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Gunton, RM, Marsh, CJ, Moulherat, S et al. (4 more authors) (2017) Multi-criterion trade-offs and synergies for spatial conservation planning. Journal of Applied Ecology, 54 (3). pp. 903-913. ISSN 0021-8901

https://doi.org/10.1111/1365-2664.12803

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

Running title: Multi-criterion trade-offs for conservation

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Word counts:
Summary: 210
Main text: 4,902
Acknowledgements: 92
References: 1,527
Tables: 120
Figure legends: 406

Element counts:
Tables: 1
Figures: 5
References: 52

Summary

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

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

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

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

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

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

Introduction

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

If the various conservation criteria reinforce each other hierarchically (Noss 1990), it should be straightforward to fulfil them simultaneously. For example, genetic diversity underpins population viability (Keller & Waller 2002; but see Tallmon, Luikart & Waples 2004), reducing local extinction rates and so promoting greater species richness, and diverse communities are thought to enhance ecosystem functioning (Klein et al. 2003; Zavaleta et al. 2010). However, spatial structure may introduce conflicts and trade-offs between conservation goals. For example, a widely-distributed habitat network might sample more environments and maximise species richness, but at the cost of protecting fewer individuals of each, increasing extinction rates (Mokany, Harwood & Ferrier 2013); or high connectivity may improve population persistence (Soulé & Simberloff 1986) but at the cost of reduced allelic richness owing to increased rates of gene-flow (Fenderson *et al.* 2014). Optimal solutions may also depend upon the taxa of concern (plants, birds, etc.), especially since differences in dispersal abilities can radically change the functional connectivity of a given landscape (Taylor *et al.* 1993). Considering ecosystem services as a conservation objective (de Groot, Wilson & Boumans 2002) adds new dimensions to the problem. For example, pollinator activity typically radiates from insect nesting habitat into croplands (Ricketts *et al.* 2008) such that crop pollination rates may increase with the habitat edge:area ratio. We can therefore imagine three situations. If all desirable criteria are linked by mutually-reinforcing effects, then for practical purposes the plurality of criteria is illusory (Fig. 1A). Otherwise, if there are certain kinds of conservation policies that fulfil all criteria (Fig. 1B), we should ask: what are the characteristics of these policies? Finally, if such win–win solutions are impractical, fragile or do not exist (e.g. Fig. 1C), then we should ask: how are the different criteria traded off so that policy-makers and conservationists may seek appropriate compromises?

These questions are especially pertinent when we consider the spatial arrangement of habitat patches. This is particularly the concern of the conservation planning literature (Miller, Bratton & White 1987). While habitat quality is of fundamental importance, in landscapes with many competing land-uses the spatial arrangement of habitat may be critical – particularly as regards the degree of fragmentation of a given area (Pardini *et al.* 2010; Doerr, Barrett & Doerr 2011). This question was previously addressed under the simplistic SLOSS framework ("single large or several small" Diamond 1975; Simberloff & Abele 1982), but contributions to that debate have rarely accounted for the full range of spatial scales at which conservation actions are undertaken, or the implications of mixed patch-sizes (but see Schwartz 1999). The diverse processes by which organisms interact with each other and with their habitat all have characteristic spatial scales (Levin 1992), so it is likely that the spatial arrangement of habitat patches will have different implications for different conservation criteria, depending on the sizes of patches, the distances between them and the characteristics of the taxa in question (With, Gardner & Turner 1997; Hodgson *et al.* 2011; Synes *et al.* accepted). The best spatial strategy for a regional scale may not simply be scaled up to give a global template for conservation planning, or scaled down for local recommendations.

There is therefore a need to investigate the value of a diverse range of spatial strategies at specific spatial scales and using a range of criteria simultaneously. Simulation models enable us to do this with some generality. Here we use four models to explore relationships among several ecological criteria as applied to configurations of habitat patches differing in their degree of fragmentation (number of fragments varying by two orders of magnitude). Considering four functional types of organism differing in population densities, dispersal distances and species richness, we explore how different landscapes perform according to the levels of genetic diversity (both heterozygosity and allelic richness), population size, species richness and pollination services that they are likely to sustain. On the basis of the reasoning given in the above examples of spatial scenarios, we predicted that (1) heterozygosity and (2) population viability would increase with decreasing fragmentation, while (3) allelic richness and (4) species richness would increase with some degree of patch separation, especially if there are any underlying habitat gradients, and subject to population viability being maintained – so these criteria would be maximized in moderately-fragmented landscapes. We expect all these benefits to be greatest for functional types with higher population densities and lower dispersal distances, but to be increasingly tempered by viability constraints when population densities are lower. Finally, (5) the export of pollination services to the matrix should benefit from higher fragmentation of landscapes. Functional connectivity – the degree to which a landscape facilitates movement for a given type of organism (Taylor *et al.* 1993; Pe'er *et al.* 2011) – must also be considered. Thus, while fragmentation is expected to cause problems under many criteria as assessed over local extents, over ranges approaching the dispersal limits of an organism we expect that landscapes with greater levels of fragmentation of a given overall habitat area will perform better, owing to reduced inter-patch distances pertaining between more-numerous fragments. Thus we expect no single habitat configuration to be optimal for all criteria (Fig. 1C).

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

Materials and Methods

Landscape patterns

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

Each of these 25 patterns ("tiles") was interpreted at two spatial scales that may be relevant to the scaling of both ecological processes and administrative regions: "local" meant a cell size of 50m, giving a tile size of 5 km × 2.5 km, while "regional" meant a cell size of 500m and tile size of 50 km × 25 km. The patterns were then tiled by transposition to add a 'border' of 50 cells (Fig. S1), to reduce edge effects; for analyses, we extracted results from only the focal tile (100 × 50 cells), referred to as the "landscape". The scaling means that all local-scale landscapes are at least as fragmented as the most fragmented regional-scale landscapes. For example, tiled arrays of the most aggregated patterns (e.g. P) at the local scale have patches of a size (25 ha in this case) equivalent to the smallest patches in a highly-fragmented pattern taken at the regional scale (e.g. Y).

Functional scenarios: species × scales

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

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

Assessment of scenarios

The scenarios were assessed using a different simulation model for each of the four main criteria: intraspecific genetic diversity, population size, species richness and pollination service. Each model was parameterised using the mean dispersal distance and corresponding carrying capacity specified by each of the functional scenarios. Further details of all models and parameter choices are given in Appendix S1 (Table S5).

1) *Genetic diversity: heterozygosity and allelic richness*

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

2) *Population size*

The stochastic patch-occupancy simulator SPOMSIM (Moilanen 2004) was used for predicting the proportion of habitat area occupied, to give a surrogate for total population size. SPOMSIM models local extinction and colonisation as functions of patch-specific carrying capacities. Extinction rates were modelled using an exponential function of patch area and population carrying capacity; colonisation was modelled as a function of patch area and the species' dispersal distance and colonisation ability, using minimum edge-to-edge distances between all pairs of patches. For every combination of landscape and species, 100 replicates were simulated over 300 time steps, starting with all patches occupied, and the mean proportion of occupied area was calculated for time steps 51-300.

