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Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones

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Summary

1. Climate change has been inducing range shifts for many species as they follow their suitable climate space and further shifts are projected. Whether species will be able to colonize regions where climate conditions become suitable, so-called 'new climate space', depends on species traits and habitat fragmentation.

2. By combining bioclimate envelope models with dispersal models, we identified areas where the spatial cohesion of the ecosystem pattern is expected to be insufficient to allow colonization of new climate space.

3. For each of three ecosystem types, three species were selected that showed a shift in suitable climate space and differed in habitat fragmentation sensitivity.

4. For the 2020 and 2050 time slices, the amount of climatically suitable habitat in northwest Europe diminished for all studied species. Additionally, significant portions of new suitable habitat could not be colonized because of isolation. Together, this will result in a decline in the amount of suitable habitat protected in Natura 2000 sites.

5. We develop several adaptation strategies to combat this problem: (i) link isolated habitat that is within a new suitable climate zone to the nearest climate-proof network; (ii) increase colonizing capacity in the overlap zone, the part of a network that remains suitable in successive time frames; (iii) optimize sustainable networks in climate refugia, the part of a species' range where the climate remains stable.

6. *Synthesis and applications*. Following the method described in this study, we can identify those sites across Europe where ecosystem patterns are not cohesive enough to accommodate species' responses to climate change. The best locations for climate corridors where improving connectivity is most urgent and potential gain is highest can then be pinpointed.

Key-words: adaptation strategies, bioclimate envelope modelling, *biodiversity* conservation, climate change, climate corridor, climate-proof networks, ecosystem networks, dispersal modelling, Natura 2000

Introduction

The number of studies reporting species' responses to climate change continues to increase (e.g. Parmesan & Yohe 2003; Root *et al*. 2003). Reported range shifts during the 20th century encompass a wide range of taxa and regions. These include poleward range expansions in plants (Tamis *et al*. 2005), butterflies (Warren *et al*. 2001) and birds (Julliard, Jiguet & Couvet 2004); expansion to higher elevations by mammals (Green & Pickering 2002); and decline at southern range margins (Lesica & McCune 2004). Bioclimate envelope modelling studies project range shifts for a variety of taxa (Araújo, Thuiller & Pearson 2006; Harrison *et al*. 2006). A basic assumption in most such studies is that geographical space is homogeneously suitable for colonization and dispersal.

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Studies that consider land-cover types, however, have shown that the effects of climate change are aggravated by land-cover changes (Sala *et al*. 2000; Berry *et al*. 2006). For nature conservation, the reported and projected changes may cause various problems, depending on scale. At the biogeographical scale, a pivotal question is whether losses in the distribution range due to unsuitable climate are compensated by colonization of regions where climate conditions become suitable, so-called 'new climate space' (Pearson *et al*. 2002). From a local perspective, a prime question is whether disappearing species are replaced by incoming species in order to maintain functional diversity (Chapin *et al*. 1997). This study seeks to address both of these questions using a multi-scale approach.

Whether species can colonize new climate space depends both on species and landscape characteristics. Warren *et al*. (2001) found that only those butterflies capable of dispersing over large distances or using widespread habitats were able to respond to climate change by expanding northwards. Hill, Thomas & Huntley (1999) showed that habitat availability is an important determinant in the northward range expansion of the speckled wood butterfly *Pararge aegeria*, with habitat fragmentation reducing both expansion rates as well as causing lower genetic diversity in climate-driven range expansion (Hill *et al*. 2006). These species-oriented studies suggest that spatial responses to climate change can be strongly inhibited by habitat fragmentation (Opdam & Wascher 2004).

In many parts of Europe, natural or semi-natural ecosystems have become fragmented and embedded in a landscape matrix with low permeability to dispersing individuals (Jongman & Pungetti 2004). Populations of species that are restricted to such remnants of suitable habitat often show characteristics of a metapopulation structure (Verboom *et al*. 1991; Hanski 1999). The persistence of such metapopulations is largely determined by the spatial cohesion of habitat networks (Opdam, Verboom & Pouwels 2003). The spatial scale of habitat networks required for population persistence (Vos *et al*. 2001) varies among species from several to hundreds of square kilometres or even larger scales (Verboom & Pouwels 2004). At a biogeographical scale, a species' range can be conceptualized as a patchwork of regions varying in the amount and density of habitat, encompassing a variety of habitat networks with different spatial cohesion, which may or may not be linked by rare long-distance dispersal (Opdam & Wascher 2004). Due to variability in network size, network density, patch quality and matrix permeability, these habitat networks may vary in their percentage of occupied patches, population growth rates and capacity to function as an effective source of colonizers for new climate space. Also, the colonization of newly suitable habitat areas requires that distances between patches or between networks can be crossed with high enough probability of success (considering distances, matrix permeability and physical barriers).

