-0.00783 (0.00022)	-0.0228 (0.0028)	-0.0228 (0.0028)	-0.000206 (0.000023)

**Table S9.** Metapopulation size: mean (standard error) proportion of total area occupied.

Landscape	Birds	Butterflies	Mammals	Trees	Birds	Mammals
	5 km	5 km	5 km	5 km	50 km	50 km
A	0.09954 (0.00005)	0.09990 (0.00002)	0.0000 (0.0000)	0.0056 (0.0012)	0.08902 (0.00237)	0.01281 (0.00215)
B	0.09978 (0.00003)	0.00628 (0.00119)	0	0.0054 (0.0013)	0.00239 (0.00058)	0.01329 (0.00222)
C	0.09977 (0.00002)	0.09999 (0.00000)	0.0183 (0.0023)	0.0032 (0.0010)	0.09858 (0.00007)	0.00786 (0.00162)
D	0.09981 (0.00002)	0.10000 (0.00000)	0.0999 (0.0000)	0.1000 (0.0000)	0.09986 (0.00001)	0.07896 (0.00043)
E	0.09974 (0.00002)	0.09998 (0.00000)	0.0838 (0.0004)	0.0204 (0.0007)	0.09927 (0.00005)	0.01044 (0.00180)
F	0.09985 (0.00001)	0.10000 (0.00000)	0.0986 (0.0001)	0.0832 (0.0006)	0.09955 (0.00002)	0.00991 (0.00137)
G	0.09993 (0.00001)	0.10000 (0.00000)	0.0989 (0.0000)	0.0970 (0.0000)	0.09966 (0.00001)	0.00234 (0.00040)
H	0.09994 (0.00000)	0.10000 (0.00000)	0.0971 (0.0000)	0.0882 (0.0000)	0.09967 (0.00001)	0.00034 (0.00005)
I	0.09996 (0.00000)	0.10000 (0.00000)	0.0980 (0.0000)	0.0868 (0.0002)	0.09965 (0.00001)	0.00772 (0.00081)
J	0.09997 (0.00000)	0.10000 (0.00000)	0.0991 (0.0000)	0.0976 (0.0000)	0.09977 (0.00000)	0.03344 (0.00071)
K	0.09997 (0.00000)	0.10000 (0.00000)	0.0989 (0.0000)	0.0940 (0.0000)	0.09975 (0.00001)	0.00893 (0.00041)
L	0.09999 (0.00000)	0.10000 (0.00000)	0.0990 (0.0000)	0.0975 (0.0000)	0.09978 (0.00000)	0.00003 (0.00001)
M	0.09999 (0.00000)	0.10000 (0.00000)	0.0995 (0.0000)	0.0992 (0.0000)	0.09984 (0.00000)	0.00182 (0.00020)
N	0.09999 (0.00000)	0.10000 (0.00000)	0.0994 (0.0000)	0.0990 (0.0000)	0.09986 (0.00000)	0.00110 (0.00012)
O	0.09999 (0.00000)	0.10000 (0.00000)	0.0996 (0.0000)	0.0996 (0.0000)	0.09991 (0.00000)	0
P	0.01873 (0.00003)	0.00050 (0.00012)	0	0.0002 (0.0001)	0.00001 (0.00000)	0.00025 (0.00012)
Q	0.01918 (0.00003)	0.00009 (0.00005)	0	0.0001 (0.0001)	0	0.00044 (0.00013)
R	0.01963 (0.00001)	0.01196 (0.00033)	0	0.0009 (0.0001)	0	0.00015 (0.00006)
S	0.01972 (0.00001)	0.01526 (0.00003)	0.0005 (0.0001)	0.0019 (0.0002)	0.01003 (0.00038)	0.00004 (0.00002)
T	0.01990 (0.00000)	0.01996 (0.00000)	0.0001 (0.0000)	0.0109 (0.0001)	0.01757 (0.00004)	0.00002 (0.00001)
U	0.01990 (0.00000)	0.01999 (0.00000)	0.0184 (0.0000)	0.0182 (0.0000)	0.01905 (0.00001)	0.00172 (0.00019)
V	0.01994 (0.00000)	0.01999 (0.00000)	0.0011 (0.0001)	0.0022 (0.0001)	0.01856 (0.00000)	0
W	0.01995 (0.00000)	0.01999 (0.00000)	0.0139 (0.0000)	0.0137 (0.0000)	0.01900 (0.00000)	0.00006 (0.00002)
X	0.01998 (0.00000)	0.02000 (0.00000)	0.0151 (0.0000)	0.0124 (0.0001)	0.01939 (0.00000)	0
Y	0.01999 (0.00000)	0.02000 (0.00000)	0.0159 (0.0000)	0.0087 (0.0000)	0.01947 (0.00000)	0

