



Habitat re-creation strategies for promoting adaptation of species to climate change

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Abstract

Creation of new habitat could help species respond to climate change by facilitating range expansion in fragmented landscapes. However, there are currently no guidelines for deciding where new habitat should be placed to promote range changes. We developed a model to simulate the expansion of populations across a heavily fragmented landscape in the United Kingdom, and investigated the effectiveness of six habitat creation strategies for woodland, grassland, heathland, and wetland habitats. A strategy aimed at linking clusters of habitat patches was most effective for three of the four habitat types. Adding habitat evenly or randomly across the landscape, or according to stakeholder suggestions, were consistently better strategies than increasing aggregation of habitat. The results highlight that the best spatial pattern to facilitate range expansion is different from the best pattern to prevent extinction.

Introduction

Climatic change drives geographic range shifts in plant and animal species (Hickling *et al.* 2006; Parmesan 2006; IPCC 2007; Thomas 2010), but species' abilities to shift are limited by habitat availability (Hill *et al.* 1999; Warren *et al.* 2001; Honnay *et al.* 2002; Skov & Svenning 2004). Habitat specialists might be most constrained because they commonly occupy less than 1% of the land surface (Cowley *et al.* 1999; Gaston & Blackburn 2002), but even generalists can lag behind climate change in heavily fragmented landscapes (Warren *et al.* 2001). If species cannot shift, or shift too slowly, they could soon face high risks of extinction (Thomas *et al.* 2004).

There is growing recognition of the need for habitat restoration/re-creation to reconnect habitat and facilitate range shifts (Heller & Zavaleta 2009; Lawler 2009),

especially where habitats are depleted and fragmented. Biogeographic and population dynamic theory indicates that increased habitat availability generally leads to larger population sizes, lower risks of extinction and faster expansion (e.g., Flather & Bevers 2002; Kinezaki *et al.* 2010). It is far less clear what spatial arrangement of habitat would maximize rates of range expansion for a given total quantity of habitat. So, although ambitious and expensive plans for landscape-scale restoration are being considered (Lawton *et al.* 2010), there is a lack of guidance on how to prioritize sites for habitat re-creation.

Spatial aggregation of habitat typically maximizes population persistence (Hill & Caswell 1999; Flather & Bevers 2002; Hanski & Ovaskainen 2003), provided that habitats are not so close as to risk simultaneous extinction (Ovaskainen 2002; Etienne 2004; McCarthy *et al.* 2005). This is not necessarily the case under climate change

because even core habitats can become unsuitable. Habitat aggregation might facilitate range expansion if it maximizes population sizes and thus the number of dispersers available (Dewhurst & Lutscher 2009). But if the gaps between the habitat aggregations are too large, then “stepping stones” or a more even distribution of habitat might increase expansion rates (McInerney *et al.* 2007; Dewhurst & Lutscher 2009; Kinezaki *et al.* 2010).

Sophisticated spatial plans can be developed to give species escape routes from climate change, if their demography and dispersal are well understood (Williams *et al.* 2005; Phillips *et al.* 2008) or at least if one is willing to trust predictions of where bioclimatic boundaries will shift in future (e.g., Vos *et al.* 2008; Carroll *et al.* 2010). However, there might be general rules of thumb that would be effective for many species in many landscape situations. Rules of thumb could be very useful where habitat re-creation strategies are based on broad habitat types, and the landscape has to allow persistence of many known and unknown, current and future species. We simulate how different spatial strategies of habitat addition could facilitate range expansions into a landscape of suitable habitat from any direction. We investigate four contrasting initial distributions of habitat and 24 combinations of species traits (dispersal and population density). To reflect real patterns of habitat fragmentation and realistic (small) amounts of proposed habitat re-creation, we use a real case-study landscape: the Yorkshire and Humber region of northern England.

Methods

We used the patch-based Incidence Function metapopulation model (IFM; Hanski 1994) to examine expansions of populations across a heavily fragmented approximately 200 × 200 km landscape in northern England. Populations inhabited one of four habitat types (woodland, heathland, wetland, grassland) that currently cover 1–7% of the landscape (Table 1, Figure 1). We examined the impact of six habitat addition (= re-creation) strategies on

expansion rates, with a variety of population parameters representing a range of species types.