3) *Species richness*

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

4) *Pollination services*

The model InVEST 2.4.2 (Nelson *et al.* 2009; Natural Capital Project 2012) provided assessments of how the scenarios may affect pollination rates of an insect-dependent (e.g. top fruit) crop grown in the surrounding matrix. Our four functional types were not relevant here, but taking habitat patches as providing both nest sites and foraging resources for pollinating insects and the matrix as a foraging resource, the model assigns an abundance of pollinators to every cell in the landscape and thence a rate of pollination to each crop cell. We parameterised it according to published recommendations (Tallis *et al.* 2011), specifying an exponential movement kernel for pollinators with a distance-decay constant of 1800 m. We also assumed a transition zone between crop and habitat equivalent to a 2-m band with zero yield around all habitat patches, reducing the cropped area of the landscape by 0.01% (least fragmented) – 2% (most fragmented), representing for example a conservation headland to protect the habitat patches, or the ecosystem disservice of reduced crop value in the vicinity of trees or other marginal habitat (Sparkes *et al.* 1998). Fruit-set values for each cell in the matrix were multiplied by potential crop cover, and the resulting values averaged to give landscape-wide relative yield.

Analyses

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

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

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

Results

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

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

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

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

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

Multi-criterion assessments by functional type

At the local scale most of the functional groups showed an interplay between low population sizes in landscapes with rather few, isolated patches vs. decreasing genetic diversities with increasing fragmentation. In trees and butterflies these factors tended to show opposite trends or none at all (Figs. 3A, 3B). In mammals and birds, severe decreases in both allelic and species richness in the most fragmented landscapes resulted in overall performance peaking in landscapes with intermediate or low levels of fragmentation (Fig. 3C, 3D).

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

Global multi-criterion assessment

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

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

Discussion

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

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

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

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

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

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

Outlook

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

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

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

Acknowledgments

This work was funded by the European Commission through SCALES, an integrating project within FP7, grant 226852 (Henle *et al.* 2010; www.scales-project.net). Sandro Azaele helped create the patch simulator, Richard German provided R functions to simulate heterogeneity, and Stephen Cornell and James Rosindell gave formative ideas. Jenny Hodgson and Jochen Krauβ provided information on butterfly traits, Christopher Wright on small mammals and Riin Taam on trees. Data from the National Forest Inventory were provided by the U.K. Forestry Commission. Joseph Bennett and two anonymous reviewers helped us clarify a number of important points.

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Supporting Information

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

Appendix S1. Details of simulation modelling

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

Table S2. Correlations between heterozygosity slopes and final estimates.

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

Fig. S5. Population sizes from MetaConnect

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

Tables

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

Functional type	**Mean dispersal distance** (m)	**Carrying capacity at 5-km scale** (inds /ha)	**Carrying capacity at 50-km scale** (inds /ha)	**Community carrying capacity** (inds /ha)	**Species richness at 5-km scale**	**Species richness at 50-km scale**
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

Figure legends

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

Figure 2. The 25 landscape tiles used, grouped by percentage of area covered and annotated with number of patches and source (either simulated or extracted from observed patterns of British woodland at either 50 m or 500 m resolutions). Landscapes are ordered first by decreasing habitat amount, then by increasing fragmentation, then by increasing edge:area ratio (Fahrig 2003).

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

Figure 4. Biplots of principle components analyses of conservation assessments of (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 pollination services assessment (unrelated to these functional types) is shown by a red arrow in the plots for butterflies (in A) and birds (in B). The loadings of landscapes (identical in each plot) are indicated by the codes A–Y; the inset plots group landscapes by percentage cover (blue region = 2%; green region = 10%), with arrows showing the directions of increasing fragmentation. The axes for the regional-scale plots have been reversed to aid comparison.

