Multicriterion trade-offs and synergies for spatial conservation planning

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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 conservation 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 conservation 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. *Policy implications.* Using four simulation models, we show that different conservation objectives must be traded off in spatial conservation planning, and that considering only a single taxon or criterion may result in suboptimal choices when planning reserve networks. Nevertheless, heterogeneous spatial patterns of habitat can provide reasonable compromises for multiple criteria.

Key-words: 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, maximizing 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, Steffan-Dewenter & Tscharntke 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 maximize 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 policymakers 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.* 2015). 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 (i) heterozygosity and (ii) population viability would increase with decreasing fragmentation, while (iii) allelic richness and (iv) 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
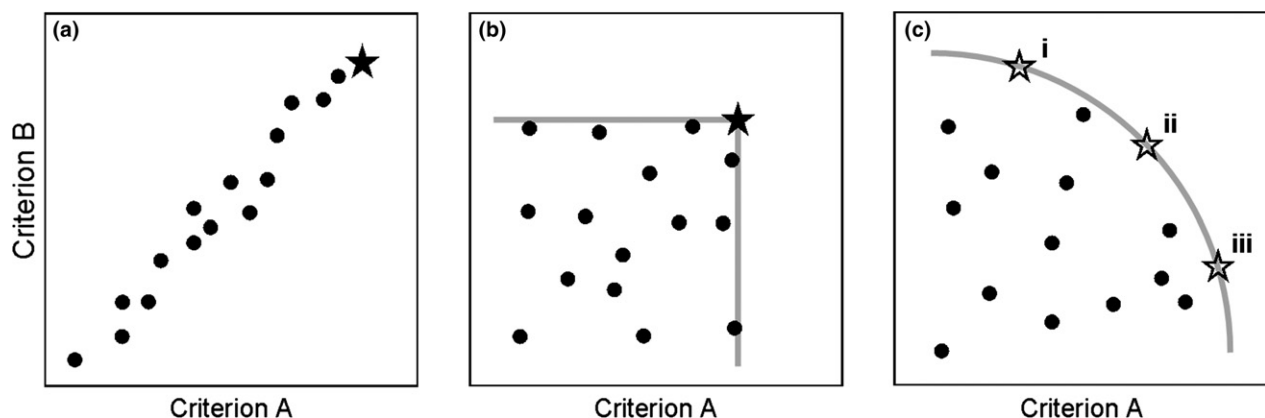

Fig. 1. Possible scenarios for the relationship between a pair of conservation criteria across the possibility space of landscape geometries: (a) positive association; (b) independence; (c) negative association. The stars indicate optimal geometries; in (c), there is an indefinite number of these and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

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, (v) 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, p107), 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, Supporting Information). 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 urbanization. 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 50 m, giving a tile size of 5 × 2·5 km, while 'regional' meant a cell size of 500 m and tile size of 50 × 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 six 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 parameterized 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).

Genetic diversity: heterozygosity and allelic richness

The individual-based, patch-focused model MetaConnect (Baguette, Clobert & Moulherat 2012; Moulherat 2014) 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 panmixia 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.

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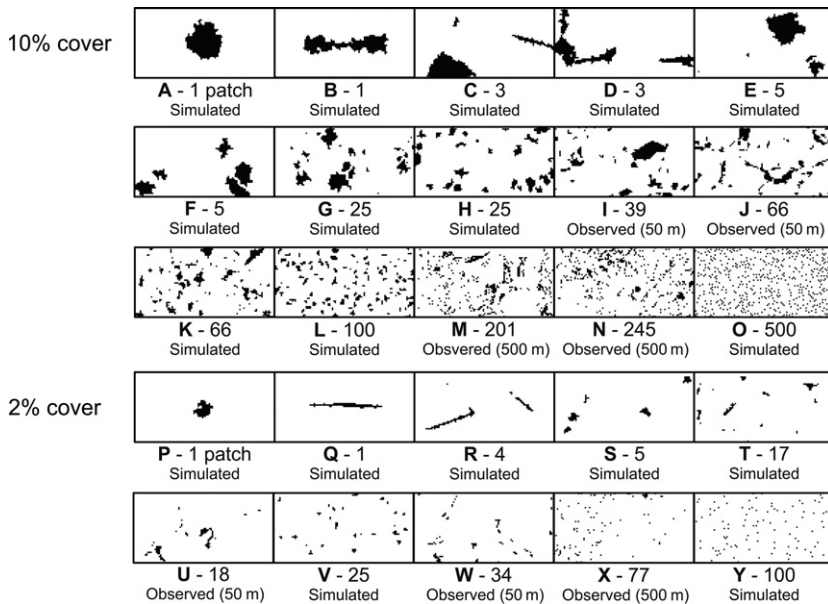
Fig. 2. The 25 landscape tiles used, grouped by percentage of area covered and annotated with number of patches and source (either simulated or extracted from observed patterns of British woodland at either 50-m or 500-m resolutions). Landscapes are ordered first by decreasing habitat amount, then by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