Habitat data and GIS layers

Vector-based maps (ESRI ArcGIS shapefiles) of the current (2004) distributions of heathland, broadleaved woodland, wetland, and grassland habitats in the Yorkshire and Humber region were obtained from Natural England (the government agency that oversees national nature conservation; Figure 1). These data are accurate to approximately 25 m resolution, and defined the baseline distribution of habitat for our scenarios and simulations.

With the exception of wetlands, we assumed additional habitats could potentially be re-created anywhere, except over existing seminatural habitat (of our four types) and urban areas. Urban areas were obtained at 25 m resolution from the satellite-based Landcover map 2000 (Fuller *et al.* 2002). Wetland re-creation was restricted to places that were geologically and hydrologically suitable for the creation of mires, fens, and lowland bogs (Penny 2005; Appendix S1).

Habitat addition scenarios

We investigated the addition of two different amounts of habitat, by six different strategies. For each habitat type, we compared the current distribution of habitat in the landscape (“Nothing” scenario) and the addition of new habitat equivalent to (1) a fixed 1% of the Yorkshire and Humber region (~150 km²), or (2) the more modest current UK biodiversity action plan targets for habitat restoration/re-creation by 2015 (0.01% to 0.46% of Yorkshire and Humber, depending on habitat type; Table 1). Thus, we examined the effectiveness of current conservation targets as well as slightly more optimistic scenarios of habitat addition.

Locations for habitat addition were selected as 4 ha blocks (200 × 200 m cells; the median of existing habitat fragment sizes). When a 4-ha cell was chosen, it was

Table 1 Summary of existing seminatural habitat areas in Yorkshire and Humber region, UK, and Biodiversity Action Plan targets for habitat restoration/re-creation by 2015. The percentage of grid squares that have none of the habitat in question is given as a rough indicator of spatial aggregation—the actual distribution of habitats is shown in Figure 1.

Habitat type	Current area, 10 ³ ha	Target re-creation for 2015, ha	Target, % of current	Current, % of Yorkshire and Humber	Target, % of Yorkshire and Humber	Aggregation in 10 km squares, % empty	Aggregation in 1 km squares, % empty
Heathland	113	180	0.16	7.24	0.01	52	81
Wetland	63	3,660	5.78	4.07	0.24	40	88
Woodland	48	7,154	14.84	3.10	0.46	44	62
Grassland	11	990	8.74	0.73	0.06	9	95

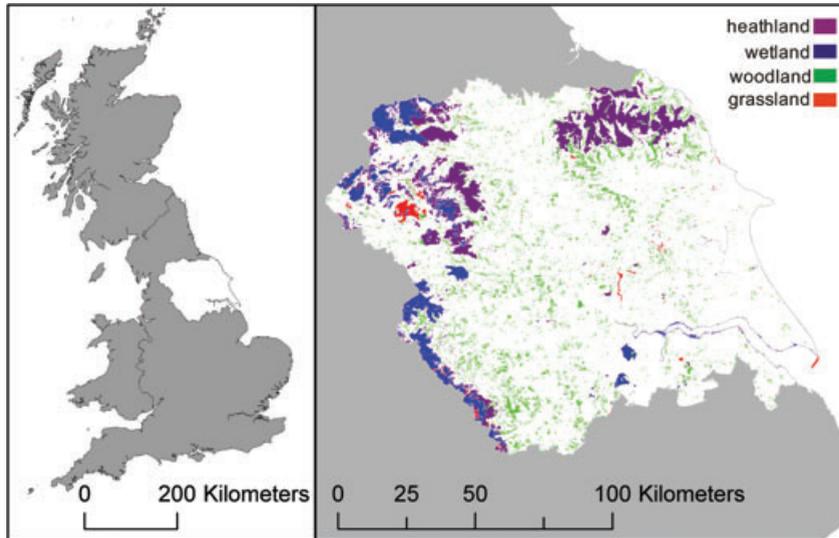


Figure 1 The study region: Yorkshire and Humber in the UK, and the seminatural habitats investigated: heathland (purple), broadleaved woodland (green), wetland (blue), and grassland (orange). Habitat data Natural England 2010, reproduced with the permission of Natural England, <http://www.naturalengland.org.uk/copyright/>; underlying OS data Crown Copyright and database right 2010. Ordnance Survey license number 100022021.