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

Fig. 1

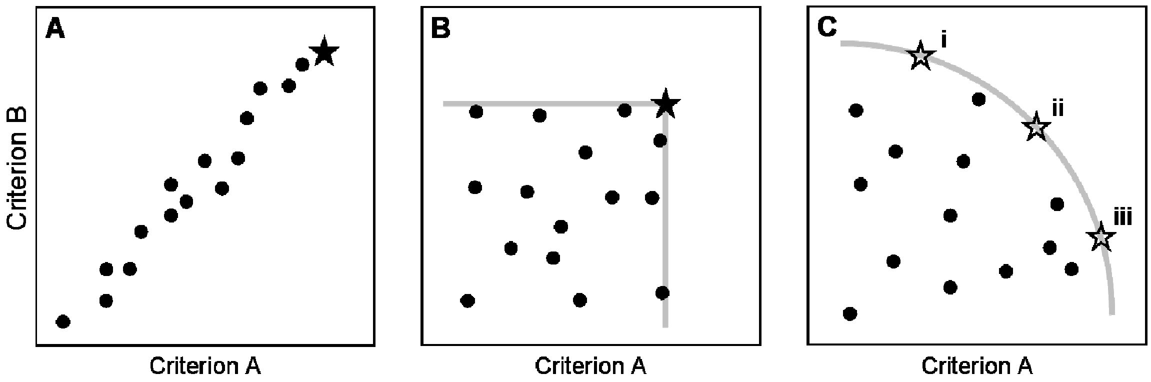
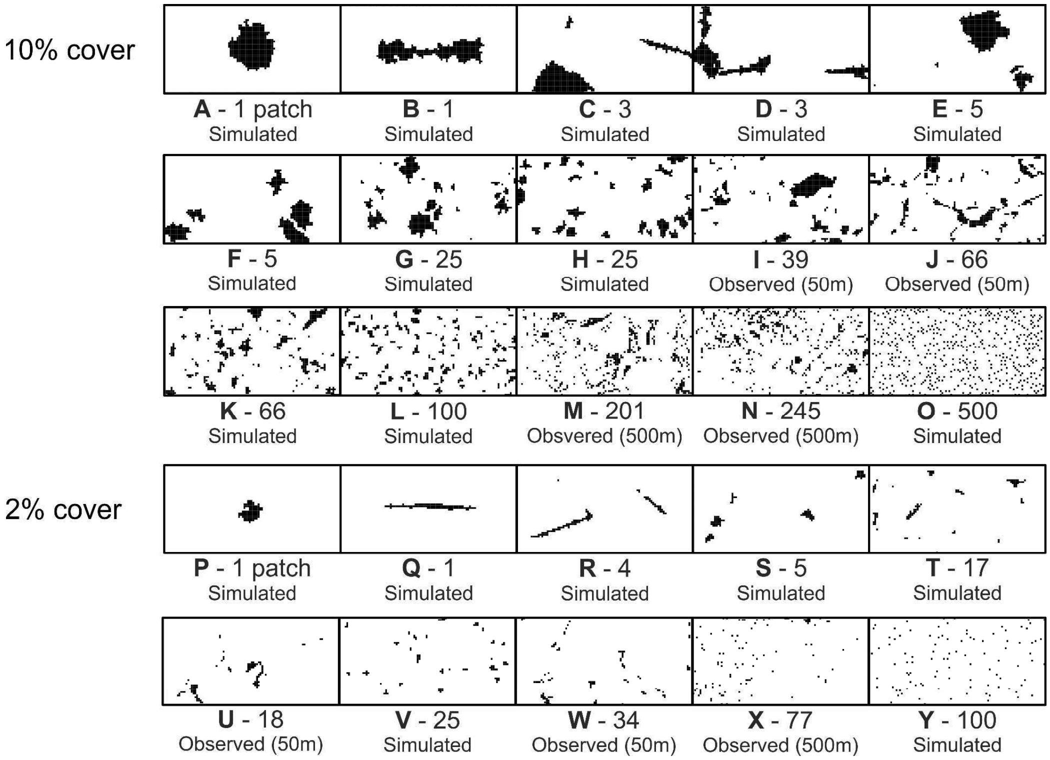
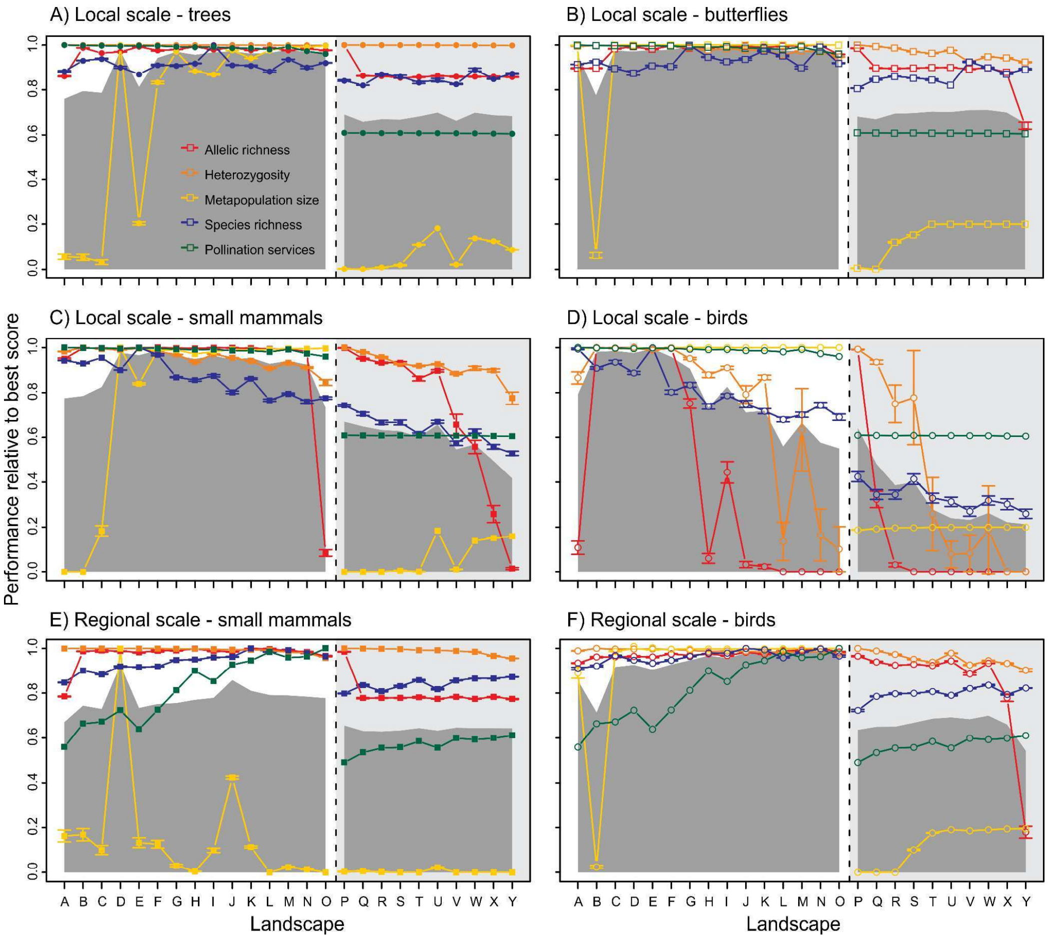


Fig. 2



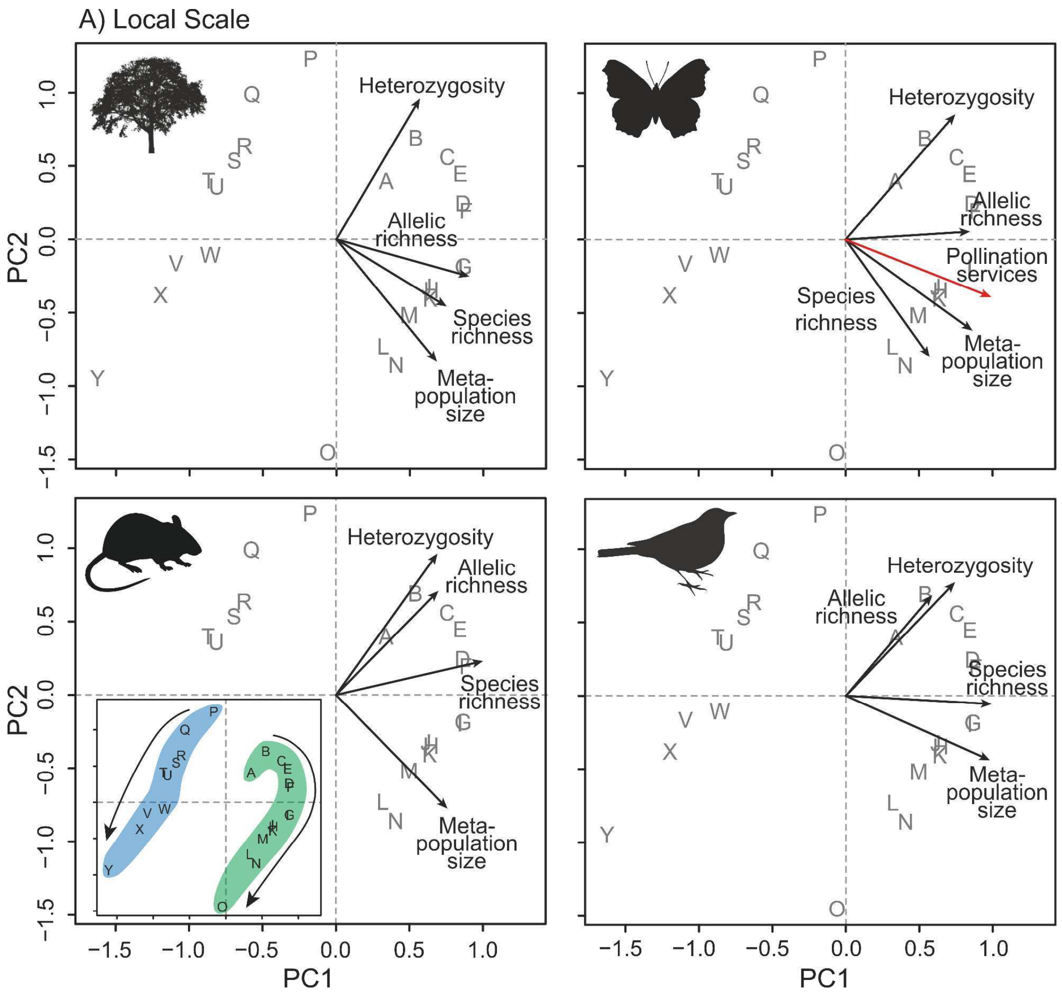
A - 1 patch Simulated
B - 1 Simulated
C - 3 Simulated
D - 3 Simulated
E - 5 Simulated
F - 5 Simulated
G - 25 Simulated
H - 25 Simulated
I - 39 Observed (50m)
J - 66 Observed (50m)
K - 66 Simulated
L - 100 Simulated
M - 201 Obsvered (500m)
N - 245 Observed (500m)
O - 500 Simulated
P - 1 patch Simulated
Q - 1 Simulated
R - 4 Simulated
S - 5 Simulated
T - 17 Simulated
U - 18 Observed (50m)
V - 25 Simulated
W - 34 Observed (50m)
X - 77 Observed (500m)
Y - 100 Simulated