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^{-1})	Carrying capacity at 50-km scale (inds ha^{-1})	Community carrying capacity (inds ha^{-1})	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

SPOMSIM models local extinction and colonization as functions of patch-specific carrying capacities. Extinction rates were modelled using an exponential function of patch area and population carrying capacity; colonization was modelled as a function of patch area and the species' dispersal distance and colonization 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.

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, e.g., a latitudinal temperature gradient) and random quasi-fractal heterogeneity with an autocorrelation coefficient based on European topographical maps (representing, e.g., 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.

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 parameterized 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 multicriterion assessments, we scaled the model outputs across landscapes as proportions of the value for the best-performing landscape. Other standardization 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 multicriterion assessment were performed. First, we averaged standardized results across multiple criteria and scenarios. The weighting of different criteria is a nontrivial decision (see 'Outlook'); we simply used relative scores (scaled to ≤1), unweighted, for illustration. More sophisticated optimization procedures, such as pareto optimization, might be useful in realistic analyses for decision-making. Secondly, to visualize 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: (i) comparing predictions for the same criterion from several models and (ii) comparing predictions for multiple criteria from a single model. For (i), we cross-correlated population size assessments as available from each of the models except InVEST, and for (ii), 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 and 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 and 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,b). 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.

MULTICRITERION 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 (Fig. 3a,b). In mammals and birds, severe decreases in both allelic and species richness in the most fragmented landscapes resulted in overall performance
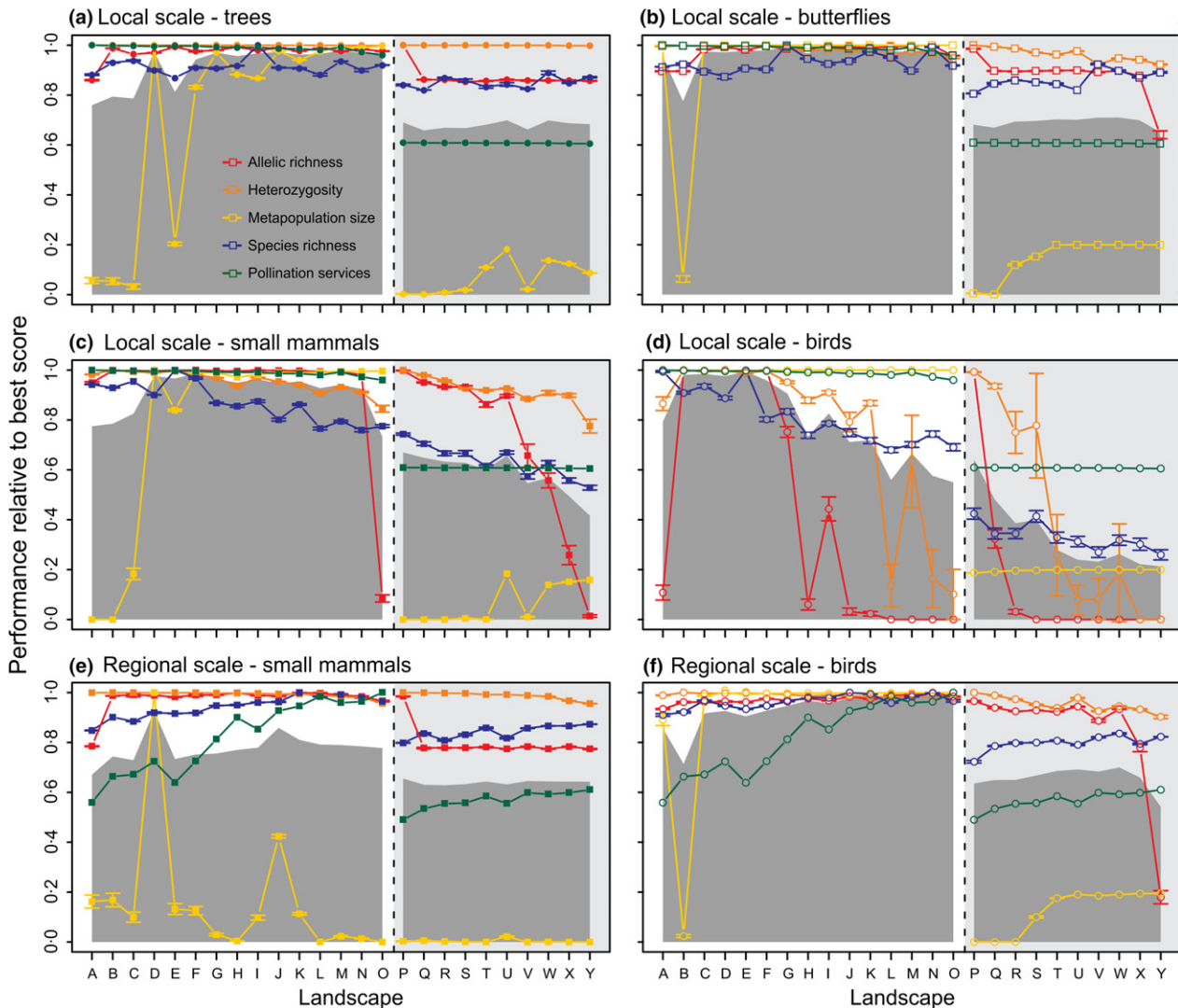
Fig. 3. Results for each functional scenario (for landscape codes see Fig. 2). Points show the scaled mean values (± 1 standard error) at the 5-km scale (a–d) and the 50-km scale (e, f), for birds (d, f), butterflies (b), small mammals (c, e) and trees (a), as assessed according to five conservation 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.

peaking in landscapes with intermediate or low levels of fragmentation (Fig. 3c,d).

At the regional scale, the fragmentation responses for birds and small mammals were largely reversed on all criteria (Fig. 3e,f). 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 MULTICRITERION 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 organization; 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 and 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 and 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, Steffen-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, Steffen-Dewenter & Holzschuh 2014), or according to the value of a key modelled parameter (Bascompte *et al.* 2007). Our results
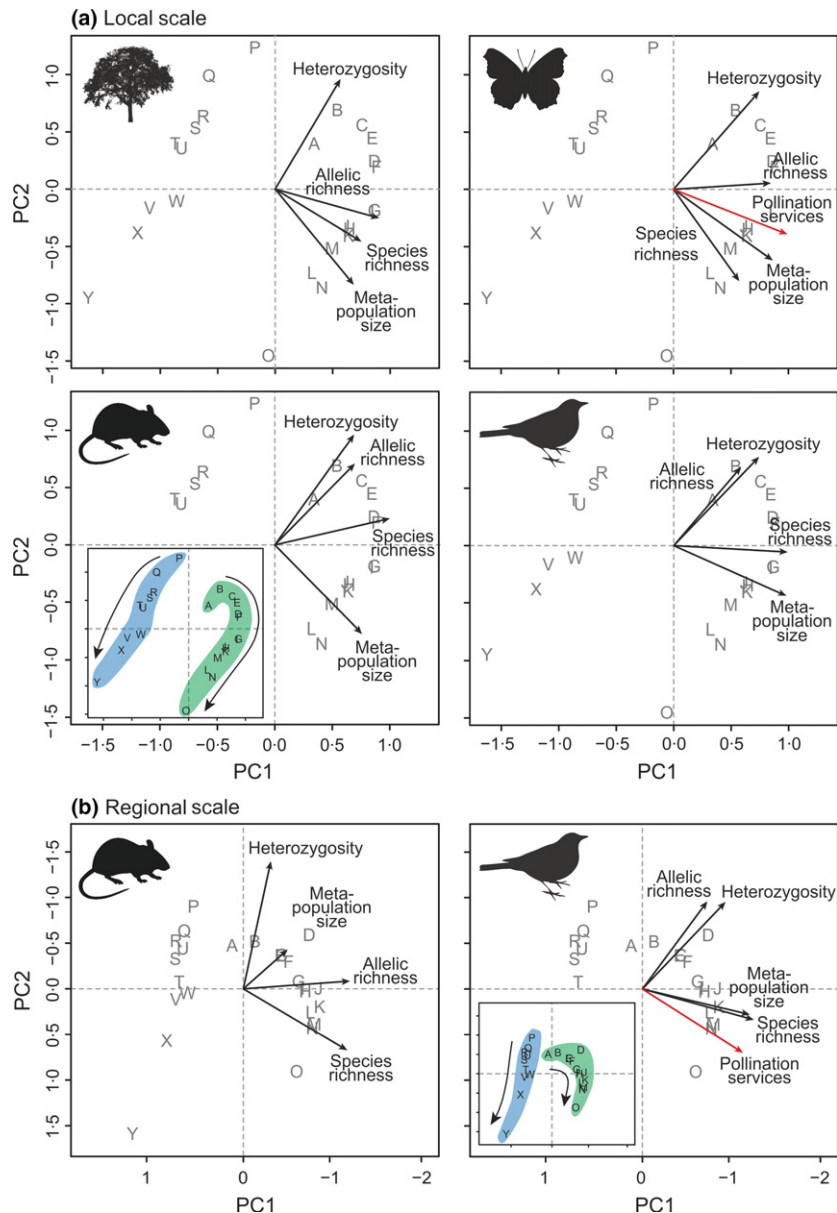