assumed that all available area (i.e., nonhabitat, known to 25 m resolution) within the cell was converted to the desired habitat. Habitat addition strategies were: (1) Quality: no new habitat area was added, but the carrying capacity of all existing habitat was increased by the same percentage as the proposed increase in area. (2) Aggregated: new habitat was added to cells that had highest connectivity to current habitat, until the target area was reached (Figure 2, red). $Connectivity_i = \sum_{j \neq i} A_j e^{-0.3d_{ij}}$, where A is the area of current habitat in cell j and d_{ij} is the Euclidian distance between the centers of cells i and j (Hanski 1994; further details in Appendix S1). (3) Random: new habitat was added to cells chosen at random. (4) Even: new habitat was added to cells with lowest connectivity (defined as above) to current habitat, to even-out the distribution of habitat availability (Figure 2, blue; further details in Appendix S1). (5) Link: this strategy linked clusters of habitat by finding and filling regional-scale bottlenecks in habitat availability (Figure 2, orange). “Clusters” were defined as the 10 km grid squares containing the most habitat (36 for each habitat type, containing $\geq 50\%$ of that habitat). The shortest straight-line routes linking clusters were identified (“minimum spanning tree”; Prim 1957), and new habitat was added to the locations of lowest connectivity (defined as above) lying within 5 km of these linkage routes. (6) Opportunities: new habitat was added at random within areas prioritized by local stakeholders. Representatives of public bodies, NGOs, and residents had been asked to identify priority areas for habitat re-creation based on their expert knowledge and after viewing maps of the four habitat types (YHBF/Natural England 2009; Appendix S1).

Running the models, and incorporating species traits

We used a version of the IFM (R code in Appendix S2) to quantify range expansion across our landscapes. In the IFM colonization depends on the location and population size of occupied patches, and extinction on population size (Hanski 1994). We assumed that expansion could occur in any direction because species might respond to different temperature and moisture gradients. At the start of each replicate simulation, a randomly selected bearing determined the origin of the expansion, then the 10% of habitat-containing cells that were closest to the origin were assigned to be occupied. Simulation was terminated when the population had reached the opposite side of the landscape, or after 100 times steps (generations) if the population had failed to expand.

To reflect a wide range of species from annual plants and invertebrates to mammals and birds, we ran simulations with three different population densities (1, 100, and 10,000 individuals per hectare of habitat), and four different realistic dispersal distances according to a literature review (Catchpole 2010; “maximum” distance between 0.5 and 16 km, see Figure 3). The area that functions as a patch (a well-mixed population) will be different for different species, and depend particularly on their dispersal ability. Therefore, we defined patches according to grids whose cell size increased with dispersal distance (200 m and 1 km grids for $\alpha = 10$; 1 km and 2 km grids for $\alpha = 3$; 2 km and 5 km grids for $\alpha = 1$; 5 km and 10 km grids for $\alpha = 0.3$). The sum of habitat area within a grid cell was multiplied by population