Fig. 3

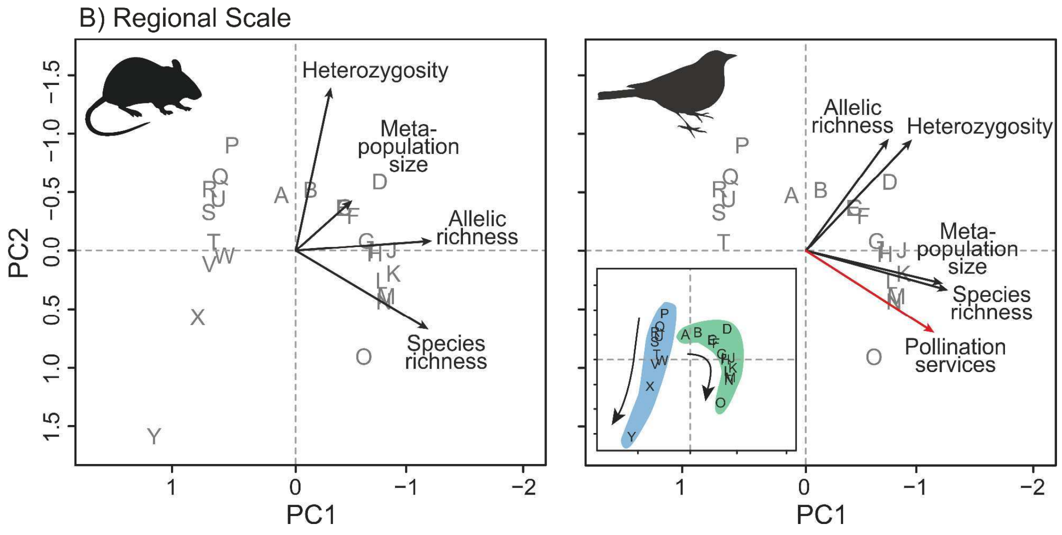


A) Local scale - trees
B) Local scale - butterflies
C) Local scale - small mammals
D) Local scale - birds
E) Regional scale - small mammals
F) Regional scale - birds
Allelic richness
Heterozygosity
Metapopulation size
Species richness
Pollination services
Performance relative to best score
0.0
0.2
0.4
0.6
0.8
1.0
A B C D E F G H I J K L M N O P Q R S T U V W X Y
Landscape

Fig. 4

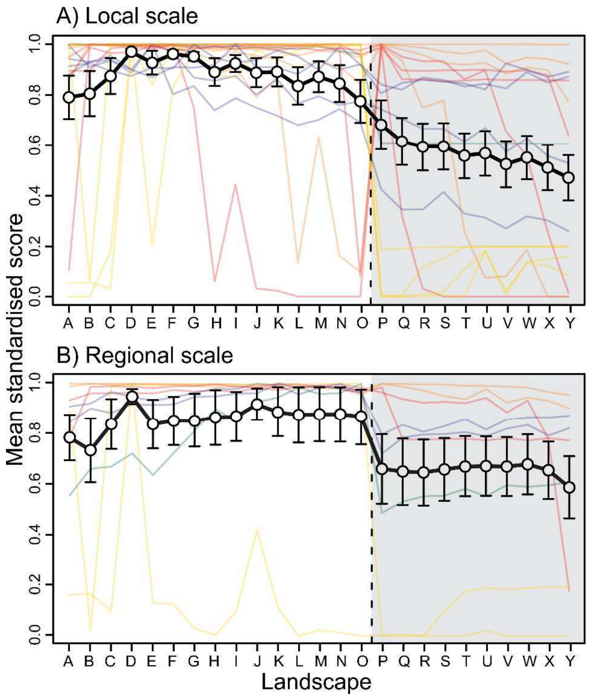


A) Local Scale



B) Regional Scale

Fig. 5


A) Local scale
B) Regional scale
Mean standardised score
0.0
0.2
0.4
0.6
0.8
1.0
A B C D E F G H I J K L M N O P Q R S T U V W X Y
Landscape

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

Contents

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).

