Ecological Informatics 30 (2015) 222–229

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape

Nicholas W. Synes [a,*], Kevin Watts [b], Stephen C.F. Palmer [c], Greta Bocedi [c], Kamil A. Bartoń [c], Patrick E. Osborne [a], Justin M.J. Travis [c]

[a] *Centre for Environmental Sciences, Faculty of Engineering and the Environment, University of Southampton, Highfield, Southampton SO17 1BJ, UK*
[b] *Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK*
[c] *Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK*

ARTICLE INFO

Article history:
Received 30 December 2014
Received in revised form 8 June 2015
Accepted 18 June 2015
Available online 25 June 2015

Keywords:
Ecological networks
Connectivity
Habitat restoration
Population dynamics
Dispersal
RangeShifter

ABSTRACT

An individual-based model of animal dispersal and population dynamics was used to test the effects of different climate change adaptation strategies on species range shifting ability, namely the improvement of existing habitat, restoration of low quality habitat and creation of new habitat. These strategies were implemented on a landscape typical of fragmentation in the United Kingdom using spatial rules to differentiate between the allocation of strategies adjacent to or away from existing habitat patches. The total area being managed in the landscape was set at realistic levels based on recent habitat management trends. Eight species were parameterised to broadly represent different stage structure, population densities and modes of dispersal. Simulations were initialised with the species occupying 20% of the landscape and run for 100 years. As would be expected for a range of real taxa, range shifting abilities were dramatically different. This translated into large differences in their responses to the adaptation strategies. With conservative (0.5%) estimates of the area prescribed for climate change adaptation, few species display noticeable improvements in their range shifting, demonstrating the need for greater investment in future adaptation. With a larger (1%) prescribed area, greater range shifting improvements were found, although results were still species-specific. It was found that increasing the size of small existing habitat patches was the best way to promote range shifting, and that the creation of new stepping stone features, whilst beneficial to some species, did not have such broad effect across different species.

1. Introduction

Climate change is expected to have increasingly detrimental effects for biodiversity, reducing available habitat (Huntley et al., 2008) and increasing extinction risk for many species (Thomas et al., 2004). Species distribution modelling studies have shown that the environmental niches of species will shift polewards under climate change (Chen et al., 2011; Hickling et al., 2006; Parmesan et al., 1999; Walther et al., 2002), meaning that existing conservation areas are likely to become less suitable for many of the species that currently occupy them (Araújo et al., 2011; Carroll et al., 2010). Furthermore, there is growing concern that habitat fragmentation, which is already a key factor in global biodiversity declines (Wilcox and Murphy, 1985), may further reduce species' abilities to shift their ranges (Fahrig, 2003; Hansen and Hoffman, 2011). These impacts from climate change and habitat fragmentation need to be considered in unison to fully understand the impacts on biodiversity (Barbet-Massin et al., 2012; Opdam and Wascher, 2004).

The selection of conservation areas generally focuses on balancing the number and size of habitat patches (Hodgson et al., 2009), and the representativeness of the desired habitats (Margules and Pressey, 2000; Thorne et al., 2011). More recently there has been a shift towards increasing connectivity to facilitate natural adaptive responses and resilience (Hansen and Hoffman, 2011; Heller and Zavaleta, 2009; Williams et al., 2005), allowing species to track their climatic niche (Araújo et al., 2011; Heller and Zavaleta, 2009).

A number of empirical studies have demonstrated that habitat corridors, stepping stones and permeable matrix features can help species move through fragmented landscapes (e.g. Aars and Ims, 1999; Fischer and Lindenmayer, 2002; Haddad and Tewksbury, 2005; Haddad et al., 2003; Robertson and Radford, 2009), but their effectiveness is variable and species-specific (Baum et al., 2004; Humphrey et al., 2014; Prevedello and Vieira, 2010). In addition, it is important to distinguish between foraging behaviour and dispersal behaviour, and between individual movements and population level benefits (which is not necessarily an implied result—Gilbert-Norton et al., 2010).

---

[*] Correspondence author. Tel.: +44 23 8059 3443.
E-mail address: n.synes@soton.ac.uk (N.W. Synes).

http://dx.doi.org/10.1016/j.ecoinf.2015.06.004
1574-9541/

Hodgson et al. (2011a) found that evidence for the benefits of habitat corridors, stepping stones and matrix improvements was weaker in comparison to the range expansion benefits provided by increasing habitat area, quality or aggregation.

Whilst previous studies have compared alternative climate change adaptation and reserve design strategies, they have often used simplistic models of dispersal (e.g. no dispersal versus universal dispersal, (Araújo et al., 2004); generic dispersal kernel across all study species, (Mokany et al., 2013)), or simplistic theoretical landscapes (e.g. binary habitat classification, (Kinezaki et al., 2010); fractal landscapes, (Hodgson et al., 2012); randomly generated fragmentation, (Bocedi et al., 2014b); habitats represented as nodes in a network, (Schoon et al., 2014)). Whilst these studies provide important theoretical insights, there is also a need to combine greater detail in dispersal and population dynamics with more realistic landscape configurations. Another important consideration is for studies to broaden the representation of species, since reserve design focussed on a single species is unlikely to provide community-wide benefits (Carroll et al., 2010; Moilanen et al., 2005). Hodgson et al. (2011b) studied the effects of climate change adaptation strategies on the range shifting of a selection of species types in a real landscape, using a modified version of the Incidence Function metapopulation model (Hanski, 1994). Further studies are required, using more detailed models of dispersal and population dynamics, to test these and other possible climate change adaptation strategies on a range of species in real landscapes.