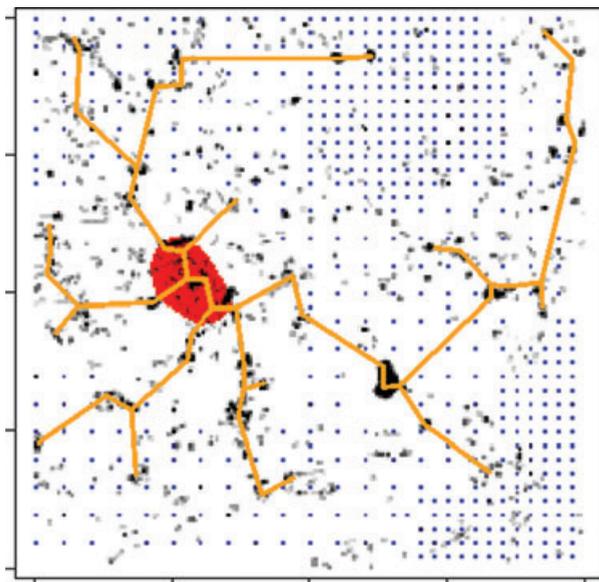


Figure 2 Illustration of the differences between the habitat addition scenarios: “aggregated” (red), “even” (blue), and “link” (orange) with a simplified example distribution of current habitat (gray-black). For the “aggregated” and “even” habitat addition scenarios we have picked 1% of the landscape to restore. For the “link” strategy, we have shown the lines that define the minimum spanning tree but there are additional steps to pick cells to restore: defining zones that are within a certain distance of the tree, then within those zones picking cells of minimum connectivity (so as to fill bottlenecks). For detailed maps of the real distribution of the four priority habitats in Yorkshire and Humber and the areas picked by these three strategies, see Figure S1.

density to give patch carrying capacity in the IFM. Extinction probability was always $1/\text{carrying capacity}$ of each patch at each time step. Altogether, this gave 24 parameter combinations that we henceforth term species types.

We ran 100 replicates of every habitat re-creation scenario for every species type. For the “Random” and “Opportunities” scenarios, the selection of locations for habitat re-creation was redone for every run.

Analysis of model outputs

From each model run, we recorded the distance of the farthest population from the origin at each time step. These data were used to compute the speed of range expansion (linear distance moved per time step). Because most simulations ended with <25 km expansion, or with colonization of the entire landscape (Figure S2), we also analyzed the binary variable that we term “getaways”: whether the population advanced at least 25 km in 100 time steps. The getaways measure shows whether strategies are helping the species that could be trapped, as opposed to making fast species even faster.

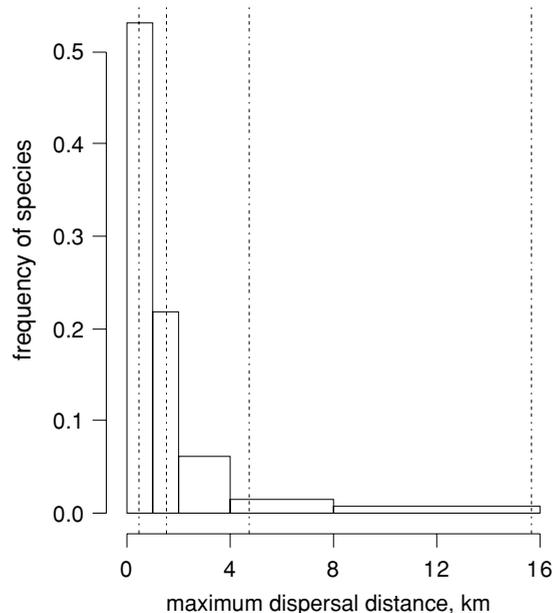


Figure 3 Distribution of maximum dispersal distance across species (histogram), and four values used for simulations (dashed vertical lines). Data come from a literature review (Catchpole 2010) covering UK native species of plants, mammals, and invertebrates that are associated with one or more seminatural habitats in our study. The alpha parameter (see connectivity equation in methods) was inferred by assuming that 5% of individuals go further than the stated maximum. The alpha values used in simulations were 0.3, 1, 3, and 10, which correspond to maximum dispersal distances of 15.7, 4.7, 1.57, and 0.47 kilometers, respectively.

Some modeled parameter combinations are likely to represent more real species than others, especially because there are more species with poor than good dispersal (Figure 3). Therefore, we report average rates of expansion and getaways after weighting simulation results by the observed frequency of dispersal distances obtained from a literature review (Figure 3). This weighting had little effect on the ranking of habitat addition strategies (see Figures S4 and 5).