In Europe, this raises the question whether current conservation strategy allows species affected by both climate change and habitat fragmentation to expand their range into new climate space. For example, it is unknown to what extent and where the spatial cohesion within the Natura 2000 network is sufficient and where isolation of protected sites will prevent the expansion of species ranges into new climate space.

In this study, we develop a method of identifying whether and where the spatial cohesion of ecosystem patterns at a large spatial scale is inadequate to allow species to respond to a changing climate. We then examine to what extent the current degree of ecosystem fragmentation of the European landscape allows species to spread into new climate space, whether this spread can compensate for losses elsewhere, and which strategies would be ecologically effective to modify the extent and configuration of the Natura 2000 sites.

Methods

We analysed the spatial cohesion of three types of ecosystems (forest, wetland and natural grassland) for northwest Europe, currently and with climate change (see Fig. 1 for a schematic overview). We estimated changes in suitable climate space using the bioclimatic model SPECIES (Pearson *et al*. 2002; Berry *et al*. 2007b). For each ecosystem type, we selected three species that have moved to new areas in response to changing environmental conditions thought to be a response to climate change (see Table 1). Secondly, species were chosen which differed in terms of habitat fragmentation sensitivity, individual area requirements per reproductive unit, dispersal capacity and sensitivity to barriers in the landscape (Table 1). For each chosen species, the configuration of networks of potential suitable habitat in northwest Europe was subsequently calculated with the GRIDWALK dispersal model (Schippers *et al*. 1996).

We analysed the projected shifts in suitable climate space and the distribution of habitat networks for each species. Climate-proof and non climate-proof networks were identified with the CENA model (Climate-based Ecological Network Analysis, Berry *et al*. 2007a). By combining these species-specific ratings, an overall ecosystem rating of spatial cohesion of the landscape emerged. Technical details of the methodology are contained in Supporting Information Appendix S1.

IDENTIFYING POTENTIALLY SUITABLE CLIMATE SPACE FOR THE BASELINE, 2020 AND 2050

The bioclimatic envelope model SPECIES (Pearson *et al*. 2002; Berry *et al*. 2007b), employs an artificial neural network (ANN) to project current and future areas of potentially suitable climate space based on correlations between species presence/absence and biologically relevant climatic variables (Table 2).These bioclimate variables were chosen based on previous studies which have demonstrated their high predictive power in terms of climatic suitability (Berry *et al*. 2003; Harrison *et al*. 2003).

The HadCM3 A2 scenario was used to project changes in potential suitable climate space (see Rounsevell, Berry & Harrison 2006 for further details). For Europe, this scenario projects an increase in mean summer temperature of 1·18 °C by 2020 and 2·5 °C by 2050 and a decrease in mean summer precipitation of 2·34 and 5·21 mm month^{-1} for 2020 and 2050 respectively. We used an A2 high-emissions climate-change scenario (IPCC 2001), which should reveal many potential bottlenecks in the risk assessment.

Model training was carried out using bioclimatic and species distribution data collected from 0·5° latitude × longitude grids. Models were then used to project changes in potentially suitable climate space for the 2020 and 2050 time slices at a 10′ latitude/longitude resolution.

