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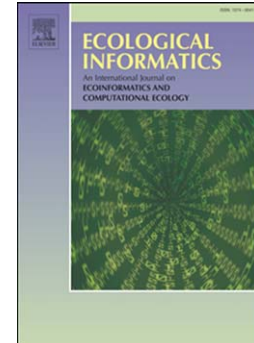
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A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape

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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.

Keywords:

Ecological networks, connectivity, habitat restoration, population dynamics, dispersal, RangeShifter

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 & 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 & 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 *et al.*, 2003; Haddad and Tewksbury, 2005; 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). 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.

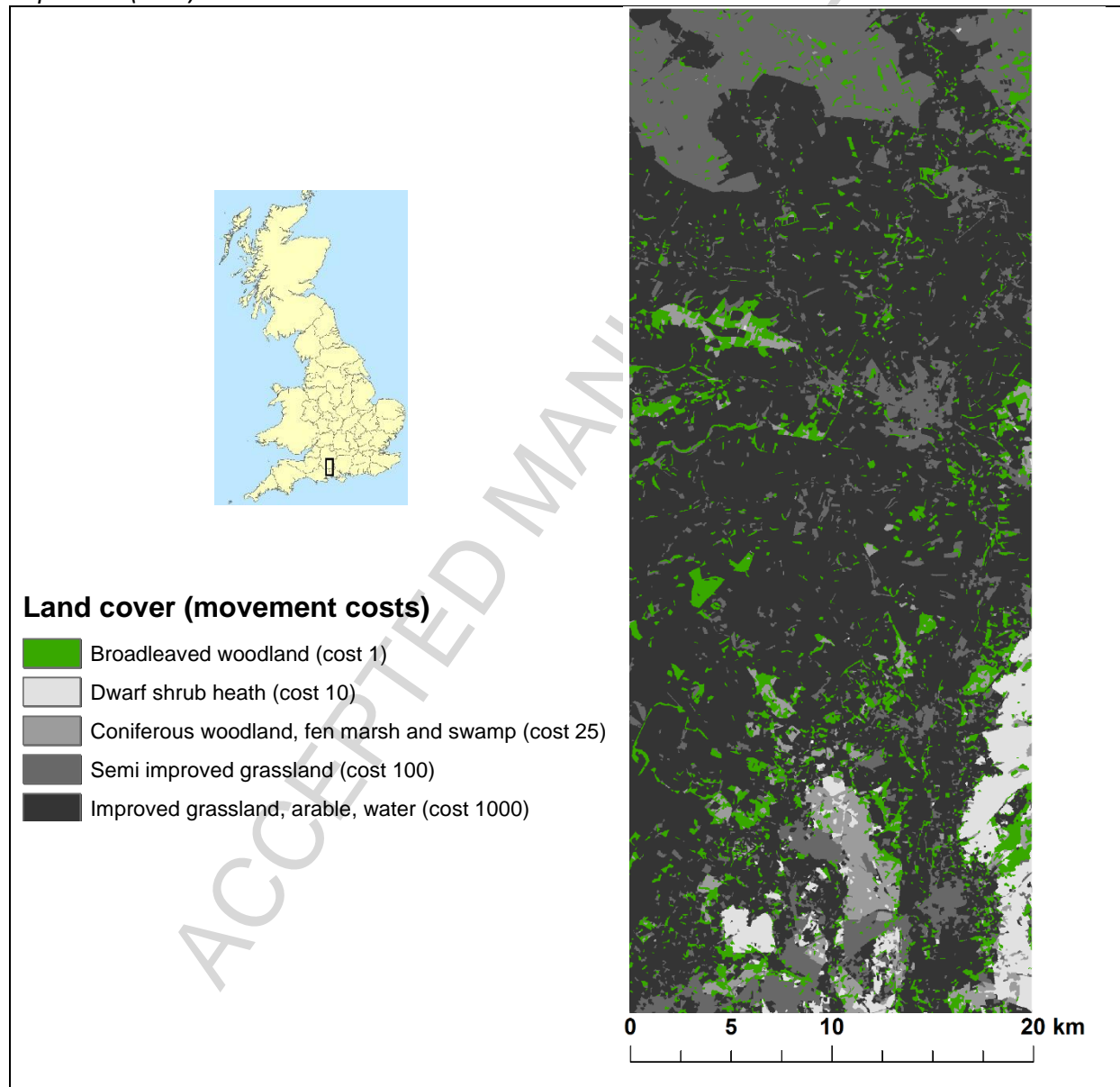
The modelling framework presented here, in contrast to many studies (although note: (Hodgson *et al.*, 2011b)), is applied to a real landscape and aims to represent climate change adaptation strategies at achievable scales (both in terms of total area prescribed for adaptation action and the size distribution 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 20km x 50km region extracted from UK Landcover Map 2007 data (Morton *et al.*, 2011) and gridded at 20m cell resolution (Figure 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.