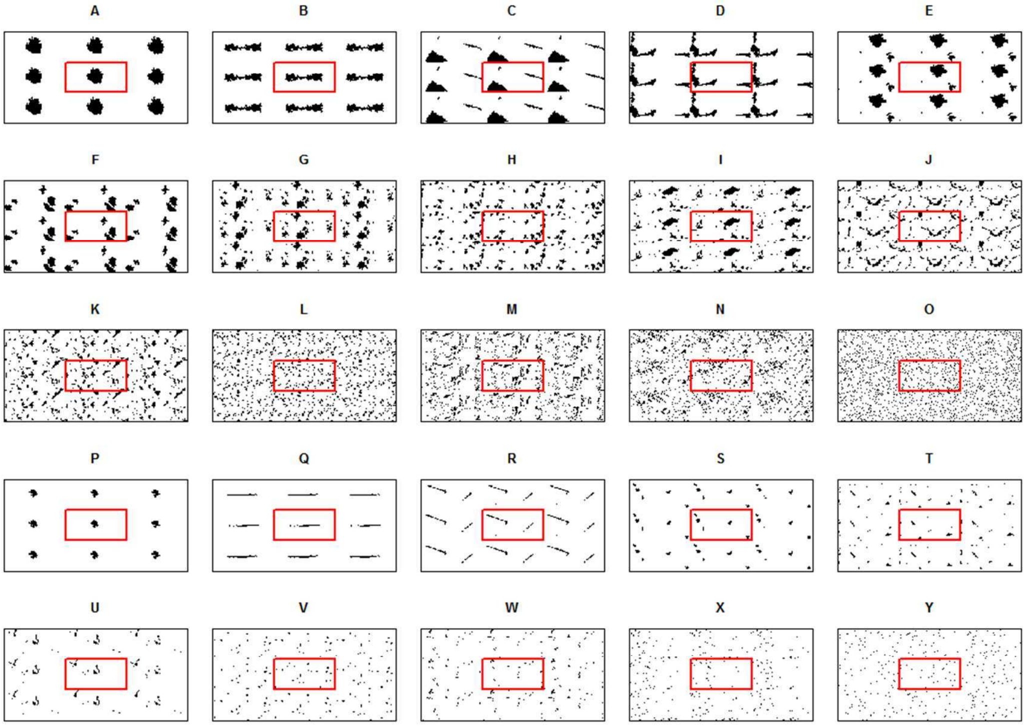
1.2 Simulated landscape patterns

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 × 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)

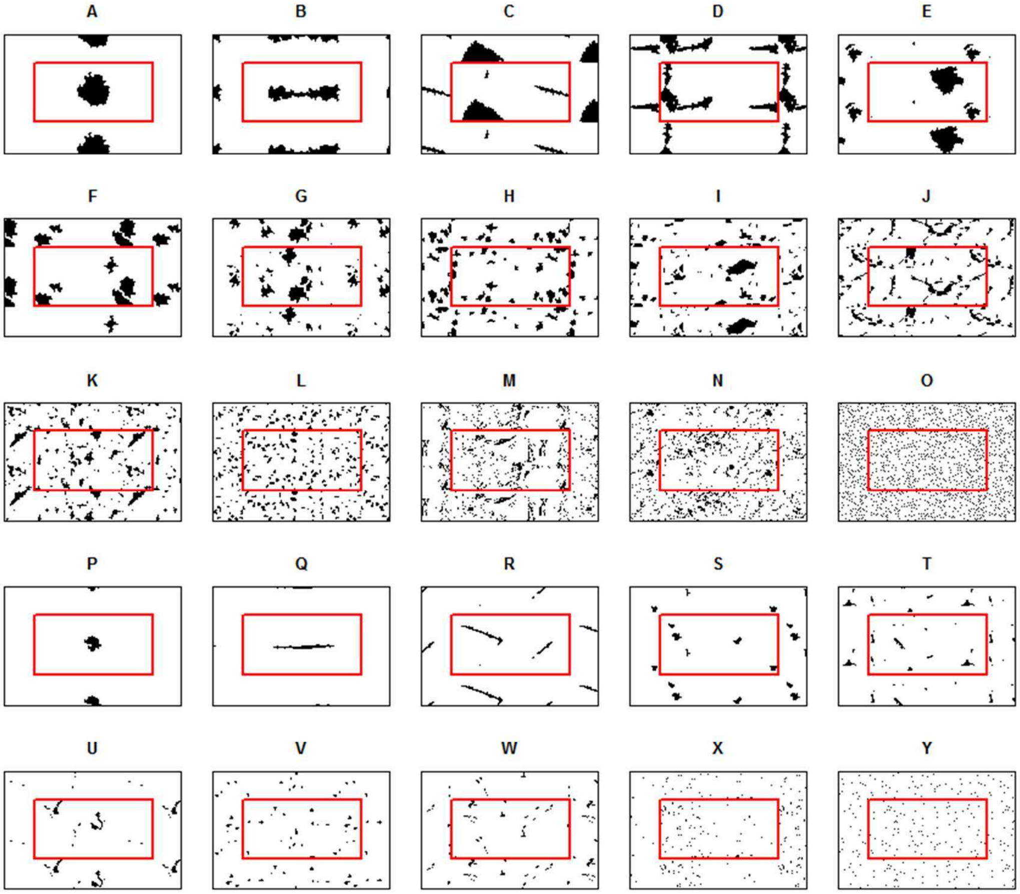


Figure S1. Tiling of patterns for (A) local-scale bird simulations and (B) all other simulations.

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^2 (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 individualsbehave 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-stepa proportion *d*of NR individuals dispersesfrom 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):

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

The constant *k* in this equation relates to the intensity of competition. Reproduction then takes place by adding a multiple $F.s_0$ 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.

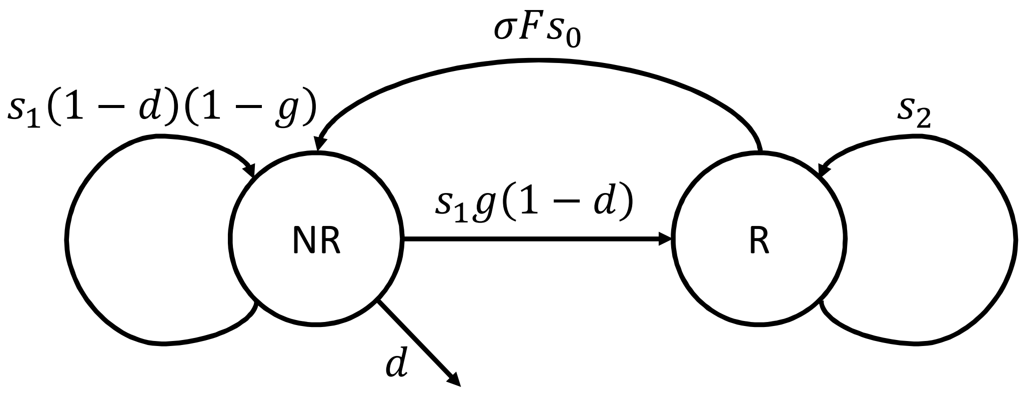


Figure S2. Generic life cycle simulated in MetaConnect, indicating how the parameters defined in the text relate to the pools of reproductive (R) and non-reproductive (NR) individuals in a single patch. Immigration from other patches is not shown since it depends upon the emergent behaviour of the whole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

Dispersal occurs by random walk. To obtain the required mean dispersal distance, the maximum number of steps moved at each dispersal eventwas made equal to the square of thespecified 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-repro-ductives** (s_1)	**Mortality of repro-ductives** (s_2)	**Disper-sal rate** (d)	**Comp-etition coef-ficient** (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 initialperiod for the model tosettle: 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	**-0.990**
Butterflies	50 km	-0.921	-0.958	-0.982	**-0.992**	-0.989
Mammals	50 km	-0.868	-0.900	-0.947	-0.973	**-0.983**
Birds	50 km	-0.161	**-0.958**	-0.865	-0.816	-0.927
Trees	500 km	-0.940	-0.996	-0.998	**-0.999**	**-0.999**
Birds	500 km	-0.821	-0.949	-0.968	-0.979	**-0.983**
	Mean	-0.696	-0.933	-0.949	-0.957	**-0.979**

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:

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

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

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

This is dependent on the distance d_{ij} between patches i and j, as well as onthe parameter α, which is defined as the reciprocalof 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:

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

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):

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

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

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

where ρ_{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.