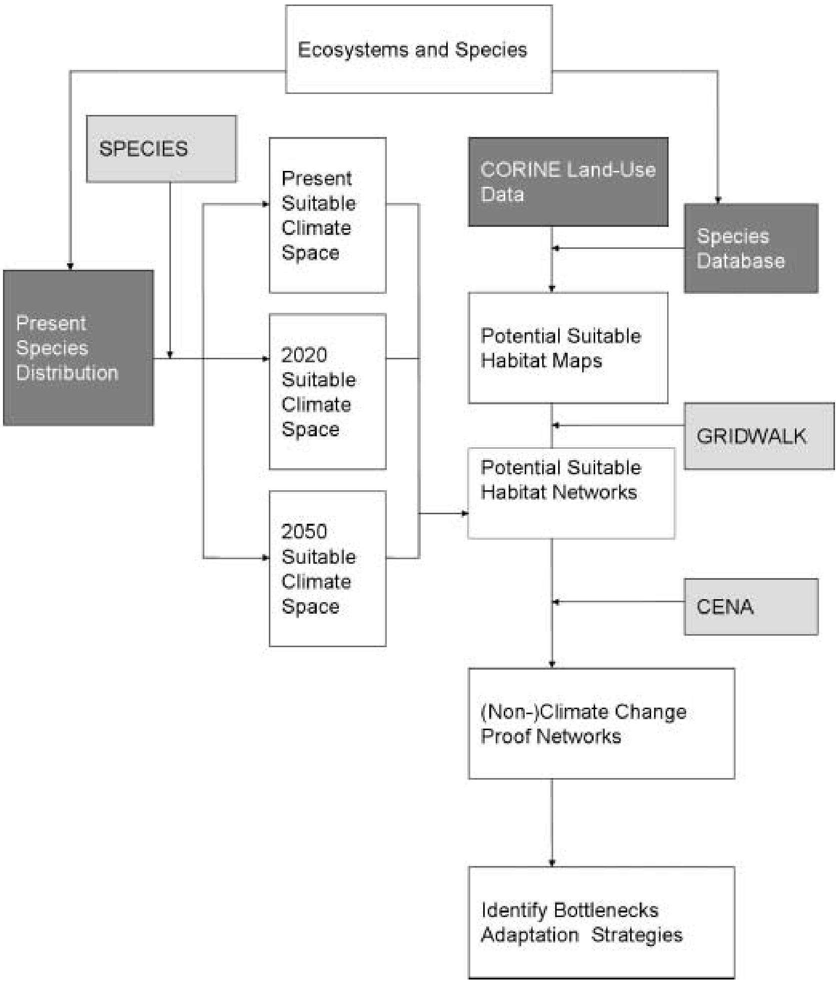

Fig. 1. Schematic overview of the analysis steps. The simulation models are indicated in grey boxes, input data in dark grey boxes.

Table 1. Species parameters. AUC and Kappa indicate the fit of the SPECIES model between observed and projected distributions. Estimated dispersal capacity (DC), area required per reproductive unit (Area RE) and barrier sensitivity (BS) is given as: – not sensitive, + sensitive, ++ highly sensitive

Ecosystem type and species	AUC	Kappa	DC (km)	Area RE (ha)	BS
Forests					
Black woodpecker *Dryocopus martius*	0·95	0·77	50	250	–
Middle spotted woodpecker *Dendrocopos medius*	0·94	0·76	10	20	–
Agile frog *Rana dalmatina*	0·95	0·75	5	5	++
Wetlands					
Bittern *Botaurus stellaris*	0·90	0·63	30	100	–
Marsh warbler *Acrocephalus palustris*	0·94	0·78	15	5	–
Large heath butterfly *Coenonympha tullia*	0·98	0·90	12	1	+
Natural grasslands					
Brown hare *Lepus europaeus*	0·98	0·86	25	500	+
Meadow pipit *Anthus pratensis*	0·95	0·76	15	5	–
Pool frog *Rana lessonae*	0·98	0·88	5	5	++

Spatial autocorrelation was not directly incorporated into the bioclimatic suitability analysis. This was not considered a significant shortcoming of the current study, given the fairly coarse resolution of the training data and given that predictions from ANN models have previously been shown to be quite robust to the presence of spatial autocorrelation (Segurado & Araújo 2004).