Results

The region we studied has little remaining seminatural habitat (15% of the landscape altogether; Table 1), and remaining habitats are spatially aggregated (Figure 1; Table 1). However, aggregation varies; heathland is concentrated in a few large blocks, whereas woodland is more widely scattered (Figure 1; Table 1).

Converting 1% of the region to additional habitat increased average range expansion rates by 40–250 m per generation (depending on habitat type, Figure 4), and average successful getaways by 6–26% (depending on habitat type, Figure 5).

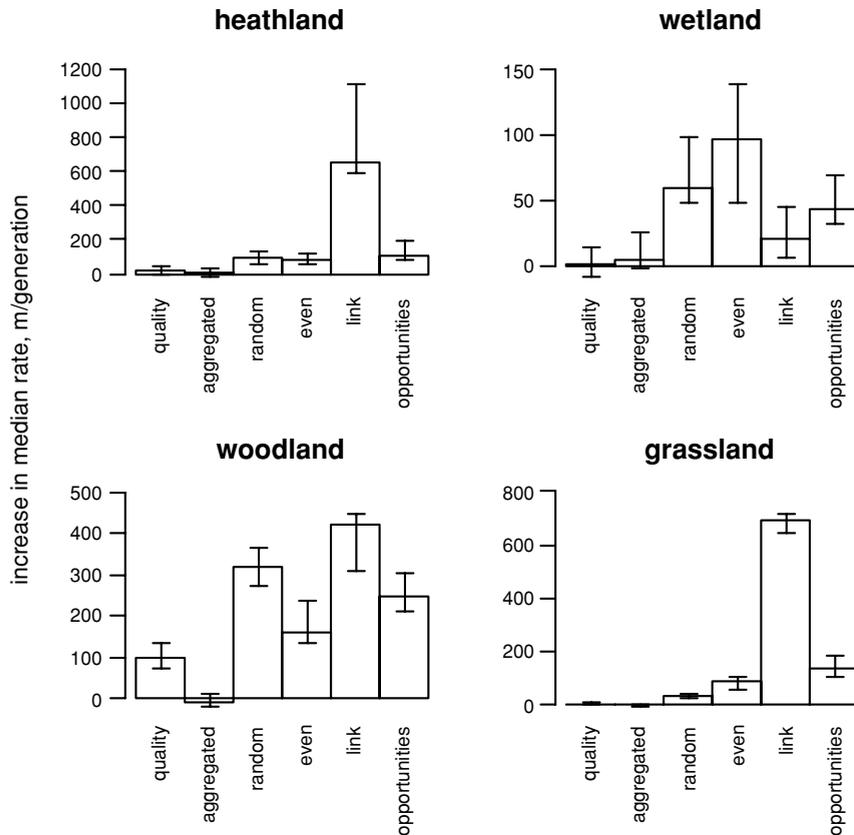


Figure 4 Differences between the six habitat addition strategies in terms of the median increase in the invasion rate relative to the “nothing” strategy. Results are weighted by the observed distribution of alpha values (see Figure 2). Ninety-five percent confidence intervals (error bars) were generated by bootstrapping with 10,001 resamples. These are intended to illustrate the precision of these observed averages, and not for hypothesis testing (with enough simulation replicates, we would be bound to find “significant” differences between simulations on different landscapes).

Habitat addition strategies varied in their success (Figures 4 and 5). The “aggregation” strategy scarcely improved average expansion rates or getaways relative to “nothing” (Figures 4 and 5). The “quality” strategy had limited impact for three out of four habitats—except for woodland, which is more evenly distributed across the region than the other habitats (Table 1). The “even,” “random,” and stakeholder-identified “opportunities” strategies were similar to each other and had consistently positive effects on rates of expansion and percentage getaways (Figures 4 and 5). The “link” strategy generated the highest expansion rates and getaways for three of the four habitats (Figures 4 and 5)—the exception was wetland, where re-creation was possible in only 7% of the study region due to the feasibility constraint.