	Extinction coefficient	**1/dispersal distance**	**Colonisation ability**
Functional type	u	α (km^{-1})	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

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 averagedover time steps 51-300 andthen 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 offive 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 and10 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 distancefor 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 potentialreproductive 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 × seed weight(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). Thesemaps 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 ~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	~B(Table S1)	Table S3	~B(0.5)	n/a
Dispersal mortality (besides failure to reach any patch)	0	n/a	0	n/a
Mortality of juveniles	~B(Table S1)	n/a	n/a	n/a
Mortality of non-reproductives	~B(Table S1)	n/a	n/a	n/a
Mortality of adults /Patch extinction rate	~B(Table S1)	Table S3	n/a	n/a
Reproduction rate (offspring per adult)	Table S1	n/a	~P(Table S4 ~Table S4)	n/a
Reproductive allocation*(=1 - Establishment allocation)	n/a	n/a	~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	~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	~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.

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

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Appendix S2: Additional results and validation

Contents

1. Additional results

2. Effects of process versus model differences

3. Raw output data

4. Standardised z-scores of output data

1. Additional results

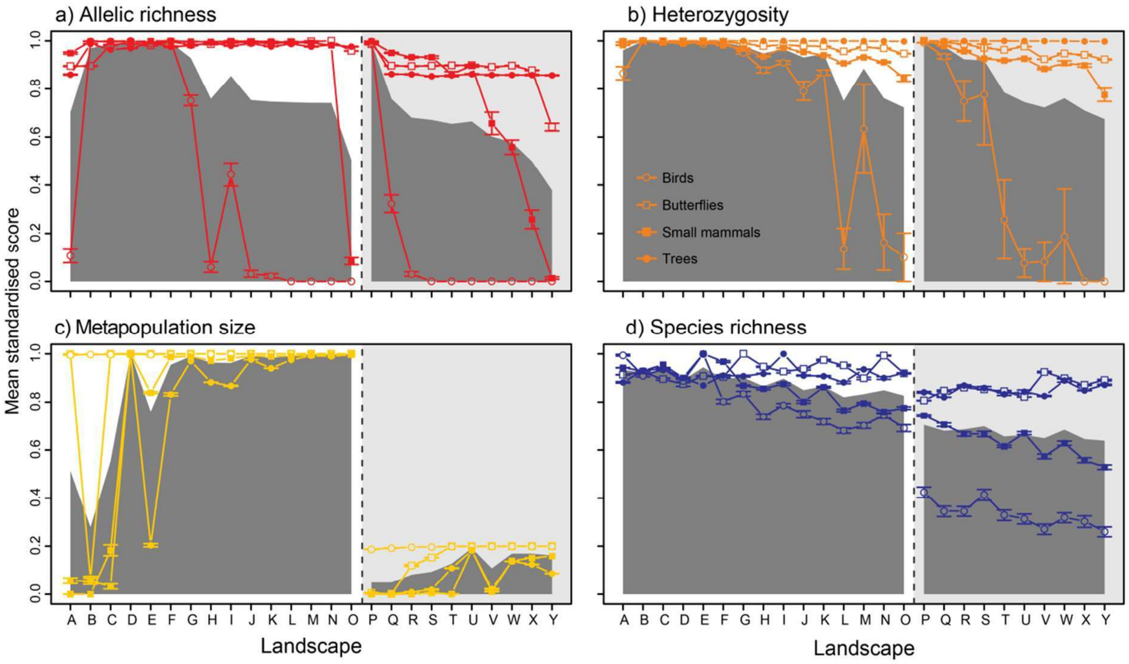


Figure S3. Results for each conservation criterion at the 5-km scale. Points are the scaled mean values (± 1 standard error) for the 25 landscapes (see Fig. 2 in main article for codes) from multiple runs of simulation models for four conservation criteria: (a) allelic richness (red), (b) heterozygosity (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.

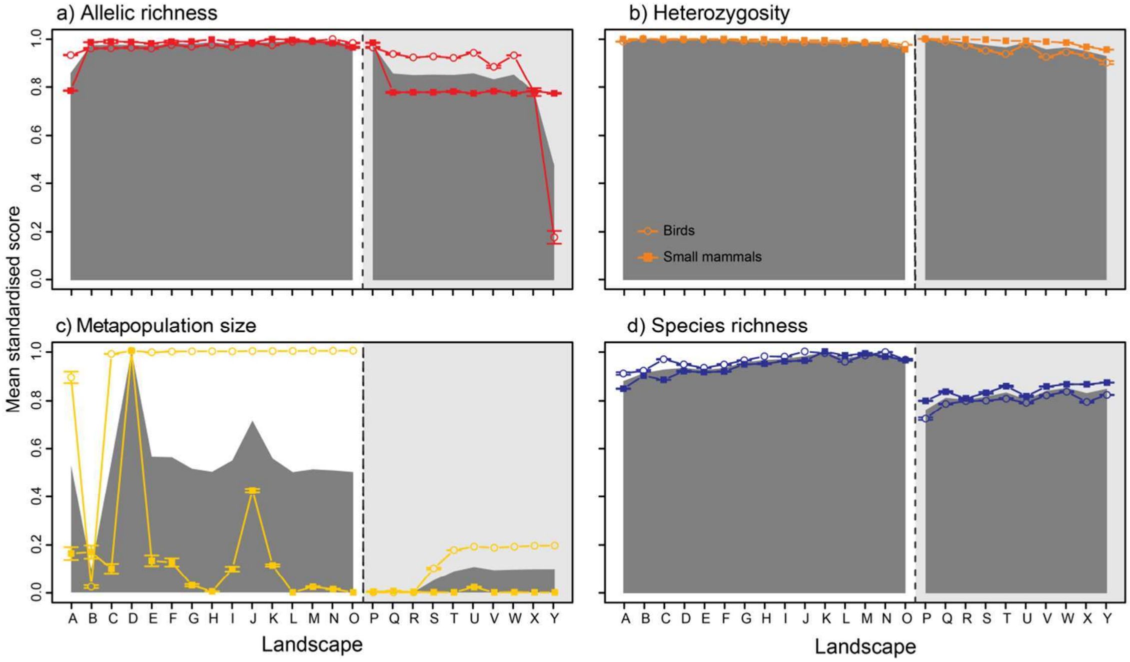


Figure S4. Results for each conservation criterion at the 50-km scale. Points are the scaled mean values (± 1 standard error) for the 25 landscapes (see Fig. 2 in main article for codes) from multiple runs of simulation models for four conservation criteria: (a) allelic richness (red), (b) heterozygosity (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.