Figure 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%).



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 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 (Walther, 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 is 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 < 3ha). 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.

*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.
liia. Create-Adjacent	New habitat patches are created within improved grassland and arable landcover types, adjacent to existing suitable breeding habitat.
liib. Create-Random	New habitat patches are created within improved grassland and arable landcover types, with no rule for adjacency to existing suitable breeding habitat.
liic. 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.

Two plausible scenarios of the area prescribed for climate change adaption actions were used: (1) 500ha (0.5% of the landscape), representing a conservative level of change; (2) 1,000ha (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 82km² of broadleaved woodland were 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.

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.

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 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 was 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.

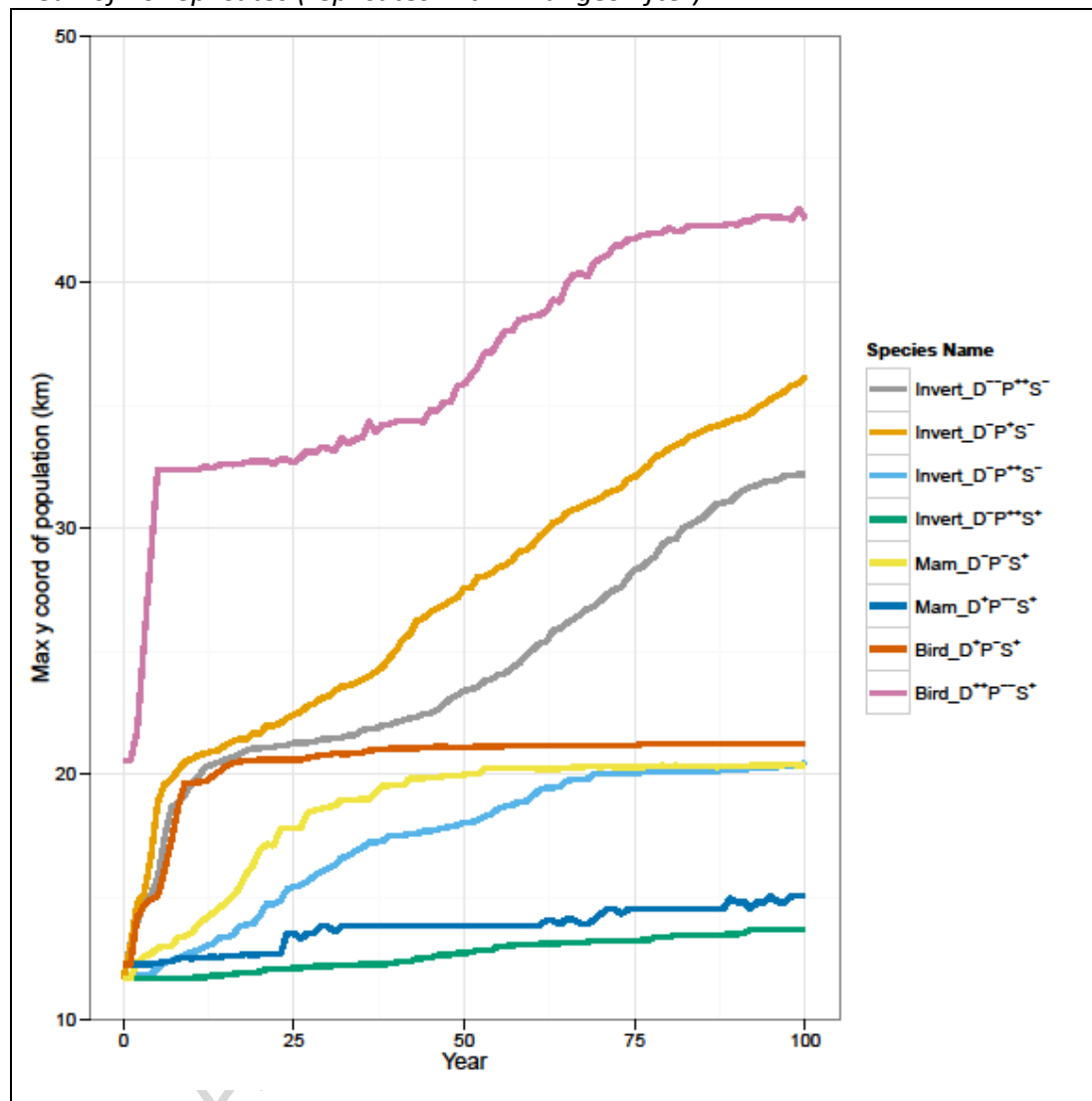
2.3.2 Main Simulations

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 (Figure 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 5km (Mam_{D⁺P⁻S⁺}, Invert_{D⁻P⁺⁺S⁺}) or 10km (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⁻}).

Figure 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).



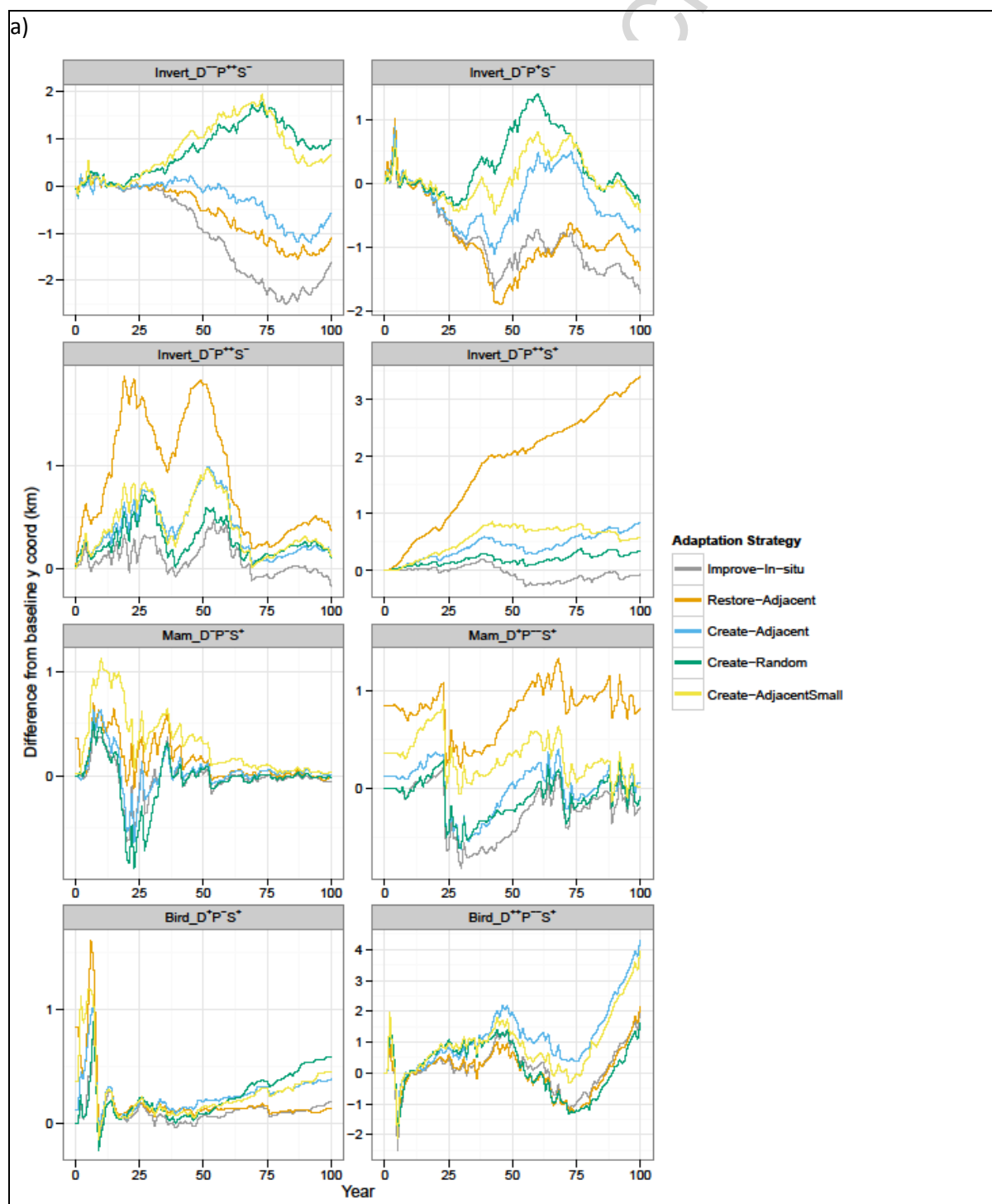
The difference between baseline range shifting and range shifting in the managed landscapes showed a variety of responses dependent on the species and management strategy (Figure 3). At 0.5% habitat change (Figure 3a), some species showed very little response to any of the adaptation strategies (Mam_D^-P^+S^+, 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 (Figure 3a and Figure 4). Invert_D⁻P⁺⁺S⁺ made large gains under the Restore-Adjacent strategy. All other species gained 1km or less in range shifting from any of the habitat management strategies over the 100 years at 0.5% habitat change (Figure 3a and Figure 4).