Despite clear differences between the habitat addition strategies, differences in expansion rate between species types were even larger, (see Figures S4 and S5). Nevertheless, most species types responded in qualitatively similar ways to the six habitat addition strategies (positive correlation of strategy rank from one species to another, Figure S3), apart from the species type with the lowest dispersal ability and lowest abundance. This type of species never achieved range expansion with 1% habitat

addition by any strategy, and populations often retreated (Figures S4 and S5).

The relative success of different habitat addition strategies was robust to the absolute amount of habitat that was added. The ranking of the six strategies for each habitat type was almost unchanged (correlation 0.99) when comparing 1% of the land area of the region being added with the target amounts of habitat (Table 1) being added. As expected, the more habitat is added, the greater the improvement in range expansion (Figure 6).

Discussion

We have shown that it is possible to increase the probability and speed of range expansion with a small amount of additional habitat. Some increase is obviously expected, since additional habitat provides additional populations producing emigrants, more targets for colonization, and on average shorter colonization distances between habitat patches. But it is important to demonstrate an appreciable increase with realistic parameters, because finding the land and funding for habitat re-creation is challenging (Lawton *et al.* 2010).

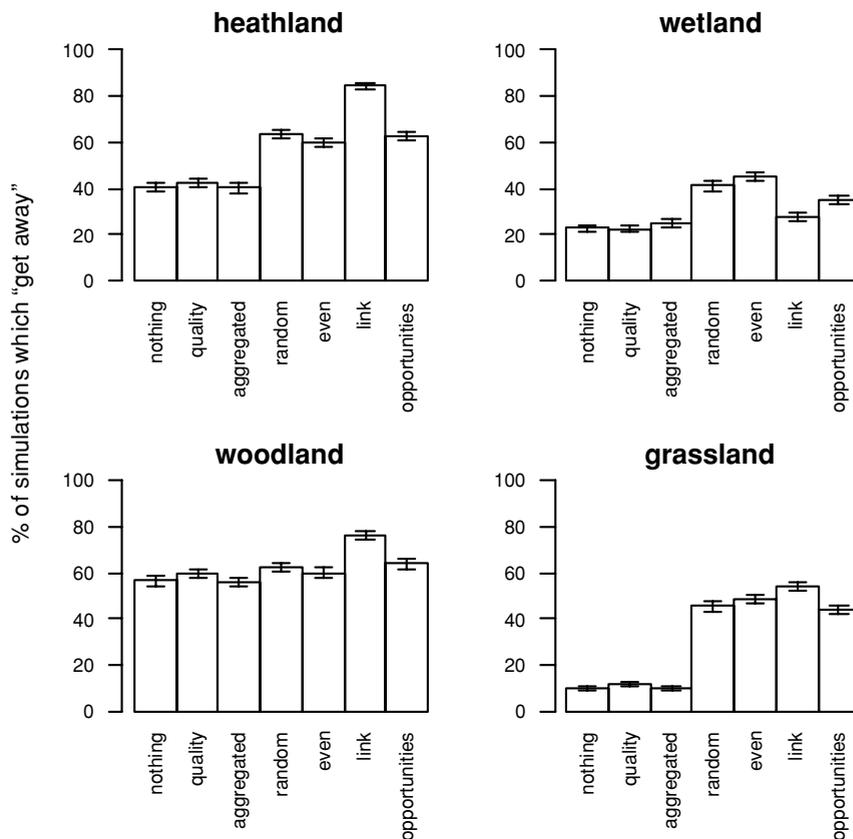


Figure 5 Differences between the six habitat addition strategies and the do nothing strategy in terms of the mean percentage of successful invasion “getaways” out of 100 simulation runs. Results are weighted by the observed distribution of alpha values (see Figure 2). Approximate 95% confidence intervals (error bars) were generated by assuming that the observed mean is the mean of a single binomial distribution with 2,400 trials.

One may argue that re-creation requires very specific spatial targeting because it is so expensive (Millennium Ecosystem Assessment 2005; Hobbs 2007), but we found three strategies that worked consistently and more or less equally well: “random,” “even,” and “opportunities.” These strategies are all very simple, so their effectiveness should encourage decision-makers that some progress can be made in the absence of a detailed plan tailored to the landscape.