The modelling framework presented here, in contrast to many studies (although note: (Hodgson et al., 2011b)), is applied to a real landscape and aims to represent climate change adaptation strategies at achievable scales (both in terms of total area prescribed for adaptation action and the size distribution of individual actions). Multiple species are separately modelled, with realistic traits and the incorporation of population dynamics and dispersal behaviour, but without considering biotic interactions. This research aims to inform the prioritisation of landscape-scale climate change adaptation strategies in order to conserve biodiversity and allow it to adapt to a changing climate. The study determines the relative impact of different adaptation strategies on the population dynamics and range-shifting potential for a number of species. The results give insights into the species-specific nature of adaptation strategy success, the importance of the spatial location of adaptation strategies, and the influence of the quantity of habitat change on their effectiveness.

2. Methods

2.1. Landscape

The study landscape was a 20 km × 50 km region extracted from UK Landcover Map 2007 data (Morton et al., 2011) and gridded at 20 m cell resolution (Fig. 1). The landscape is dominated by agriculture (~66% by area), with broadleaved woodland making up only ~8% of the total area, and represents typical fragmentation comparable with the UK national average: 50% agriculture, 6% broadleaved woodland (Morton et al., 2011). The remainder of the landscape is made up of semi-natural habitat (~16%), coniferous woodland (~4%) and built up areas (~6%). Broadleaved woodland was defined as the breeding habitat for our study species, and other habitat types formed the inter-patch matrix, each having its own associated movement cost.

2.1.1. Climate change adaptation strategies

We applied a number of climate change adaptation strategies to our study landscape as defined by Oliver et al. (2012), namely: (i) improvement of existing habitat, (ii) restoration of low quality

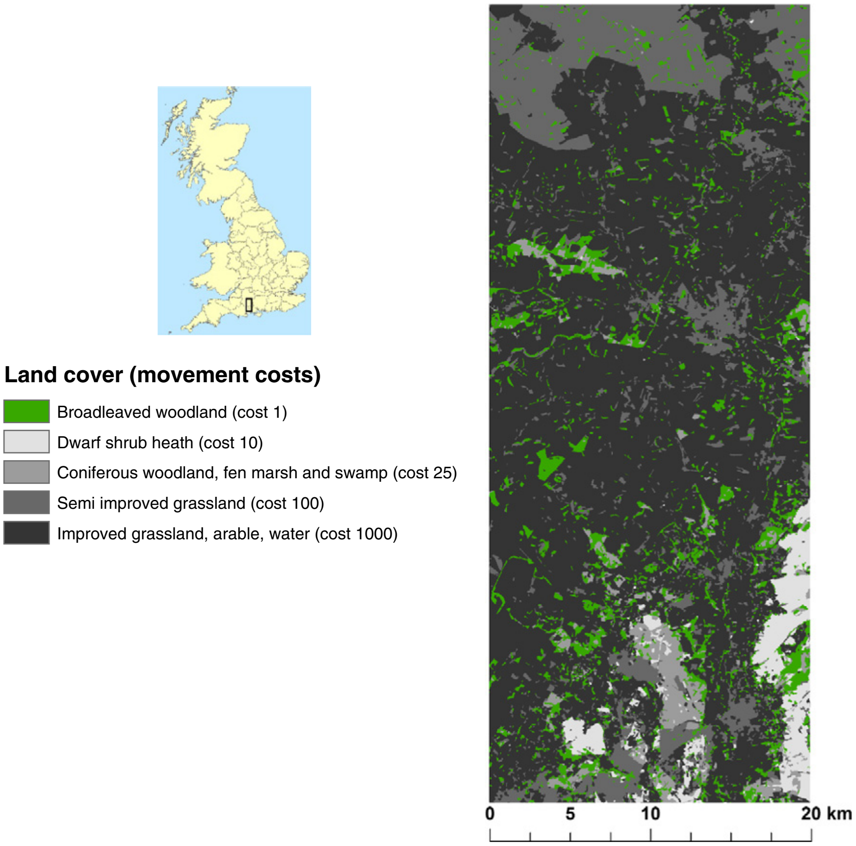

Fig. 1. The study landscape. Breeding habitat patches (broadleaved woodlands) are green, all other habitat types are grey. The study landscape is dominated by agriculture (~66% by area), with broadleaved woodland making up ~8% of the total area. The remainder of the landscape is made up of semi-natural habitat (~16%), coniferous woodland (~4%) and built up areas (~6%).

Table 1
The climate change adaptation strategies, as collated by Oliver et al. (2012), which were applied to our study landscape.

Name	Details
i. Improve-In-situ	Existing habitat patches are improved (e.g. plant diversity increased, or non-desirable plant species removed), increasing their carrying capacity.
ii. Restore-Adjacent	Existing low quality patches which are not currently suitable breeding habitat and are adjacent to existing suitable breeding habitat, are improved to become suitable breeding habitat.
Iiia. Create-Adjacent	New habitat patches are created within improved grassland and arable landcover types, adjacent to existing suitable breeding habitat.
Iiib. Create-Random	New habitat patches are created within improved grassland and arable landcover types, with no rule for adjacency to existing suitable breeding habitat.
Iiic. Create-AdjacentSmall	New habitat patches are created within improved grassland and arable landcover types adjacent to existing suitable breeding habitat below a size threshold of 3 ha.

habitat, and (iii) creation of new habitat (Table 1). The improvement strategy increased the carrying capacity of existing broadleaved woodlands by 10%. Although habitat quality does not always correlate with population density (Van Horne, 1983), there are many examples of quality having a positive correlation with abundance for butterflies (Pöyry et al., 2009; Thomas et al., 2011), small mammals (Corbalán et al., 2006; Haughland and Larsen, 2004; Peles and Barrett, 1996) and birds (Lloyd, 2008). Thus our simplification and generalisation of habitat quality across species are considered a reasonable representation of current knowledge of the potential effects of improving existing breeding habitat. The restoration strategy represents the conversion of unsuitable non-broadleaved woodland (i.e. conifer), which was adjacent to broadleaved woodland, into suitable breeding habitat. The creation strategy was split into three sub-categories based on different spatial rules: (a) adjacent to existing habitat, (b) randomly within the landscape, to act as stepping stones, or (c) adjacent to small patches (defined as <3 ha). Under each creation strategy new patches of habitat were formed from an initial cell (pixel) in the correct spatial location (Table 1). In order to create realistic woodlands, the new habitat patch was then expanded from these starting cells to reach the desired patch size derived from the size frequency distribution of existing broadleaved woodlands in the study landscape.