POTENTIALLY SUITABLE HABITAT NETWORKS

For each species, we analysed the spatial configuration of the northwest European landscapes in three steps: (i) habitat mapping, (ii) delineation of habitat networks, and (iii) assessment of these networks under climate change. The network analysis is based on

Table 2. Bioclimatic input variables used by the SPECIES model

Birds	Other taxa
Growing degree days > 5 °C	Growing degree days > 5 °C
Absolute minimum temperature expected over a 20-year period	Absolute minimum temperature expected over a 20-year period
Mean summer temperature (May to July)	Annual maximum temperature
Mean summer precipitation (May to July)	Accumulated annual soil water deficit
Mean winter precipitation (December, January and February)	Accumulated annual soil water surplus
Mean summer water availability (May to July)	

species-specific landscape indices (Table 1): habitat sites (based on the amount of habitat required for one reproductive unit), the maximum distance between habitat sites (based on estimated maximum dispersal distance), and the permeability of the landscape matrix between sites (based on the preference for habitat types and sensitivity to barriers of dispersing individuals). All estimates of habitat suitability, area requirements per reproductive unit, dispersal distance and habitat preference or avoidance during dispersal were derived from the literature or estimated by species experts (see Supporting Information Appendix S1).

For each species, patches of suitable reproduction habitat were defined based on the CORINE (2005) land-use data. Major roads were derived from the ESRI data base (ESRI 2002), incorporating motorways and federal (dual) highways. For barrier-sensitive species, patches separated by major roads were divided in two separate habitat patches.

DELINEATION OF HABITAT NETWORKS

Functional connectivity between habitat sites was estimated as the probability that an individual leaving one patch would arrive in another patch. Arrival probability was calculated from stochastic simulations of cell-to-cell movement of individuals. The movement between these 1-km^2 cells was determined by the maximum dispersal distance of a species and the preference value of the cells, which was derived from the amount of good dispersal habitat and barriers within each cell. To calculate connectivity, the probabilities of moving from one patch to another were multiplied by the number of reproductive units inside the source patch and the number of dispersers on average produced per reproductive unit, resulting in a matrix of immigration flows between patches. Patches were defined as belonging to the same network when the total flow of immigrants from the patch into the network, or from the network into this patch, exceeded a threshold value of two individuals (one reproductive unit) per dispersal period.

CLIMATE-CHANGE-PROOF ASSESSMENT OF HABITAT NETWORKS

The climate-change-proof assessment was based on the new method called CENA. Potentially suitable networks were delineated within the shifting climate space for three scenarios: baseline, 2020, and 2050. For each scenario, networks were defined based on the calculated connectivity of the patches that were suitable under this scenario. Thus, patches were considered to belong to the same network when: (i) the patches were within the same suitable climate zone, and (ii) the connectivity between patches was sufficient.

To be climate-change-proof in 2020 or 2050, a network had to be located at least partly within a suitable climate in the previous time interval. This can be visualized in Fig. 2a, where the light network is climate-proof until 2020 and the dark network is not. Although the dark network is situated in a climate space that becomes suitable in 2020, the species will not be able to colonize it, as there is no overlap with a network in the current suitable climate space. If located in a zone where the climate is projected to become unsuitable, the sub-area of a previously delineated network was no longer considered climate-change-proof.

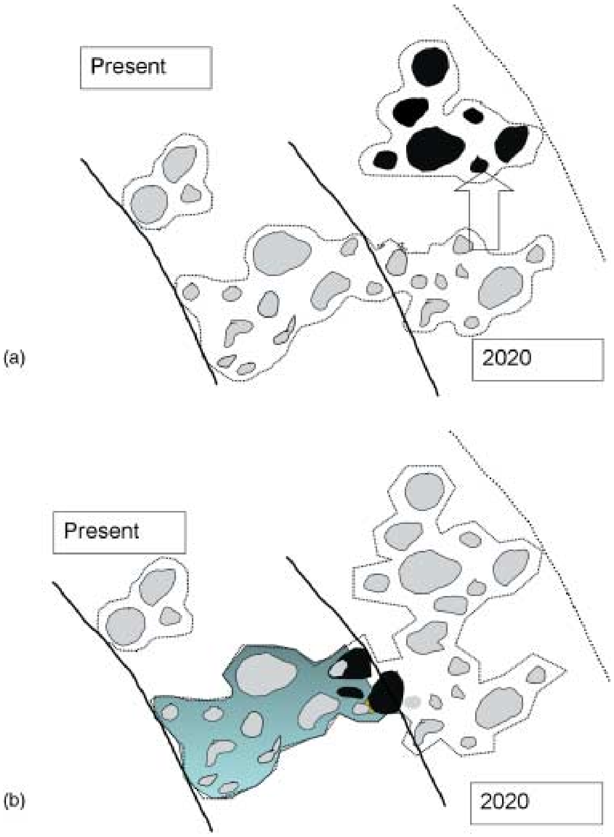

Fig. 2. (a) Link to climate-proof network. Although the dark network is situated in a climate space that becomes suitable in 2020, it is not climate proof as it is too isolated to become colonized. The arrow indicates the search area for adaptation measures. (b). Increase colonizing capacity. The shaded area indicates the overlap zone in the habitat network between two successive climatic time frames. The expanding capacity is improved by creating new habitat patches or enlarging existing habitat patches in the overlap zone (dark areas).