**Table S10.** Species richness: mean (standard error) number of remaining species.

<b>Landscape</b>	<b>Birds 5 km</b>	<b>Birds 50 km</b>	<b>Butterflies 5 km</b>	<b>Mammals 5 km</b>	<b>Mammals 50 km</b>	<b>Trees 5 km</b>
<b>A</b>	1.87 (0.13)	15.20 (0.36)	4.96 (0.20)	2.94 (0.11)	7.49 (0.21)	3.44 (0.14)
<b>B</b>	1.71 (0.12)	15.39 (0.34)	5.02 (0.24)	2.90 (0.10)	7.96 (0.21)	3.63 (0.13)
<b>C</b>	1.76 (0.13)	16.17 (0.32)	4.86 (0.23)	2.98 (0.11)	7.81 (0.21)	3.66 (0.15)
<b>D</b>	1.67 (0.12)	15.82 (0.33)	4.75 (0.25)	2.81 (0.10)	8.12 (0.24)	3.51 (0.15)
<b>E</b>	1.88 (0.12)	15.59 (0.30)	4.93 (0.20)	3.12 (0.11)	8.09 (0.22)	3.39 (0.13)
<b>F</b>	1.51 (0.12)	15.81 (0.33)	4.91 (0.23)	3.02 (0.12)	8.11 (0.22)	3.55 (0.15)
<b>G</b>	1.57 (0.12)	16.10 (0.30)	5.43 (0.23)	2.71 (0.11)	8.37 (0.22)	3.54 (0.15)
<b>H</b>	1.39 (0.11)	16.37 (0.30)	5.14 (0.21)	2.67 (0.11)	8.39 (0.20)	3.58 (0.14)
<b>I</b>	1.48 (0.11)	16.35 (0.30)	5.03 (0.24)	2.73 (0.11)	8.48 (0.23)	3.90 (0.15)
<b>J</b>	1.41 (0.12)	16.70 (0.30)	5.09 (0.24)	2.50 (0.11)	8.50 (0.24)	3.55 (0.14)
<b>K</b>	1.35 (0.11)	16.59 (0.23)	5.29 (0.24)	2.69 (0.11)	8.83 (0.23)	3.54 (0.15)
<b>L</b>	1.28 (0.10)	16.00 (0.28)	5.17 (0.24)	2.39 (0.10)	8.69 (0.23)	3.44 (0.15)
<b>M</b>	1.32 (0.11)	16.43 (0.31)	4.88 (0.23)	2.48 (0.10)	8.76 (0.20)	3.65 (0.14)
<b>N</b>	1.40 (0.11)	16.66 (0.28)	5.39 (0.24)	2.37 (0.11)	8.65 (0.21)	3.51 (0.16)
<b>O</b>	1.30 (0.11)	16.14 (0.36)	4.99 (0.22)	2.42 (0.10)	8.52 (0.22)	3.59 (0.14)
<b>P</b>	0.80 (0.09)	12.07 (0.30)	4.38 (0.19)	2.32 (0.10)	7.05 (0.19)	3.28 (0.14)
<b>Q</b>	0.65 (0.08)	13.12 (0.27)	4.60 (0.21)	2.20 (0.10)	7.38 (0.22)	3.20 (0.12)
<b>R</b>	0.65 (0.08)	13.32 (0.31)	4.67 (0.20)	2.08 (0.10)	7.14 (0.21)	3.39 (0.14)
<b>S</b>	0.78 (0.09)	13.35 (0.26)	4.63 (0.20)	2.08 (0.11)	7.34 (0.23)	3.35 (0.15)
<b>T</b>	0.62 (0.08)	13.48 (0.29)	4.59 (0.21)	1.92 (0.08)	7.58 (0.22)	3.25 (0.14)
<b>U</b>	0.59 (0.08)	13.20 (0.28)	4.46(0.19)	2.09(0.09)	7.22(0.22)	3.29 (0.15)
<b>V</b>	0.51 (0.07)	13.71 (0.29)	5.02(0.20)	1.79(0.10)	7.57(0.21)	3.22 (0.13)
<b>W</b>	0.60 (0.08)	13.96 (0.30)	4.88(0.22)	1.96(0.10)	7.65(0.20)	3.47 (0.16)
<b>X</b>	0.57 (0.08)	13.26 (0.29)	4.73(0.21)	1.74(0.09)	7.65(0.21)	3.31 (0.12)
<b>Y</b>	0.49 (0.07)	13.74 (0.26)	4.84(0.22)	1.65(0.09)	7.71(0.21)	3.40 (0.14)