Two plausible scenarios of the area prescribed for climate change adaption actions were used: (1) 500 ha (0.5% of the landscape), representing a conservative level of change; (2) 1000 ha (1% of the landscape), representing a more ambitious level of change. These scenarios relate to the observed change in woodland area in the UK from 9% of total land area in 1980 to 12.9% in 2014 (Forestry Commission, 2014a). However, these values do not differentiate between broadleaved and conifer planting. Furthermore, due to limitations of land ownership and funding, the rate of woodland planting has decreased in recent years. Since 2009, an average of 82 km^2 of broadleaved woodland was planted in the UK each year, with 58% of this planting occurring in Scotland (Forestry Commission, 2014b). If this rate were maintained for the next 15 years, this would equate to 0.5% of UK land area being planted with new broadleaved woodland. Since the strategies are applied to the landscape using a stochastic spatial algorithm, ten replicates of each of the five strategies (see Table 1) were created. At the 1% level of prescribed change, the Restore-Adjacent strategy was not possible due to insufficient conifer woodlands adjacent to broadleaved woodlands in the study landscape.

2.2. Species

A number of artificial species were modelled, parameterised to represent a range of taxa having different population densities, stage structuring, dispersal abilities and lifespans (Table 2 and Appendix A). The species are not designed to represent real species accurately, but rather to represent a broad range of realistic characteristics, including density dependence and accounting for inter-specific variation in behaviour during transfer through the landscape matrix.

For species modelled with dispersal kernels (see Table 2 and Appendix A), distinct breeding habitat patches were defined as contiguous areas of habitat only. For species modelled with mechanistic dispersal, for which we estimated a perceptual range, patches were defined using a least-cost network methodology (Watts et al., 2010). This approach applies a cost distance analysis to generate a buffer around each distinct habitat patch, using the permeability of the surrounding matrix (taken from the Delphi analysis of Eycott et al. (2011)) as the cost values and our estimate of perceptual range as the maximum distance. Where multiple distinct patches were contained within a buffer, these were defined as a single home range patch.

2.3. The model

Species were simulated in the study landscape using RangeShifter (Bocedi et al., 2014a), a platform for spatially explicit individual-based modelling of population dynamics and dispersal. An important feature of RangeShifter is that dispersal is modelled in terms of its three fundamental phases: emigration, transfer and settlement. This level of detail in dispersal is often neglected in simulation models, but is crucial for determining species responses to environmental change and therefore for conservation planning (Travis et al., 2013). Moreover, RangeShifter incorporates optional mechanistic modelling of transfer limited by perceptual range using the 'stochastic movement simulator' (SMS; Palmer et al., 2011); simulating perceptual range in individual-based models has been demonstrated as a crucial factor in differentiating movement success through a fragmented landscape (Pe'er and Kramer-Schadt, 2008).

2.3.1. Simulation run-in

Due to the stochastic nature of the population dynamics and dispersal in RangeShifter, "run-in" simulations are important to determine a stable starting population for each species. For run-in simulations, the

Table 2
Species characteristics (SMS—stochastic movement simulator (Palmer et al., 2011), a mechanistic model of dispersal; Kernel—standard dispersal kernel). For detailed RangeShifter parameter values, see Appendix A.

Group	Dispersal ability (D)	Abundance/population density (P)	Reproduction (S)	Dispersal method	Name (letters and symbols indicate key species parameters)
Invertebrates	Low ($^{--}$)	Very high ($^{++}$)	Asexual[a] ($^{-}$)	SMS	Invert_D^{--}P^{++}S^{-}
	Medium ($^{-}$)	High ($^{+}$)	Asexual[a] ($^{-}$)	SMS	Invert_D^{-}P^{+}S^{-}
	Medium ($^{-}$)	Very high ($^{++}$)	Asexual[a] ($^{-}$)	Kernel	Invert_D^{-}P^{++}S^{-}
	Medium ($^{-}$)	Very high ($^{++}$)	Sexual ($^{+}$)	Kernel	Invert_D^{-}P^{++}S^{+}
Mammals	Medium ($^{-}$)	Medium ($^{-}$)	Sexual ($^{+}$)	SMS	Mam_D^{-}P^{-}S^{+}
	High ($^{+}$)	Low ($^{--}$)	Sexual ($^{+}$)	SMS	Mam_D^{+}P^{--}S^{+}
Birds	High ($^{+}$)	Medium ($^{-}$)	Sexual ($^{+}$)	SMS	Bird_D^{+}P^{-}S^{+}
	Very high ($^{++}$)	Low ($^{--}$)	Sexual ($^{+}$)	SMS	Bird_D^{++}P^{--}S^{+}

[a] In this context, an 'asexual' species does not necessarily imply asexual reproduction. This form of simulation may represent invertebrate species which mate upon emergence into the adult stage within the natal patch, and then fertilised females disperse and are able to found a new colony alone; hence dispersal of males does not need to be modelled.

landscape was reduced to the southern 20% only, and each species was initialised at half its carrying capacity in every habitat patch. Ten replicates of the simulations were run for a period of 50 years each, and the final patch occupancy and mean density of each species were used to initialise all subsequent simulations from which the results in this paper were gathered. This initialisation in the southern 20% of the study landscape represents the population prior to a northward shift.