The initial delineation of habitat networks was a critical step in identifying climate-proof networks. Therefore, we varied the network threshold, the number of exchanging individuals required to belong to the same network, and the weight of barriers under standard, minimum and maximum scenarios. In the minimum scenario, a habitat network had an exchange threshold of one individual between patches with no barriers in the matrix. In the maximum scenario, barrier effects were high and the network threshold was the exchange of at least four individuals between patches.

IDENTIFYING BOTTLENECKS AND LANDSCAPE ADAPTATION STRATEGIES

We defined a bottleneck as a part of the (shifting) distribution range where low connectivity or too-little habitat area inhibits the spatial response of a species to climate change. A bottleneck therefore identifies regions where, due to climate change and habitat fragmentation, biodiversity policy targets might not be met. We distinguished three bottleneck types, each with a related landscape adaptation strategy. Using these strategies, we identified search areas where adaptation is needed. We explored how the relative urgency for adaptation measures could be inferred from a comparison of the three network delineation scenarios. We illustrated the method in more detail for the middle spotted woodpecker and explored the areas where adaptation is needed for the forest ecosystem, integrating the results of the forest species.

LANDSCAPE ADAPTATION STRATEGY I: LINK TO THE NEAREST CLIMATE-PROOF NETWORK

The first type of bottleneck (Type I) emerges when habitat networks of one or more patches have moved into a newly suitable climate zone but are too distant from a climate-proof network, based on species dispersal capacity. Hence, by linking bottleneck areas to the nearest climate-proof network, they become climate-proof (Fig. 2a).

LANDSCAPE ADAPTATION STRATEGY II: INCREASE COLONIZING CAPACITY

The size of populations in the overlap zone, the part of a network that is suitable in successive time frames, is important in the overall robustness of a climate-proof network. When this overlap is especially small, it is unlikely that species will be able to colonize any new climate space because the dispersal flow is too low. We designated this bottleneck (Type II) when less than 50% overlap exists between consecutive suitable climate zones. An appropriate adaptation strategy, therefore, is to increase the amount of suitable habitat in the overlap zone in order to promote a greater colonization capacity (Fig. 2b).

LANDSCAPE ADAPTATION STRATEGY III: OPTIMIZE SUSTAINABLE NETWORKS WITHIN CLIMATE REFUGIA

From a species' perspective, it is important that it is well protected in the climatically stable parts of its range (e.g. the brown areas in Fig. 3A). These regions form climate refugia from which a species might be able to expand if climatic conditions become favourable again. A potentially effective adaptation strategy in this case is to improve favourable environmental and spatial conditions in the climate refugia, so that the species' persistence is maximized.

Results

A comparison of the total suitable area of the baseline with 2020 and 2050 shows a range reduction within the study area for all nine species (see Supporting Information Appendix S1, for more details). The amount of habitat protected under Natura 2000 also declines for all species. Differences between species are large; for some, the reduction is limited (agile frog 6% and bittern 8%), while for others, considerable (black woodpecker, marsh warbler and meadow pipit 70%).

The total suitable habitat is divided into two categories: climate-proof networks and bottlenecks. The fraction in need of adaptation in 2020 and 2050 encompasses, on average, 5% and 4% of the total suitable area, respectively. Again, differences between species are large. For the bittern, adaptation areas add up to 33% and 24% of the total suitable habitat in 2020 and 2050, respectively, while the marsh warbler map shows no (apparent) adaptation need.

Comparing the standard with the minimum and maximum scenarios for delineating networks, in the minimum scenario, the amount of adaptation required is reduced by approximately 50%. We consider the locations shown by this scenario as most urgent. In the maximum scenario, the adaptation task is on average three times greater than in the default scenario, showing many places where the cohesion of ecosystem networks is relatively weak.