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 (Figure 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% (Figure 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 (Figure 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⁺ (Figure 3b and Figure 4).

Figure 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 x 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).



b)

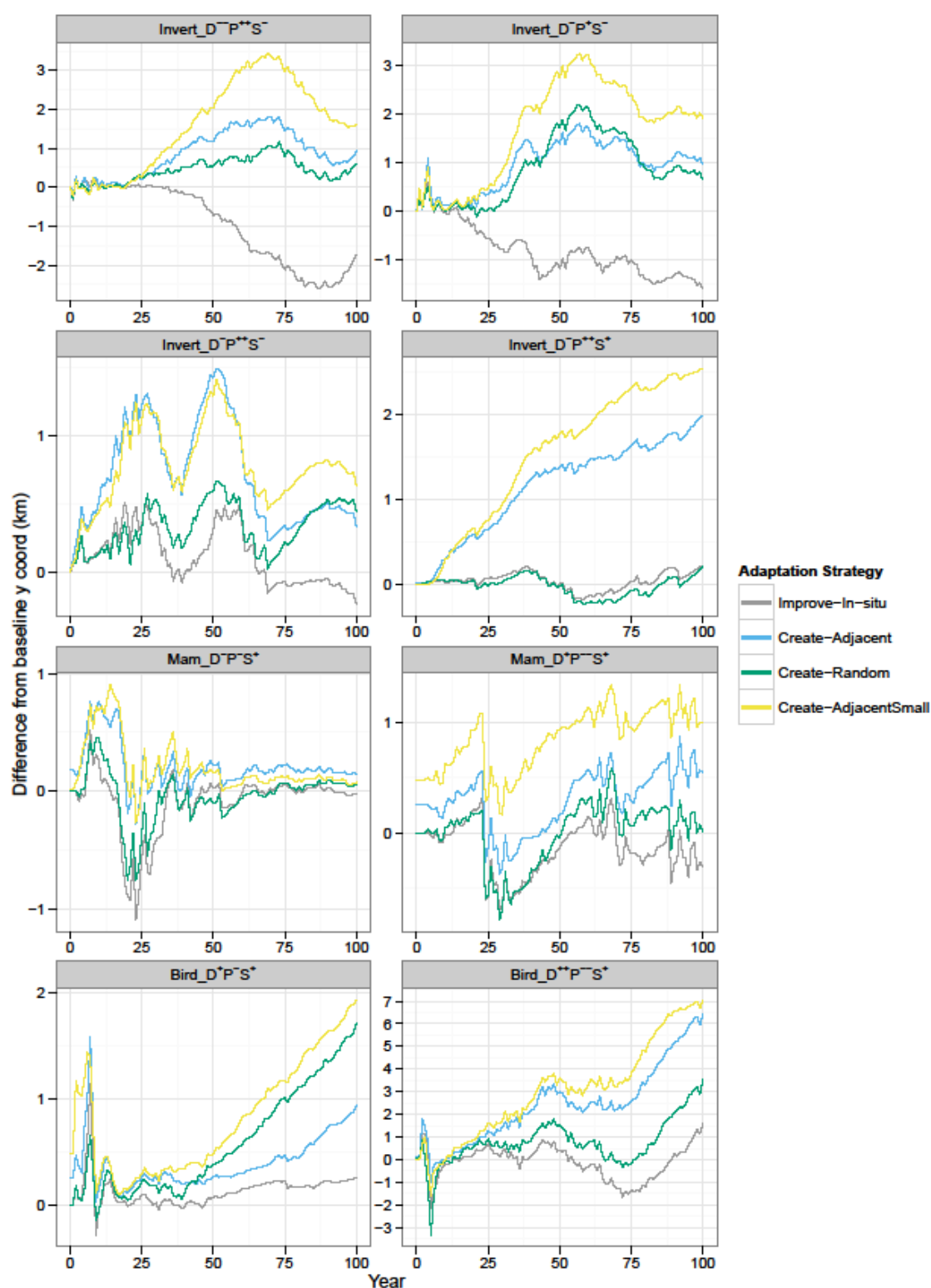
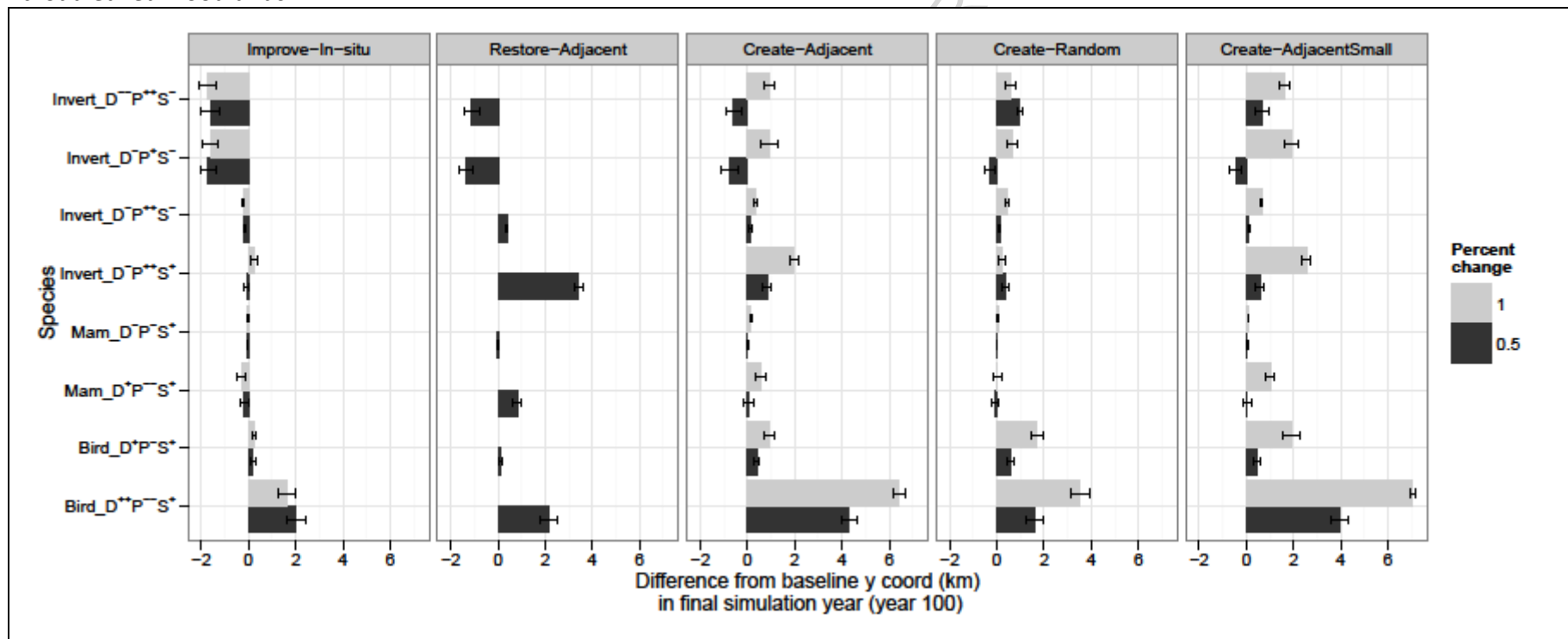


Figure 4: Difference in range shifting response between five adaptation strategies and the baseline simulation (unchanged landscape), measured by the location after 100 years of the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for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



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 hectares) 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 (Figure 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 (Figure 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 1km over the 100 year period at the 0.5% level of change (Figure 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 (Figure 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_ $D^{++}S^{-}$ - Figure 3a; Bird_ $D^{+}P^{+}S^{+}$ - Figure 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) 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 - Figure 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_ $D^{+}P^{+}S^{+}$ - Figure 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 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.

5 Acknowledgements

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Highlights

- We study species range shifting under climate change adaptation strategies
- An individual-based model of dispersal and population dynamics was used
- Strategies are based on habitat improvement, restoration and creation
- Broadest benefits came from habitat creation adjacent to small habitat patches
- At conservative levels of habitat management, range shifting benefits are minimal