2.3.2. Main simulations

Ten replicate simulations were run in RangeShifter for each of the eight species on the full landscape to generate baseline measures of range shifting. Range shifting was measured as the northern edge of the most northern patch containing an individual for asexual species, or a breeding pair for sexual species. Each replicate was initialised in the specific patches and at the mean population density from the run-in simulations in the southern 20% of the landscape only, and run for 100 years. For the ninety landscape adaptation scenarios created (two quantities for area of change; five adaptation strategies at 0.5%, four adaptation strategies at 1%; ten replicates of each), and for each of the eight species, ten replicate 100-year simulations were run (initialised as above).

3. Results

The baseline simulations for each species on the original landscape demonstrated the huge disparity in range shifting potential that results from differences in species characteristics (Fig. 2). Whilst some species were able to shift their range through almost the entire landscape (Bird_D^{++}P^{--}S^{+}), others barely expanded their range by more than 5 km (Mam_D^{+}P^{--}S^{+}, Invert_D^{-}P^{++}S^{+}) or 10 km (Mam_D^{-}P^{-}S^{+}, Bird_D^{+}P^{-}S^{+}, Invert_D^{-}P^{++}S^{-}). The species most successful at range shifting in the original landscape were those with a very high dispersal ability and low population density (Bird_D^{++}P^{--}S^{+}) or a high to very high population density and low to medium dispersal ability (Invert_D^{--}P^{++}S^{-}, Invert_D^{-}P^{+}S^{-}).

The difference between baseline range shifting and range shifting in the managed landscapes showed a variety of responses dependent on the species and management strategy (Fig. 3). At 0.5% habitat change (Fig. 3a), some species showed very little response to any of the adaptation strategies (Mam_D^{-}P^{-}S^{+}, Bird_D^{+}P^{-}S^{+}, Invert_D^{-}P^{++}S^{-}). There was evidence that the Create-AdjacentSmall strategy can be one of the best for increasing the range shifting distance for some species (Invert_D^{--}P^{++}S^{-}, Bird_D^{++}P^{--}S^{+}); Restore-Adjacent also provided a clear increase in range shifting for some species (Mam_D^{+}P^{--}S^{+}, Invert_D^{-}P^{++}S^{+}). There were also species-specific benefits from the Create-Random (Invert_D^{--}P^{++}S^{-}) and Create-Adjacent (Bird_D^{++}P^{--}S^{+}) strategies. Total gains over the baseline range shifting after 100 years were small, with the greatest gains for Bird_D^{++}P^{--}S^{+} under the Create-Adjacent strategy and Create-AdjacentSmall strategy (Figs. 3a and 4). Invert_D^{-}P^{++}S^{+} made large gains under the Restore-Adjacent strategy. All other species gained 1 km or less in range shifting from any of the habitat management strategies over the 100 years at 0.5% habitat change (Figs. 3a and 4).

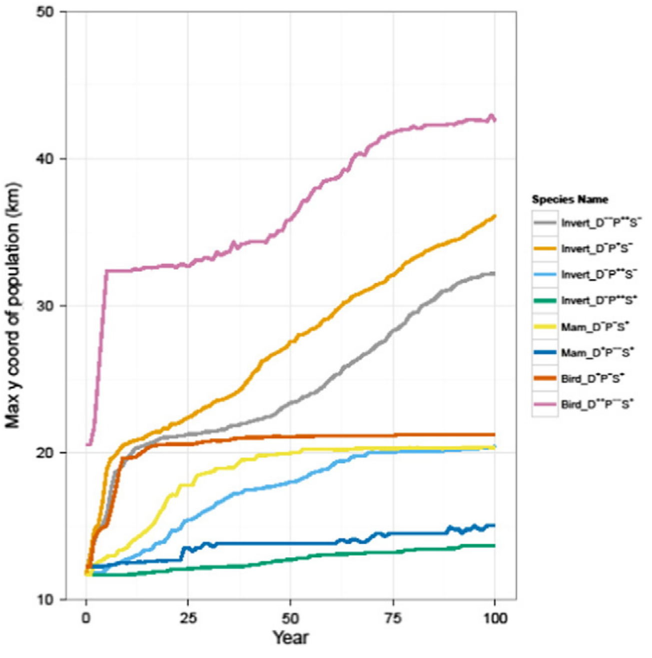

Fig. 2. Time series of range shifting in the baseline simulations (unchanged landscape), measured by the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Each line represents the mean of 10 replicates (replicates within RangeShifter).

Increasing the percentage of habitat change from 0.5% to 1% led to a consistent, but not guaranteed, increase in range shifting distance for the creation strategies (Fig. 4). Differences were still very limited for some species (Mam_D^{-}P^{-}S^{+}, Invert_D^{-}P^{++}S^{-}), and the Create-Random strategy resulted in a lower range shifting distance for some low to medium dispersal ability species (Invert_D^{--}P^{++}S^{-}, Invert_D^{-}P^{++}S^{+}) when increasing the percentage of habitat change from 0.5% to 1% (Fig. 4). Whilst the difference in range shifting distance from their baseline was different between species, the Create-AdjacentSmall strategy gave the greatest increase in range shifting distance for all species except Mam_D^{-}P^{-}S^{+} at the higher percentage of habitat change (Fig. 4). Create-Adjacent also increased range shifting distance for Bird_D^{++}P^{--}S^{+} and Invert_D^{-}P^{++}S^{-}, whilst Create-Random increased range shifting distance for Bird_D^{+}P^{-}S^{+} (Figs. 3b and 4).