EXAMPLE – *MIDDLE SPOTTED WOODPECKER* DENDROCOPUS MEDIUS

Figure 3A illustrates how climate envelopes shift across the study area. A contraction of suitable habitat in France is projected, and an expansion is predicted in Ireland, the Netherlands and Denmark. In southern England, some contraction of suitable climate space occurs while climate suitability expands towards the north of England and Scotland. The brown areas depict parts of the range unaffected by climate change, at least until 2050.

The maps for 2020 (Fig. 3B) and 2050 (Fig. 3C) show considerable bottlenecks in Belgium, the Netherlands, northwest Germany and Denmark, where climate becomes suitable but patches are too isolated to be colonized. The species shows potential range expansion towards Britain and Ireland. However, considering its present distribution, this expansion will probably be prevented by the sea barrier. Additionally, forested areas in Ireland and southern England are too fragmented to allow expansion. The climate-proof networks in England, in 2020, are light green, indicating that the overlap zone is less than 20%. Thus, the capacity to colonize this new climate space is limited.

The adaptation strategies for all forest species are illustrated in Fig. 4. The black woodpecker, middle spotted woodpecker and agile frog show different responses to climate change. The former shows a large eastward contraction, with habitat becoming unsuitable in large parts of the study area. On the other hand, habitat suitability for the agile frog, and to a lesser extent for the middle spotted woodpecker, does show potential expansion, provided adaptation measures are taken. The red areas are only reachable if connected to the nearest climate-proof network (adaptation strategy I). The green areas are small, and thus, the colonizing capacity needs to be increased