**Table S11.** Pollination service: percentage crop yield.

<b>Landscape</b>	<b>5 km</b>	<b>50 km</b>
<b>A</b>	0.4985	0.2771
<b>B</b>	0.4974	0.3289
<b>C</b>	0.4971	0.3331
<b>D</b>	0.4960	0.3589
<b>E</b>	0.4972	0.3168
<b>F</b>	0.4966	0.3595
<b>G</b>	0.4947	0.4031
<b>H</b>	0.4937	0.4464
<b>I</b>	0.4943	0.4228
<b>J</b>	0.4916	0.4598
<b>K</b>	0.4915	0.4690
<b>L</b>	0.4888	0.4885
<b>M</b>	0.4944	0.4758
<b>N</b>	0.4849	0.4780
<b>O</b>	0.4785	0.4961
<b>P</b>	0.3037	0.2430
<b>Q</b>	0.3034	0.2650
<b>R</b>	0.3031	0.2751
<b>S</b>	0.3034	0.2764
<b>T</b>	0.3030	0.2898
<b>U</b>	0.3030	0.2754
<b>V</b>	0.3028	0.2968
<b>W</b>	0.3026	0.2938
<b>X</b>	0.3020	0.2968
<b>Y</b>	0.3017	0.3027

### 3. Standardised z-scores of output data

**Table S12.** Allelic richness

Landscape	Butterflies	Birds	Mammals	Trees	Birds	Mammals
	5km	5km	5km	5km	50km	50km
A	-0.534	-0.470	0.365	-1.171	0.089	-1.139
B	-0.528	1.600	0.530	0.883	0.259	0.791
C	0.597	1.600	0.527	0.504	0.265	0.819
D	0.717	1.605	0.527	0.593	0.277	0.798
E	0.570	1.582	0.533	0.966	0.259	0.742
F	0.762	1.603	0.537	0.696	0.347	0.812
G	0.619	1.028	0.527	0.764	0.306	0.819
H	0.632	-0.582	0.523	0.958	0.347	0.895
I	0.726	0.311	0.533	0.756	0.300	0.798
J	0.742	-0.647	0.530	0.902	0.394	0.777
K	0.684	-0.668	0.527	0.709	0.341	0.909
L	0.740	-0.721	0.517	0.877	0.429	0.881
M	0.786	-0.721	0.510	0.704	0.447	0.819
N	0.813	-0.721	0.476	0.816	0.499	0.756
O	0.273	-0.721	-2.565	0.702	0.400	0.590
P	0.629	1.586	0.530	1.085	0.283	0.770
Q	-0.516	0.030	0.369	-1.138	0.119	-1.209
R	-0.538	-0.649	0.308	-1.150	0.031	-1.202
S	-0.518	-0.721	0.308	-1.282	0.054	-1.202
T	-0.499	-0.721	0.070	-1.224	0.019	-1.174
U	-0.488	-0.721	0.187	-1.143	0.148	-1.244
V	-0.580	-0.721	-0.626	-1.195	-0.209	-1.160
W	-0.513	-0.721	-0.962	-1.195	0.084	-1.244
X	-0.762	-0.721	-1.977	-1.198	-0.877	-1.160
Y	-3.814	-0.721	-2.804	-1.218	-4.613	-1.244