4. Discussion

It is often suggested that conservation strategies and nature reserve design should aim to provide habitat and connectivity measures that will benefit as many species as possible (Carroll et al., 2010; Moilanen et al., 2005; Nicholson et al., 2006). Our work demonstrates how difficult it can be to target multiple species when resources for climate change adaptation are limited. At the 0.5% (500 ha) level of change, the improvements in range shifting are unremarkable, with some species achieving no increase in their range. In fact, an adaptation strategy can benefit range shifting for some species, but be detrimental for others. For example, the Restore-Adjacent strategy (Fig. 4) was beneficial for three species (Invert_D^{-}P^{++}S^{+}, Mam_D^{+}P^{--}S^{+} and Bird_D^{++}P^{--}S^{+}), but detrimental for others (Invert_D^{-}P^{+}S^{-} and Invert_D^{-}P^{++}S^{-}); the strategy was neutral or only slightly beneficial for the remaining species. When the adaptation strategy is focussed on increasing the quality or area of existing habitats independent of their size (Improve-In-situ, Restore-Adjacent, Create-Adjacent), species with high to very high population density and only low to medium dispersal ability (Invert_D^{--}P^{++}S^{-}, Invert_D^{-}P^{+}S^{-}) may make smaller gains than they would have made in the unchanged landscape (Fig. 3). No species makes more than a 4.3 km increase in their range compared with the baseline (i.e. range shifting in the unchanged landscape), and most species gain no more than 1 km over the 100 year period at the 0.5% level of change (Fig. 4). However it is important to note that this result may illustrate one of the problems with focussing on connectivity as a measure of the success of conservation actions. Conservation objectives strongly influence which habitat configuration will be most suitable (Margules and Pressey, 2000). Some strategies may be better suited to increasing in-situ population size, for example strategies that increase the size or quality of existing habitat. The proximity of new habitat to existing habitat can influence the lag in habitat growth and restoration, and may have a significant effect on the time it takes for new habitat to be colonised (Huxel and Hastings, 1999). This factor is rarely considered in reserve design or climate change adaptation studies, and was also not modelled in this study. Future work should incorporate habitat growth and restoration lag to determine its influence on the efficacy of different climate change adaptation strategies.

Increasing the percentage of habitat change from 0.5% to 1% leads to greater increases in range shifting distances (Fig. 4), demonstrating that one of the key factors in improving habitat connectivity is simply increasing the amount of habitat. This suggests that there are no cheap or shortcut solutions. Stepping stones (our Creation-Random strategy) proved only to be one of the best strategies for two species (Invert_D^{--}P^{++}S^{-}—Fig. 3a; Bird_D^{+}P^{-}S^{+}—Fig. 3b) that have vastly different population densities and dispersal abilities, both of which contribute towards a species' gap-crossing ability (e.g.: Awade and Metzger, 2008; Creegan and Osborne, 2005; Robertson and Radford, 2009). If the total habitat area remains low, the creation of small stepping stone features cannot fix centuries of habitat fragmentation. Different species will benefit from alternative strategies and have varying thresholds for the size of gaps that they can cross, meaning that the dominant use of a single strategy will not provide connectivity for all species, especially where the amount of habitat change is low. Mokany et al. (2013)