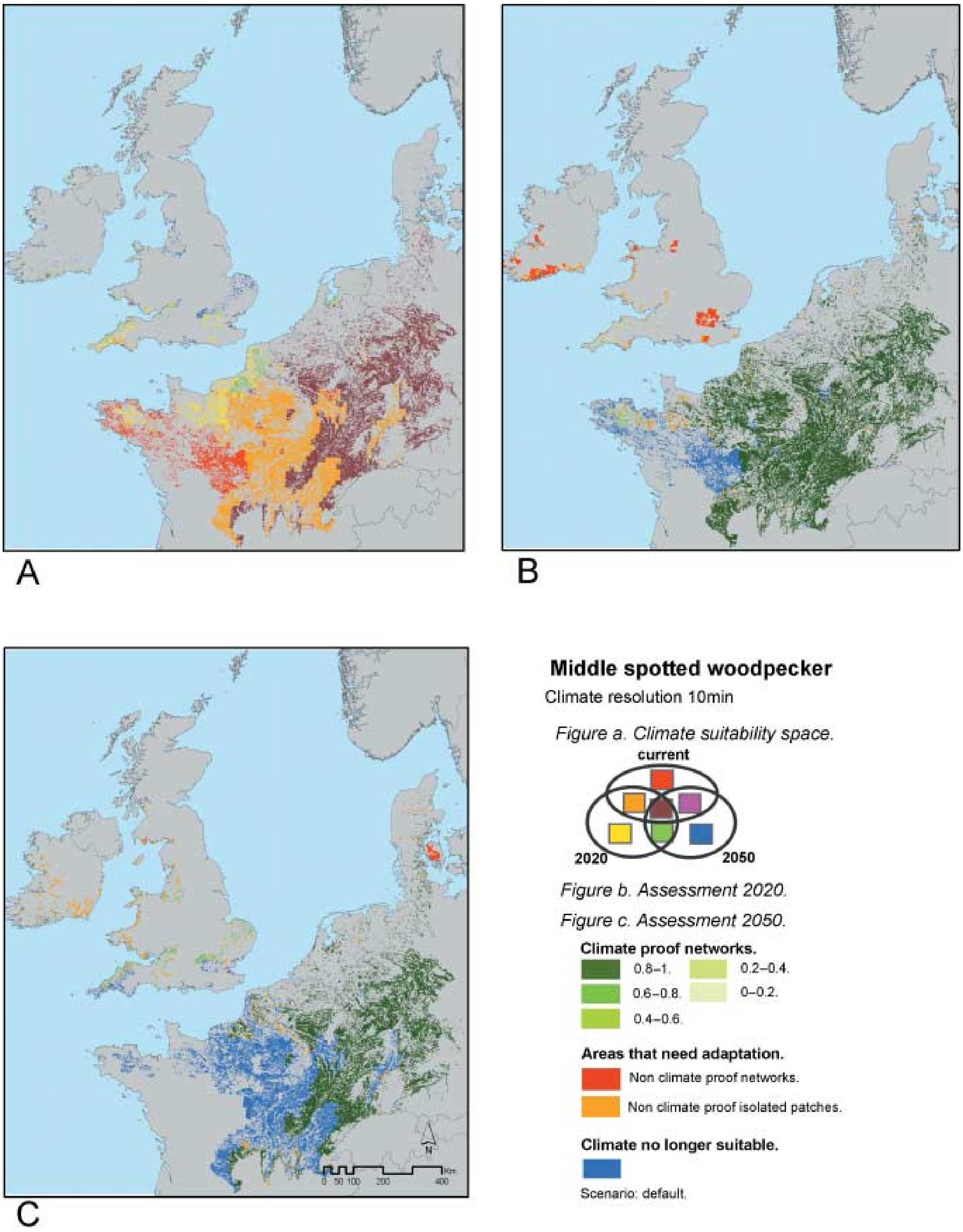

Fig. 3. Climate-change-proof assessment for the middle spotted woodpecker. In 3A, the suitable climate space for the current situation, 2020 and 2050 is projected over the potential suitable habitat (broad-leaved forests). 3B (2020) and 3C (2050), green areas indicate climate-proof networks. The darkest green networks are the most robust (sharing a large part of their network with the previous climate zone). The red and orange areas need adaptation, having a suitable climate but too isolated to become colonized. In the blue areas, the climate is no longer suitable.

(adaptation strategy II). Finally, the grey areas show zones that are not affected by climate change. These areas form relatively stable climate refugia at least until 2050. Here, conservation efforts should be focussed on optimizing network sustainability (adaptation strategy III). The adaptation measures for all three forest species are integrated in Fig. 4 (bottom right). If these species are considered as representative for the response of biodiversity in forest ecosystems, this map indicates where adaptation would be recommended.

Discussion

The approach developed here allows managers to identify the locations across Europe where ecosystem patterns are not cohesive