**Table S13.** Heterozygosity

<b>Landscape</b>	<b>Butterflies 5km</b>	<b>Birds 5km</b>	<b>Mammals 5km</b>	<b>Trees 5km</b>	<b>Birds 50km</b>	<b>Mammals 50km</b>
<b>A</b>	0.895	0.635	0.812	0.642	0.521	0.691
<b>B</b>	1.017	0.974	1.137	0.803	0.941	0.712
<b>C</b>	1.003	0.961	1.018	0.836	0.813	0.704
<b>D</b>	0.995	0.968	0.946	0.744	0.832	0.691
<b>E</b>	1.008	0.944	1.060	0.769	0.839	0.692
<b>F</b>	0.911	0.966	0.801	0.668	0.790	0.678
<b>G</b>	0.630	0.851	0.561	0.400	0.616	0.572
<b>H</b>	0.173	0.669	-0.077	0.394	0.442	0.544
<b>I</b>	0.412	0.747	0.591	0.643	0.495	0.478
<b>J</b>	0.201	0.450	0.278	0.472	0.434	0.282
<b>K</b>	0.137	0.641	0.023	0.289	0.339	0.286
<b>L</b>	-0.795	-1.204	-0.604	0.034	0.283	0.066
<b>M</b>	-0.031	0.052	-0.141	-0.570	0.381	-0.551
<b>N</b>	-0.220	-1.134	-0.521	-0.813	0.377	-0.802
<b>O</b>	-1.182	-1.292	-1.775	-2.591	0.025	-2.593
<b>P</b>	1.102	0.955	1.143	0.775	0.930	0.731
<b>Q</b>	0.823	0.811	0.758	0.562	0.506	0.680
<b>R</b>	0.524	0.344	0.338	0.100	-0.085	0.569
<b>S</b>	-0.167	0.413	-0.240	0.220	-0.895	0.496
<b>T</b>	-0.512	-0.897	-0.383	0.612	-1.384	0.111
<b>U</b>	0.074	-1.351	-0.247	-0.014	0.131	0.097
<b>V</b>	-2.195	-1.338	-1.037	-0.135	-1.865	-0.159
<b>W</b>	-1.166	-1.073	-0.583	-0.303	-1.126	-0.455
<b>X</b>	-1.410	-1.546	-0.772	-1.985	-1.600	-1.828
<b>Y</b>	-2.227	-1.546	-3.086	-2.552	-2.740	-2.693

**Table S14.** Metapopulation viability

<b>Landscape</b>	<b>Butterflies 5km</b>	<b>Birds 5km</b>	<b>Mammals 5km</b>	<b>Trees 5km</b>	<b>Birds 50km</b>	<b>Mammals 50km</b>
<b>A</b>	0.860	0.792	-1.068	-0.900	0.640	0.309
<b>B</b>	-1.273	0.797	-1.068	-0.905	-1.296	0.338
<b>C</b>	0.862	0.797	-0.679	-0.954	0.854	0.012
<b>D</b>	0.863	0.798	1.058	1.212	0.882	4.284
<b>E</b>	0.862	0.796	0.716	-0.570	0.869	0.167
<b>F</b>	0.863	0.799	1.031	0.837	0.875	0.135
<b>G</b>	0.862	0.801	1.036	1.145	0.878	-0.320
<b>H</b>	0.862	0.802	0.998	0.949	0.878	-0.440
<b>I</b>	0.863	0.802	1.018	0.916	0.878	0.003
<b>J</b>	0.863	0.802	1.040	1.158	0.880	1.549
<b>K</b>	0.863	0.802	1.036	1.079	0.880	0.076
<b>L</b>	0.863	0.803	1.039	1.156	0.881	-0.459
<b>M</b>	0.863	0.803	1.048	1.195	0.882	-0.352
<b>N</b>	0.863	0.803	1.047	1.190	0.882	-0.395
<b>O</b>	0.863	0.803	1.051	1.204	0.883	-0.461
<b>P</b>	-1.405	-1.224	-1.068	-1.021	-1.350	-0.446
<b>Q</b>	-1.415	-1.213	-1.068	-1.023	-1.350	-0.434
<b>R</b>	-1.144	-1.201	-1.068	-1.006	-1.350	-0.452
<b>S</b>	-1.069	-1.199	-1.058	-0.984	-1.126	-0.458
<b>T</b>	-0.962	-1.195	-1.067	-0.782	-0.957	-0.459
<b>U</b>	-0.961	-1.195	-0.677	-0.619	-0.924	-0.358
<b>V</b>	-0.961	-1.194	-1.046	-0.977	-0.935	-0.461
<b>W</b>	-0.961	-1.194	-0.773	-0.719	-0.925	-0.457
<b>X</b>	-0.961	-1.193	-0.746	-0.748	-0.916	-0.461
<b>Y</b>	-0.961	-1.193	-0.730	-0.832	-0.915	-0.461