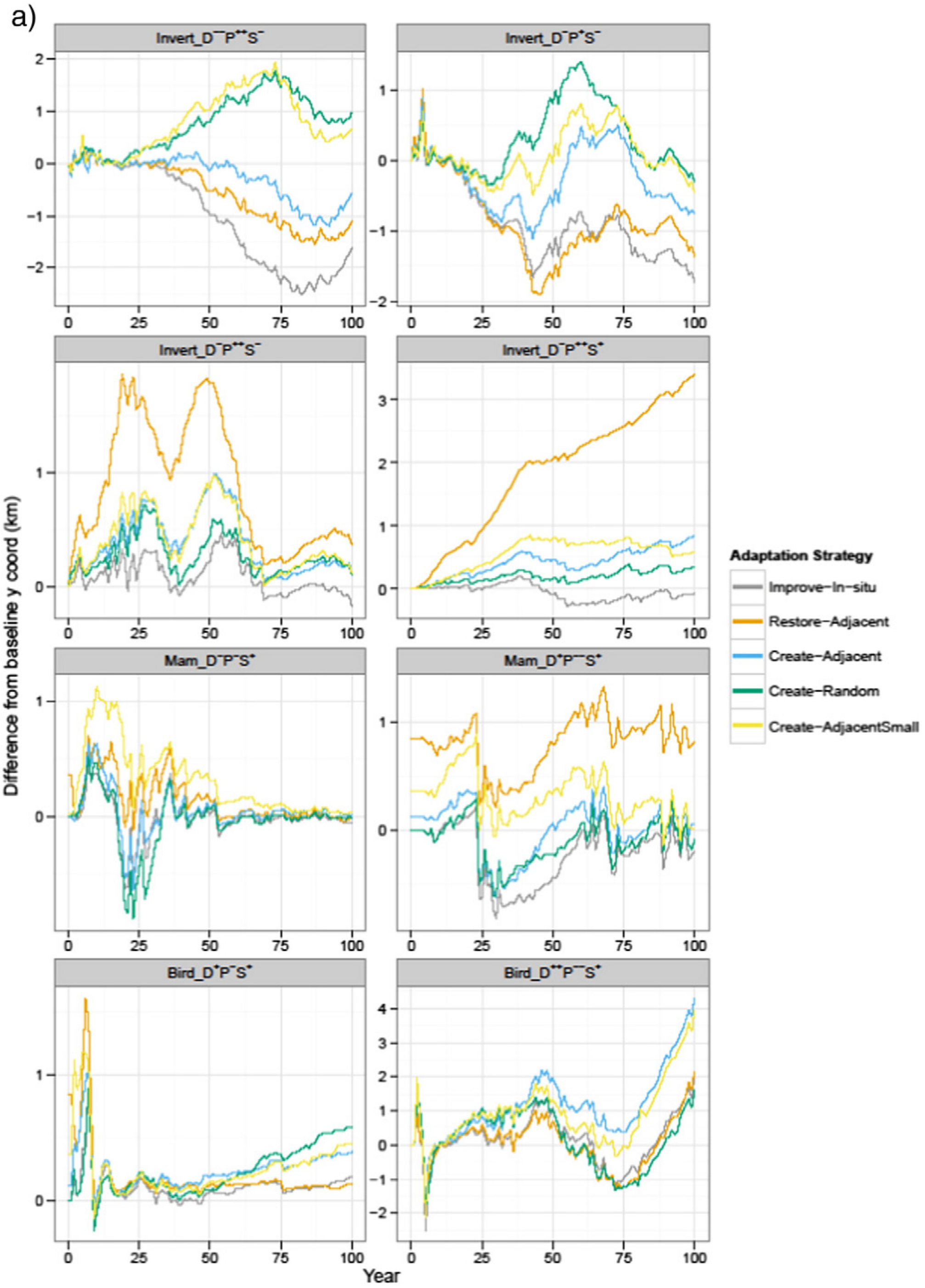

Fig. 3. Time series (for each species) of the difference in range shifting response between the adaptation strategy (with (a) 0.5% and (b) 1% habitat change) and the baseline simulation (unchanged landscape), measured by the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Each line represents the mean of 100 replicates (10 strategy replicates × 10 RangeShifter replicates). Note that fluctuations in "Difference from baseline y coord" are the result of both baseline range shifting (where the fluctuation will be visible across every adaptation strategy in the species' graph), and adaptation strategy range shifting (where the fluctuation will only be visible in the relevant adaptation strategy in the species' graph).

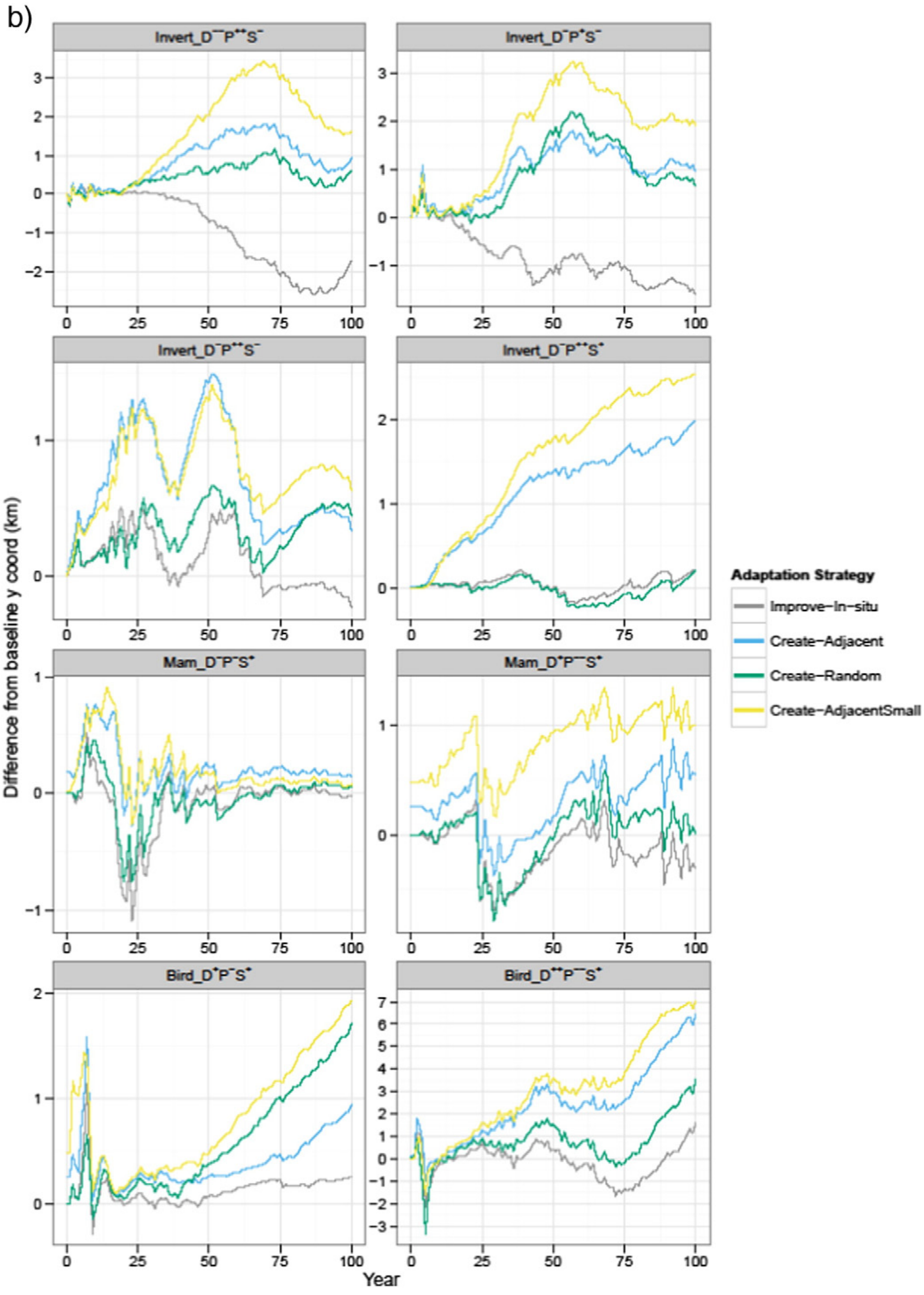

Fig. 3 (*continued*).

demonstrated the importance of using a balanced set of strategies, rather than focussing exclusively on connectivity, aggregation or representativeness. This study adds further evidence to this argument, but also demonstrates that in terms of range shifting, not all climate change adaptation strategies are equal; some provide greater benefits across broader groups of species (e.g. Create-AdjacentSmall—Fig. 4). Even though making changes to 1% of the landscape did increase range shifting, the improvement is not huge, and species that exist in medium population densities and with medium dispersal ability will still struggle (e.g. Mam_D^{-}P^{-}S^{+}—Fig. 4). It is important to note that this study used only one landscape for all simulations so perhaps there are landscape specific effects. Landscape configuration is known to play a crucial role in determining the success of different habitat management strategies (Hodgson et al., 2011a; Mokany et al., 2013), so an important future area of research is to test how influential this effect was over the results of this study.