Fig. 4. Biplots of principle components analyses of conservation assessments of (a) local-scale landscapes and (b) regional-scale landscapes. For each scale, a single biplot was produced, and each plot here is a layer of that biplot for one of the functional types, showing how the assessments for that 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.
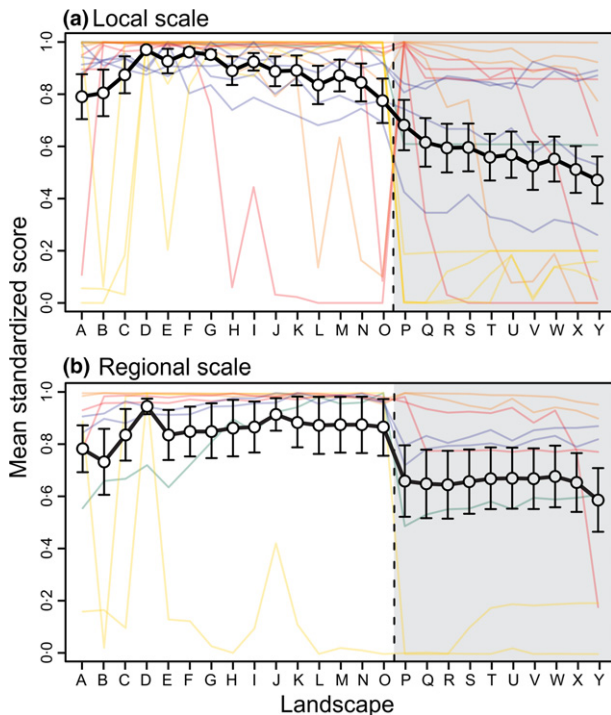
Fig. 5. Mean overall landscape conservation values (for landscape codes see Fig. 2). Values are averages of all the mean scaled values for criteria and functional types, which are overlain as lines for allelic richness (red), heterozygosity (orange), population size (yellow), species richness (blue) and pollination service (green). Vertical bars indicate standard errors.

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, nonuniform 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 parameterization of SPOMSIM seems to have produced rather high patch extinction and colonization 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 maximizing 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. Secondly, 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. Policymakers 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 nontranslatable 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 multicriterion, multiscale 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 colonized 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 generalizing 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. Secondly, 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, multicriterion assessment methods will surely remain important. Ecologists and policymakers 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 multicriterion methods (Smith & Theberge 1987). Our study shows how some of the most important decisions may lie in optimizing the geometry of habitat networks in a scale-sensitive way and with the needs of particular types of organisms in view (Wiggering & Steinhardt 2015).