However, it is possible to improve on the simplest strategies: in our case study the “link” strategy was most effective for three out of the four habitats. We think that its success arises from identifying locations where a small amount of habitat can cause a large improvement to the probability of colonizing large clusters of unoccupied habitat (i.e., identifying habitat bottlenecks). The link strategy is more complicated than the others and requires two key decisions: which are the important existing habitat clusters (that require linking), and how wide should the linking routes be? Future work should develop some guidelines on implementing this strategy given different initial distributions of habitat. It would be especially useful to find a robust way of rerouting the links if the shortest links are through regions that are unfeasible for

habitat re-creation (as occurred in our case study with the wetland habitat, Figure S1).

Our model did not consider the relative cost and feasibility of the different strategies. The ranking of benefits achieved with a given area (e.g., 1% of the landscape, Figures 4 and 5) might be less practically relevant than the ranking of benefits achieved with a given budget. The more habitat area (or carrying capacity) can be added, the faster the rate of expansion, such that the benefits of a larger total area of a cheaper strategy could outweigh the benefits of a smaller area of better spatial strategy (e.g., Figure 6). The “quality” and “opportunities” strategies are notable examples that are likely to be cheaper and more feasible. The “quality” strategy corresponds to improving the management of existing habitat so that it can support bigger populations; methods to do this are often better understood than methods to create habitat (Hobbs 2007). The “opportunities” areas were chosen by local stakeholders, who were aware of competing land uses, public support for nature conservation, and other socioeconomic issues.

One striking result is that the aggregated strategy was the least effective at facilitating range expansion. This has significant implications because many existing