The strategy that gives the most consistent benefit across species is the creation of new habitat adjacent to existing small patches (Create-AdjacentSmall). Hodgson et al. (2011b), on the other hand, found that their "random" (new habitat added to cells chosen at random) and "even" (new habitat added to cells with lowest connectivity) strategies gave the most consistent increases in range expansion speed, and that "aggregation" was the least effective at facilitating range expansion. Whilst these findings are in stark contrast to ours, it is important to note some key differences between the studies. Firstly, the two studies are based on different landscapes and at different scales; as discussed

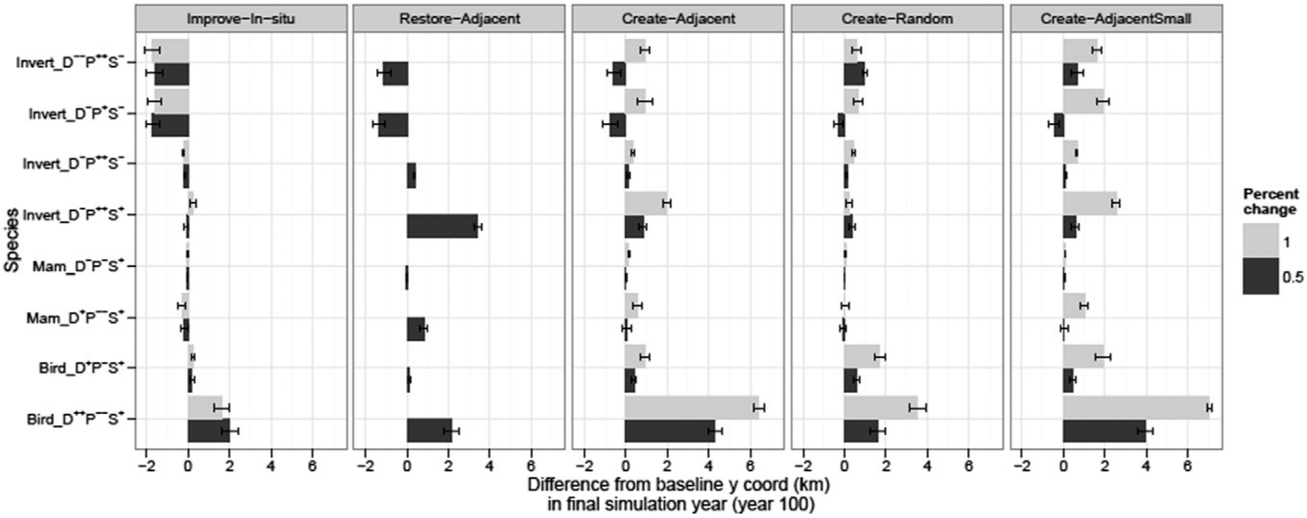

Fig. 4. Difference in range shifting response between five adaptation strategies and the baseline simulation (unchanged landscape), measured by the location after 100 years of the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Error bars represent standard error from 100 replicates (10 strategy replicates × 10 RangeShifter replicates). The Restore-Adjacent strategy was not possible with 1% prescribed for change due to insufficient conifer woodlands adjacent to broadleaved woodlands.

above, landscape configuration is an important factor in the success of habitat management strategies. Secondly, different adaptation strategies are used and whilst some are similar, none is identical; future work could study the effect of small variations in the way adaptation strategies are implemented. Thirdly, different models are used for the species populations; future studies to compare results from different population and dispersal models would be useful. The key is that a balanced approach should be used whereby different strategies are used for different regions and species (Mokany et al., 2013). Our study demonstrates that increasing the size of small patches may be the best method for improving connectivity for a number of different species simultaneously. In a world where conservation is increasingly restricted by land ownership and where budget is a limiting factor, focusing on increasing the size of small patches may be the best and most realistic option. However, landscape specific studies are crucial to ensure that the adaptation strategies chosen are best suited to the configuration of existing habitat and to the target species.

Acknowledgements

N.S. was supported by an EPSRC Doctoral Training Centre grant (EP/G03690X/1). K.B. was supported by the EU (FP7-IEF) Marie Curie Fellowship, project RANGESHIFT (Grant Agreement number: 302546). This work was also supported by the Natural Environment Research Council (NE/J008001/1), and funding from the Forestry Commission.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.ecoinf.2015.06.004.

References

Aars, J., Ims, R.A., 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. Ecology 80, 1648–1655.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14, 484–492.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob. Chang. Biol. 10, 1618–1626.

Awade, M., Metzger, J.P., 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral. Ecol. 33, 863–871. http://dx.doi.org/10.1111/j.1442-9993.2008.01857.x.

Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. Glob. Chang. Biol. 18, 881–890.

Baum, K.A., Haynes, K.J., Dillemuth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85, 2671–2676.

Bocedi, G., Palmer, S.C.F., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K., Travis, J.M.J., 2014a. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. Methods Ecol. Evol. 5, 388–396.

Bocedi, G., Zurell, D., Reineking, B., Travis, J.M.J., 2014b. Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. Ecography 37, 1240–1253.

Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Glob. Chang. Biol. 16, 891–904.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.

Corbalán, V., Tabeni, S., Ojeda, R.A., 2006. Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. Mamm. Biol. 71, 227–237. http://dx.doi.org/10.1016/j.mambio.2006.02.002.

Creegan, H.P., Osborne, P.E., 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. J. Appl. Ecol. 42, 678–687.

Eycott, A.E., Marzano, M., Watts, K., 2011. Filling evidence gaps with expert opinion: the use of Delphi analysis in least-cost modelling of functional connectivity. Landsc. Urban Plan. 103, 400–409.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 487–515.