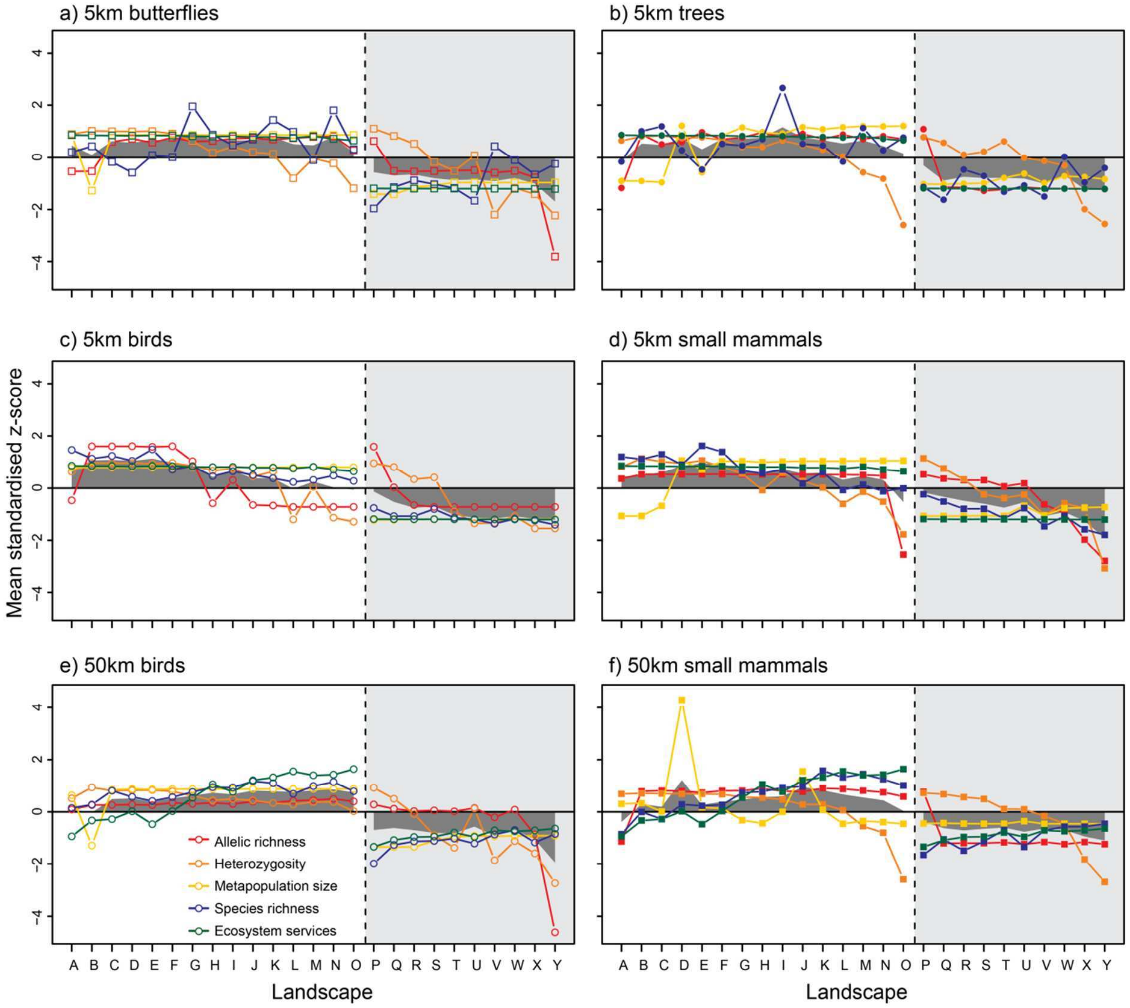


Figure S5. Standardised results for each functional scenario. Points indicate z-scores at the 5-km scale (a-d) and the 50-km scale (e, f), for birds (c, e), butterflies (a), small mammals (d, f) and trees (b), as assessed according to five conservation criteria evaluated by our simulation models: allelic 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).