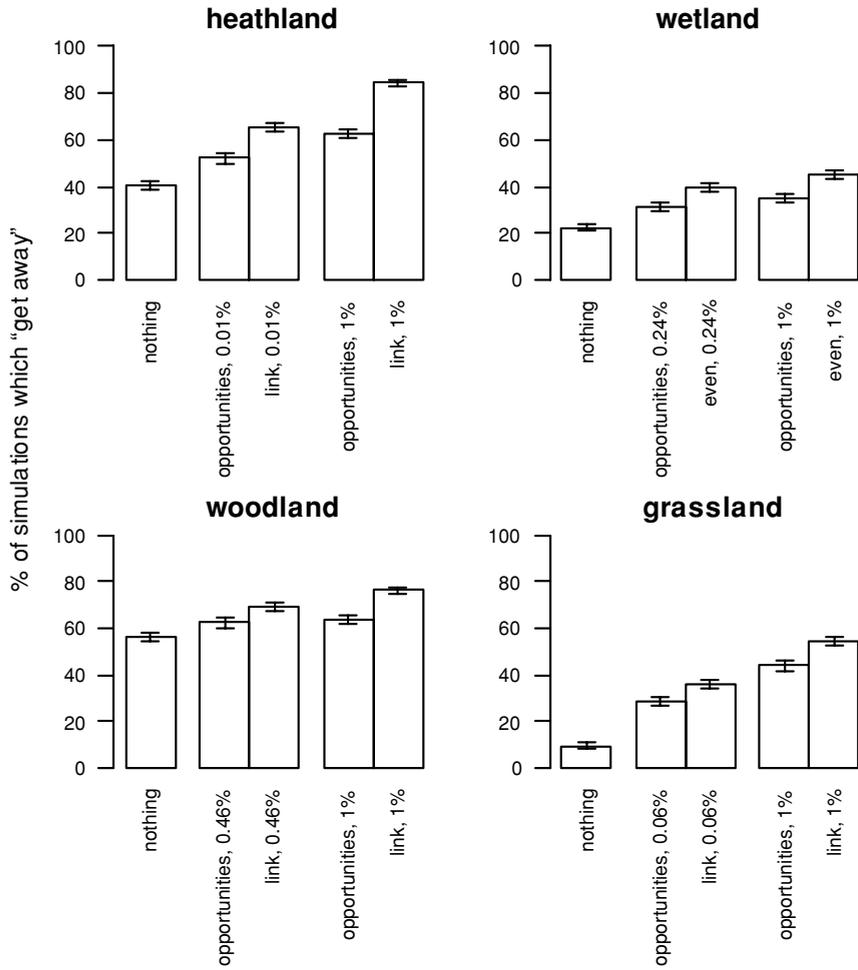


Figure 6 How getaways increase with increasing amounts of habitat added to the landscape: either the amounts of habitat re-creation that are planned for the different habitat types (see also Table 1), or 1% of Yorkshire and Humber. The weighted mean percentage of getaways, with binomial 95% CI (error bars), is plotted for the opportunities strategy and for the best observed strategy (“even” for wetland, “link” for the other habitats).

conservation planning guidelines and tools favor aggregated patterns (e.g., prioritizing large patches and minimizing interpatch distances or boundary lengths, Margules & Pressey 2000; Sarkar *et al.* 2006). They do this because much theoretical and empirical evidence shows that small isolated patches of habitat usually hold fewer species, and populations within them are less viable (Margules & Pressey 2000). However, our results and other recent work (Kinezaki *et al.* 2010) suggest that the best spatial pattern for rapid range expansion is different from the best spatial pattern to prevent extinction (assuming habitat remains suitable). To appreciate this difference, consider our four example habitats (Figure 1): they cover a low proportion of the Yorkshire and Humber landscape, and are already highly aggregated. This leads to high population and metapopulation viability in some areas (e.g., within a few 10 km squares), but leaves large gaps at the regional scale that pause or even halt range expansion.

This gives us a new source of trade-offs between the needs of different species, and between short and long-

term priorities for conservation. Some species in some regions do not need to undertake rapid range expansion, for example, because a large part of their current range will remain suitable, or because they can move up an elevational gradient (Thuiller *et al.* 2006; Huntley *et al.* 2008; Hole *et al.* 2009). Other species have essentially no chance of expanding their range because their habitat is much too rare and fragmented (Warren *et al.* 2001). Such species will be highly reliant on the biggest existing clusters of habitat to prevent extinction in short term. So any rule of thumb that increases range expansion speed (e.g., a variant of our link strategy) will need to be used in conjunction with other measures (including identifying and protecting refugia, and possible assisted colonization, Lawler 2009).

It is always difficult to incorporate all the important variables and trade-offs into a spatial conservation plan (Margules & Pressey 2000). The selection of sites could undoubtedly be made more effective if we knew exactly what species to plan for, where they exist currently, what subset of habitat would be suitable for them now and

in the future under climate change, and how much it would cost to create that habitat on different land parcels. The methods to predict species range shifts are improving rapidly (reviewed in Huntley *et al.* 2010), and some sophisticated planning for multiple species has already been attempted (Phillips *et al.* 2008). Our approach to modeling is more tactical. We look for general-purpose strategies that might on average help the set of species dependent on a particular habitat. When we find results that are consistent across species and habitats, they give some insight into the underlying drivers of range expansion speed. The most consistent result is that the “random” and “even” strategies increase range expansion speed more than the “aggregated” strategy. We know that in theory, given our model assumptions, the “aggregated” strategy would minimize the extinction risk in an already occupied landscape (Hanski & Ovaskainen 2003). This highlights the fact that expansion speed is not synonymous with population viability, even though both will generally increase the more habitat is added to the landscape (Kinezaki *et al.* 2010). The speed of expansion is a critical factor in species’ ability to adapt to climate change: some climatic zones are predicted to shift at tens of kilometers per decade (Huntley *et al.* 2008). Therefore, expansion speed should be considered as a possible conservation metric alongside the ability of a certain area to support a viable population, especially in regions that are predicted to have high species turnover under climate change.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

- Figure S1**
- Figure S2**
- Figure S3**
- Figure S4**

Figure S5

Appendix S1: extra methodological details

Appendix S2: R version of the Incidence Function Model: help page and code

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