Fischer, J., Lindenmayer, D.B., 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. Biodivers. Conserv. 11, 833–849.

Forestry Commission, 2014a. Forestry statistics 2014 [WWW Document] URL, http://www.forestry.gov.uk/website/forstats2014.nsf/TopContents?Open&ctx=5BFAF7169C6D2E038025735D00349319 (accessed 12.2.14).

Forestry Commission, 2014b. Forestry statistics 2014—new planting and restocking [WWW Document] URL, http://www.forestry.gov.uk/website/forstats2014.nsf/0/4F09640F0B6F8C27802573760033DE64 (accessed 12.2.14).

Gilbert-Norton, L., Wilson, R., Stevens, J.R., Beard, K.H., 2010. A meta-analytic review of corridor effectiveness. Conserv. Biol. 24, 660–668.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. Ecology 84, 609–615.

Haddad, N.M., Tewksbury, J.J., 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecol. Appl. 15, 250–257.

Hansen, L.J., Hoffman, J.R., 2011. The role of connectivity. Climate Savvy. Springer, pp. 136–146.

Hanski, I., 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 151–162.

Haughland, D.L., Larsen, K.W., 2004. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. J. Mammal. 85, 225–236.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142, 14–32. http://dx.doi.org/10.1016/j.biocon.2008.10.006.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Chang. Biol. 12, 450–455.

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011a. Habitat area, quality and connectivity: striking the balance for efficient conservation. J. Appl. Ecol. 48, 148–152.

Hodgson, J.A., Thomas, C.D., Cinderby, S., Cambridge, H., Evans, P., Hill, J.K., 2011b. Habitat re-creation strategies for promoting adaptation of species to climate change. Conserv. Lett. 4, 289–297. http://dx.doi.org/10.1111/j.1755-263X.2011.00177.x.

Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J., Cornell, S.J., 2012. The speed of range shifts in fragmented landscapes. PLoS One 7, e47141.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. J. Appl. Ecol. 46, 964–969.

Humphrey, J.W., Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peace, A.J., Park, K.J., 2014. What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. Landsc. Ecol. 1–30.

Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E., 2008. Potential impacts of climatic change on European breeding birds. PLoS One 3, e1439.

Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. Restor. Ecol. 7, 309–315.

Kinezaki, N., Kawasaki, K., Shigesada, N., 2010. The effect of the spatial configuration of habitat fragmentation on invasive spread. Theor. Popul. Biol. 78, 298–308.

Lloyd, H., 2008. Influence of within-patch habitat quality on high-Andean Polylepis bird abundance. Ibis 150, 735–745. http://dx.doi.org/10.1111/j.1474-919X.2008.00843.x.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. R. Soc. B Biol. Sci. 272, 1885–1891.

Mokany, K., Harwood, T.D., Ferrier, S., 2013. Comparing habitat configuration strategies for retaining biodiversity under climate change. J. Appl. Ecol. 50, 519–527.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., Simpson, I., 2011. Final report for LCM2007—the new UK land cover map. Countryside Survey Technical Report No 11/07.

Nicholson, E., Westphal, M.I., Frank, K., Rochester, W.A., Pressey, R.L., Lindenmayer, D.B., Possingham, H.P., 2006. A new method for conservation planning for the persistence of multiple species. Ecol. Lett. 9, 1049–1060.

Oliver, T.H., Smithers, R.J., Bailey, S., Walmsley, C.A., Watts, K., 2012. A decision framework for considering climate change adaptation in biodiversity conservation planning. J. Appl. Ecol. 49, 1247–1255.

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol. Conserv. 117, 285–297.

Palmer, S.C.F., Coulon, A., Travis, J.M.J., 2011. Introducing a “stochastic movement simulator” for estimating habitat connectivity. Methods Ecol. Evol. 2, 258–268.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579–583.

Pe'er, G., Kramer-Schadt, S., 2008. Incorporating the perceptual range of animals into connectivity models. Ecol. Model. 213, 73–85. http://dx.doi.org/10.1016/j.ecolmodel.2007.11.020.

Peles, J.D., Barrett, G.W., 1996. Effects of vegetative cover on the population dynamics of meadow voles. J. Mammal. 857–869.

Pöyry, J., Paukkunen, J., Heliölä, J., Kuussaari, M., 2009. Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. Oecologia 160, 577–587. http://dx.doi.org/10.1007/s00442-009-1328-7.

Prevedello, J.A., Vieira, M.V., 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodivers. Conserv. 19, 1205–1223.

Robertson, O.J., Radford, J.Q., 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral. Ecol. 34, 435–446. http://dx.doi.org/10.1111/j.1442-9993.2009.01945.x.

Schoon, M., Baggio, J.A., Salau, K.R., Janssen, M., 2014. Insights for managers from modeling species interactions across multiple scales in an idealized landscape. Environ. Model Softw. 54, 53–59.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., 2004. Extinction risk from climate change. Nature 427, 145–148.

Thomas, J.A., Simcox, D.J., Hovestadt, T., 2011. Evidence based conservation of butterflies. J. Insect Conserv. 15, 241–258.

Thorne, J.H., Huber, P.R., Harrison, S., 2011. Systematic conservation planning. Serpentine 309.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., 2013. Dispersal and species' responses to climate change. Oikos 122, 1532–1540.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manag. 893–901.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Watts, K., Eycott, A.E., Handley, P., Ray, D., Humphrey, J.W., Quine, C.P., 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landsc. Ecol. 25, 1305–1318.

Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. Am. Nat. 879–887.

Williams, P., Hannah, L., Andelman, S., Midgley, G., AraúJo, M., Hughes, G., Manne, L., Martinez-Meyer, E., Pearson, R., 2005. Planning for climate change: identifying minimum-dispersal corridors for the cape proteaceae. Conserv. Biol. 19, 1063–1074.