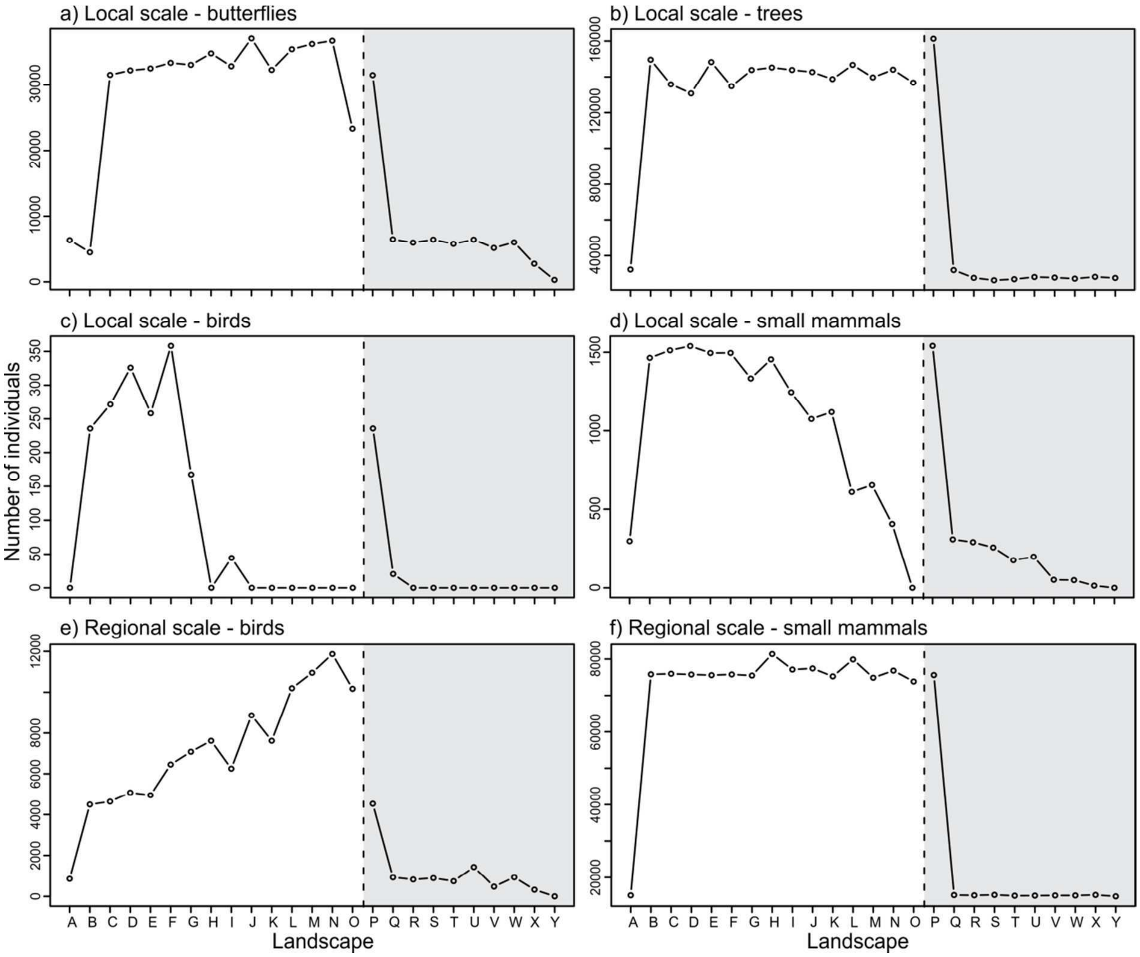
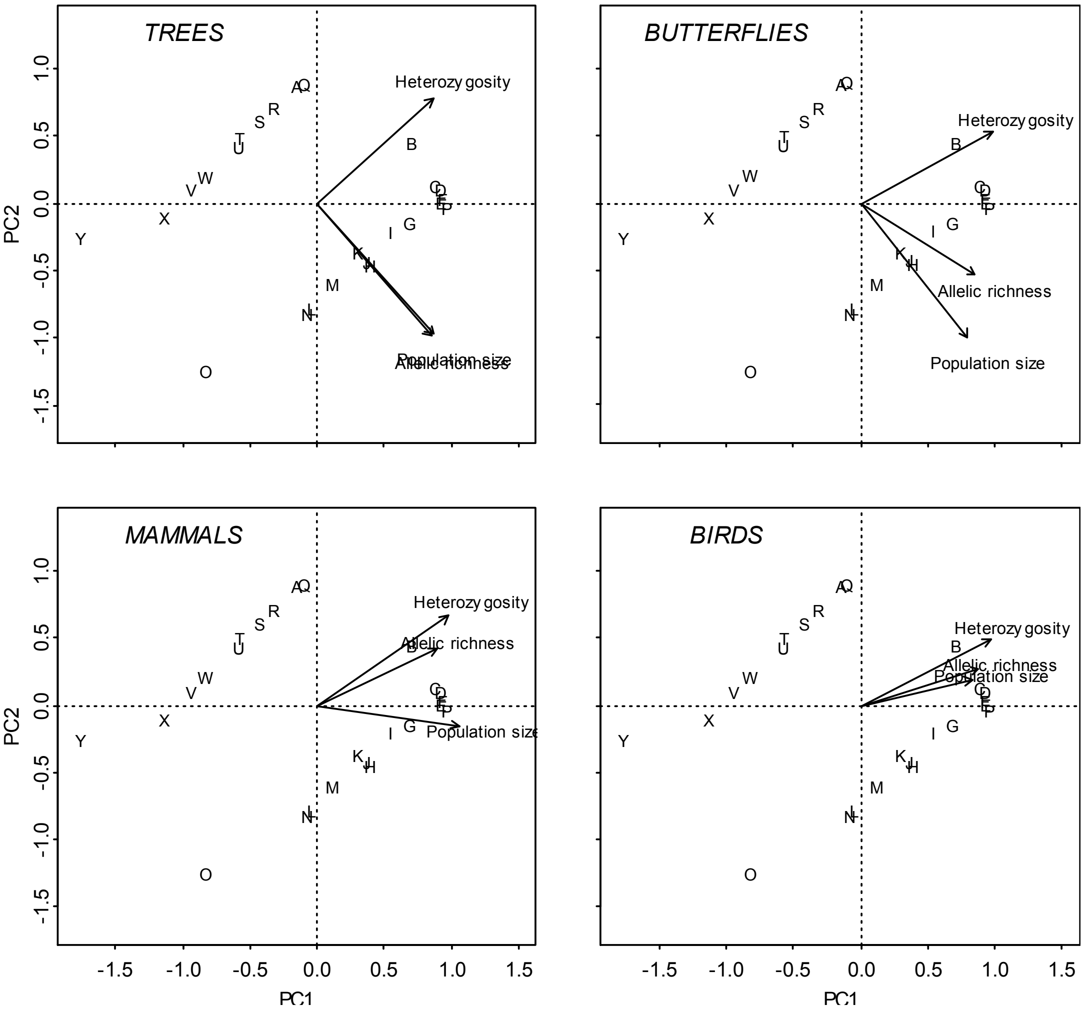


Figure S6. Mean total population sizes (number of individuals) estimated from 10 MetaConnect simulations parameterised for local scale butterflies (a), trees (b), birds (c) and small mammals (d) and regional scale birds (e) and small mammals (f).

A) Local Scale



B) Regional Scale

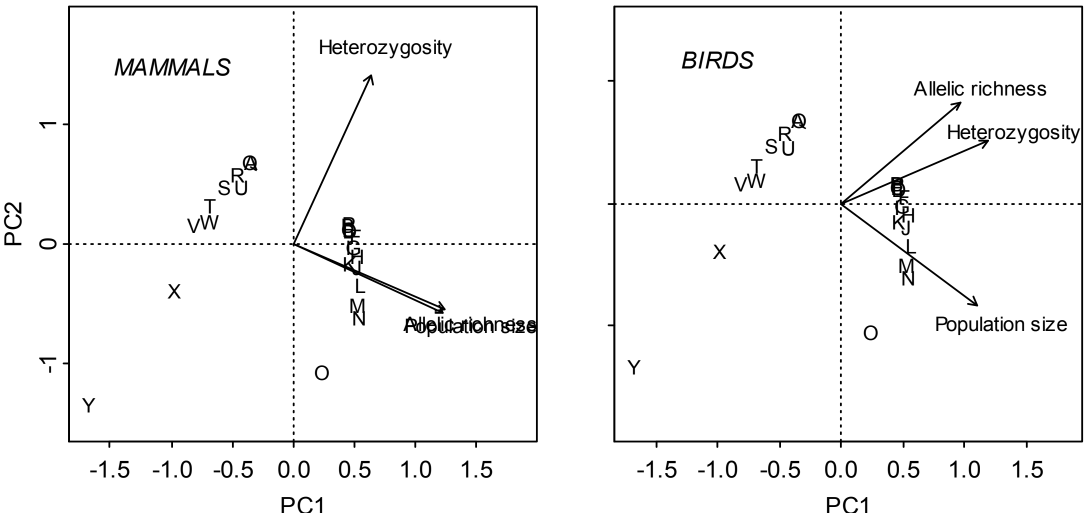


Figure S7 – Biplots of principle components analyses (PCA) from MetaConnect results for (A) local-scale landscapes and (B) regional-scale landscapes. For each scale a single biplot was produced, and each plot here is a layer of that biplot for one of the functional types, showing how the assessments 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.

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

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

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

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

3. Standardised z-scores of output data

Table S12. Allelic richness

Landscape	Butterflies 5km	Birds 5km	Mammals 5km	Trees 5km	Birds 50km	Mammals 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

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

Table S14. Metapopulation viability

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

Table S15. Species richness

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

Table S16. Pollination service

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