Acknowledgements

Data accessibility

The model parameters used are provided in Appendix S1. Summary output data from the simulation models are provided in Appendix S2. Text files specifying the landscape patterns are provided in Appendix S3.

References

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Baguette, M., Clobert, J. & Moulherat, S. (2012) Population viability across scales. Project SCALES. Report for European Commission FP7 Environment, Brussels.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T. *et al.* (2014) Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science*, **345**, 1041–1045.

Bascompte, J., Luque, B., Olarrea, J. & Lacasa, L. (2007) A probabilistic model of reserve design. *Journal of Theoretical Biology*, **247**, 205–211.

Bocedi, G. (2010) *A general framework for modelling metacommunity dynamics under environmental changes*. MSc thesis, University of Aberdeen, Aberdeen.

Bocedi, G., Gunton, R.M. & Kunin, W.E. (2011) Comparative analysis of putative drivers and parameterization of disturbance scaling simulation model. Project SCALES. Report for European Commission FP7 Environment, Brussels.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cimon-Morin, J., Darveau, M. & Poulin, M. (2013) Fostering synergies between ecosystem services and biodiversity in conservation planning: a review. *Biological Conservation*, **166**, 144–154.

Diamond, J. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129–146.

Doerr, V.A.J., Barrett, T. & Doerr, E.D. (2011) Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. *Journal of Applied Ecology*, **48**, 143–147.

Ekroos, J., Olsson, O., Rundlof, M., Watzold, F. & Smith, H.G. (2014) Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation*, **172**, 65–71.

Evans, M.R., Norris, K.J. & Benton, T.G. (2012) Predictive ecology: systems approaches: introduction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **367**, 163–169.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.

Fenderson, L.E., Kovach, A.I., Litvaitis, J.A., O'Brien, K.M., Boland, K.M. & Jakubas, W.J. (2014) A multiscale analysis of gene flow for the New England cottontail, an imperiled habitat specialist in a fragmented landscape. *Ecology and Evolution*, **4**, 1853–1875.

Gaston, K.J., Blackburn, T.M. & Gregory, R.D. (1999) Does variation in census area confound density comparisons? *Journal of Applied Ecology*, **36**, 191–204.

de Groot, R.S., Wilson, M.A. & Boumans, R.M.J. (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, **41**, 393–408.

Gunton, R.M., Firbank, L.G., Inman, A. & Winter, D.M. (2016) How scalable is sustainable intensification? *Nature Plants*, **2**, 16065.

Harfoot, M., Newbold, T., Tittensor, D., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M.J., Scharlemann, J.P. & Purves, D.W. (2014) Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *Plos Biology*, **12**, e1001841.

Henderson, I.G., Holland, J.M., Storkey, J., Lutman, P., Orson, J. & Simper, J. (2012) Effects of the proportion and spatial arrangement of un-cropped land on breeding bird abundance in arable rotations. *Journal of Applied Ecology*, **49**, 883–891.

Henle, K., Kunin, W., Schweiger, O., Schmeller, D., Grobelnik, V., Matsinos, Y. *et al.* (2010) Securing the conservation of biodiversity across administrative levels and spatial, temporal, and ecological scales: research needs and approaches of the SCALES project. *Gaia – Ecological Perspectives for Science and Society*, **19**, 187–193.

Hodgson, J.A., Thomas, C.D., Cinderby, S., Cambridge, H., Evans, P. & Hill, J.K. (2011) Habitat re-creation strategies for promoting adaptation of species to climate change. *Conservation Letters*, **4**, 289–297.

Hopfenmüller, S., Steffan-Dewenter, I. & Holzschuh, A. (2014) Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS ONE*, **9**, e104439.

Humphrey, J.W., Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peace, A.J. & Park, K.J. (2015) What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landscape Ecology*, **30**, 21–50.

Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230–241.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 955–961.

Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J. *et al.* (2010) Making Space for Nature: a review of England's wildlife sites and ecological network. Report for Defra, London.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I. & Metzger, J.P. (2012) Associations of forest cover, fragment area, and connectivity

with neotropical understory bird species richness and abundance. *Conservation Biology*, **26**, 1100–1111.