**Table S15.** Species richness

<b>Landscape</b>	<b>Butterflies 5km</b>	<b>Birds 5km</b>	<b>Mammals 5km</b>	<b>Trees 5km</b>	<b>Birds 50km</b>	<b>Mammals 50km</b>
<b>A</b>	0.203	1.463	1.201	-0.156	0.150	-0.859
<b>B</b>	0.426	1.130	1.108	1.005	0.280	-0.004
<b>C</b>	-0.170	1.234	1.294	1.188	0.814	-0.277
<b>D</b>	-0.579	1.047	0.899	0.271	0.574	0.286
<b>E</b>	0.091	1.484	1.619	-0.462	0.417	0.232
<b>F</b>	0.016	0.715	1.387	0.516	0.567	0.268
<b>G</b>	1.953	0.839	0.667	0.455	0.766	0.741
<b>H</b>	0.873	0.465	0.575	0.699	0.951	0.777
<b>I</b>	0.463	0.652	0.714	2.655	0.937	0.941
<b>J</b>	0.687	0.507	0.180	0.516	1.176	0.977
<b>K</b>	1.431	0.382	0.621	0.455	1.101	1.577
<b>L</b>	0.985	0.236	-0.075	-0.156	0.697	1.323
<b>M</b>	-0.095	0.319	0.134	1.127	0.992	1.450
<b>N</b>	1.804	0.486	-0.122	0.271	1.149	1.250
<b>O</b>	0.314	0.278	-0.006	0.760	0.793	1.014
<b>P</b>	-1.957	-0.762	-0.238	-1.134	-1.993	-1.659
<b>Q</b>	-1.138	-1.074	-0.516	-1.623	-1.274	-1.059
<b>R</b>	-0.877	-1.074	-0.794	-0.462	-1.137	-1.495
<b>S</b>	-1.026	-0.804	-0.794	-0.706	-1.116	-1.131
<b>T</b>	-1.175	-1.136	-1.166	-1.318	-1.027	-0.695
<b>U</b>	-1.659	-1.199	-0.771	-1.073	-1.219	-1.350
<b>V</b>	0.426	-1.365	-1.467	-1.501	-0.870	-0.713
<b>W</b>	-0.095	-1.178	-1.073	0.027	-0.699	-0.568
<b>X</b>	-0.654	-1.240	-1.583	-0.951	-1.178	-0.568
<b>Y</b>	-0.244	-1.407	-1.792	-0.401	-0.850	-0.459

**Table S16.** Pollination service

<b>Landscape</b>	<b>5km</b>	<b>50km</b>
<b>A</b>	0.857	-0.945
<b>B</b>	0.845	-0.333
<b>C</b>	0.842	-0.284
<b>D</b>	0.831	0.021
<b>E</b>	0.843	-0.476
<b>F</b>	0.837	0.028
<b>G</b>	0.817	0.542
<b>H</b>	0.806	1.053
<b>I</b>	0.813	0.775
<b>J</b>	0.784	1.211
<b>K</b>	0.783	1.320
<b>L</b>	0.755	1.550
<b>M</b>	0.814	1.400
<b>N</b>	0.714	1.426
<b>O</b>	0.647	1.640
<b>P</b>	-1.190	-1.347
<b>Q</b>	-1.193	-1.087
<b>R</b>	-1.196	-0.968
<b>S</b>	-1.193	-0.953
<b>T</b>	-1.197	-0.795
<b>U</b>	-1.197	-0.965
<b>V</b>	-1.200	-0.712
<b>W</b>	-1.202	-0.747
<b>X</b>	-1.208	-0.712
<b>Y</b>	-1.211	-0.642