Miller, R.I., Bratton, S.P. & White, P.S. (1987) A regional strategy for reserve design and placement based on an analysis of rare and endangered species distribution patterns. *Biological Conservation*, **39**, 255–268.

Moilanen, A. (2004) SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. *Ecological Modelling*, **179**, 533–550.

Mokany, K., Harwood, T.D. & Ferrier, S. (2013) Comparing habitat configuration strategies for retaining biodiversity under climate change. *Journal of Applied Ecology*, **50**, 519–527.

Moulherat, S. (2014) Toward the development of predictive systems ecology modeling: MetaConnect and its use as an innovative modeling platform in theoretical and applied fields of ecological research. PhD thesis, Université de Toulouse, Toulouse.

Natural Capital Project (2012) *InVEST*. http://www.naturalcapitalproject.org/, http://www.naturalcapitalproject.org/ (accessed 23 December 2012).

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R. *et al.* (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, **7**, 4–11.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.

Pardini, R., Bueno, A.D., Gardner, T.A., Prado, P.I. & Metzger, J.P. (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, **5**, e13666.

Pe'er, G., Henle, K., Dislich, C. & Frank, K. (2011) Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. *PLoS ONE*, **6**, e22355.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A. *et al.* (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, **11**, 499–515.

Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J. *et al.* (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications*, **13**, S199–S214.

Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, **179**, 209–222.

Schwartz, M.W. (1999) Choosing the appropriate scale of reserves for conservation. *Annual Review of Ecology and Systematics*, **30**, 83–108.

Simberloff, D. & Abele, L.G. (1982) Refuge design and island biogeographic theory: effects of fragmentation. *The American Naturalist*, **120**, 41–50.

Smith, P.G.R. & Theberge, J.B. (1987) Evaluating natural areas using multiple criteria: theory and practice. *Environmental Management*, **11**, 447–460.

Soulé, M.E. & Simberloff, D. (1986) What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation*, **35**, 19–40.

Sparkes, D.L., Jaggard, K.W., Ramsden, S.J. & Scott, R.K. (1998) The effect of field margins on the yield of sugar beet and cereal crops. *The Annals of Applied Biology*, **132**, 129–142.

Sutherland, C., Elston, D.A. & Lambin, X. (2012) Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. *Ecology*, **93**, 2465–2473.

Synes, N.W., Watts, K., Palmer, S.C.F., Bocedi, G., Bartoń, K.A., Osborne, P.E. & Travis, J.M.J. (2015) A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. *Ecological Informatics*, **30**, 222–229.

Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Sharp, R., Nelson, E. *et al.* (2011) *InVEST 2.4.3 User's Guide*. Stanford, CA, USA. http://www.naturalcapitalproject.org/.

Tallmon, D.A., Luikart, G. & Waples, R.S. (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, **19**, 489–496.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571–573.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.

Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kazmierczak, A., Niemela, J. & James, P. (2007) Promoting ecosystem and human health in urban areas using Green Infrastructure: a literature review. *Landscape and Urban Planning*, **81**, 167–178.

Wiggering, H. & Steinhardt, U. (2015) A conceptual model for site-specific agricultural land-use. *Ecological Modelling*, **295**, 42–46.

Wilson, K.A., Carwardine, J. & Possingham, H.P. (2009) Setting conservation priorities. *Annals of the New York Academy of Sciences*, **1162**, 237–264.

With, K.A., Gardner, R.H. & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, **78**, 151–169.

Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, G.D. (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 1443–1446.

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 parameterize the MetaConnect model.

Table S2. Correlations between heterozygosity slopes and final estimates.

Table S3. Values used to parameterize the SPOMSIM model.

Table S4. Details of species-specific traits used to parameterize the community model.

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

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

Fig. S2. Generic life cycle simulated in MetaConnect.

Appendix S2. Additional results and validation.

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

Tables S7–S11. Raw output data.

Tables S12–S16. Standardized output data.

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

Fig. S4. Between-criteria trade-offs (standardized data).

Fig. S5. Population sizes from MetaConnect.

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

Appendix S3. Collection of 25 text files specifying landscape patterns.