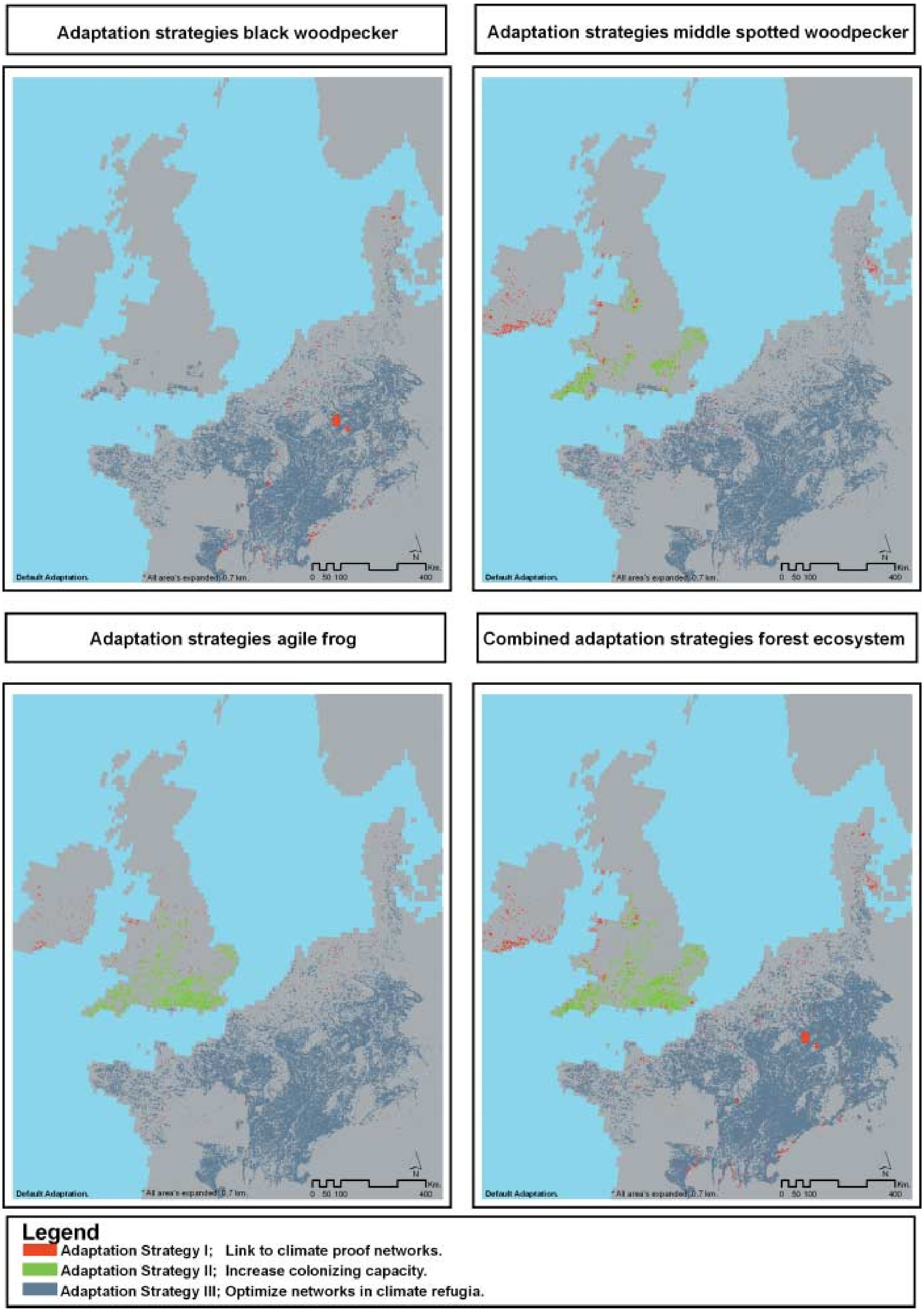

Fig. 4. Search areas for adaptation for the black woodpecker, the middle spotted woodpecker and the agile frog and the combined adaptation measures for the forest ecosystem.

enough to accommodate species responses to global warming. We discuss some caveats and necessary improvements for further implementation of the method, and propose how it can support future European policy on climate-change adaptation.

Bioclimate envelope models have received criticism for the assumption that species are in equilibrium with climate and that climate is the major factor affecting distribution. A fuller discussion in relation to the SPECIES model is provided by

Berry *et al*. (2007b). Although our analysis does not solve all methodological caveats, the combined application of a bioclimate model, a dispersal model and actual data on the distribution of suitable habitat offers, for the first time, a tool for identifying adaptation priorities at a large spatial scale. We predict that species' ranges might shrink, causing loss of biodiversity at the European level, due to two factors. First, the amount of climate-proof habitat in northwest Europe diminishes, and secondly, the current degree of habitat fragmentation for most species is too high, leading to additional range reductions. Due to these two factors, the amount of suitable habitat protected in Natura 2000 sites was projected to decline for all nine species studied here. This effect is aggravated because there is less suitable habitat in the expansion zone than in the contracting zone. The amount of broad-leaved forest, for instance, declines from southeast to northwest. Therefore, we conclude that our approach contributes to quantification of the impacts of climate change on the current common biodiversity policy in Europe.

Modelling-based studies have inherent limitations, assumptions and uncertainties. In this study, limitations include the small number of species analysed per ecosystem. However, using a set of species that represent variations in spatial functioning (so-called 'ecoprofiles'; Vos *et al*. 2001; Opdam *et al*. 2008), the integrated results do encompass a range of species traits, and can therefore, be interpreted as identifying strong and weak spatial cohesion of ecosystem networks. However, we are unsure as to what extent the selected species are representative of the variety of climate-change response patterns. The limited spatial resolution of the CORINE land-cover data is, for now, a limitation in reliably applying the method for species needing small mosaics of patches, such as amphibians. Additional detailed regional land-cover data are necessary.

Climate uncertainty stems from the emissions scenarios and the response of the climate system to them as captured by Global Climate Models (GCMs). As our main concern was proof of concept, in this study, we used only one emission scenario (A2) from one GCM (Had CM3). This GCM/scenario combination falls along the upper range for increased temperature change projections for Europe, and thus, the results should indicate the levels of adaptation necessary to cope with moderate to severe climate change.

To test whether differences in resolution between the climate suitability maps and the habitat maps affected our results, we conducted a sensitivity analysis for the middle spotted woodpecker, interpolating the climate suitability from a 10′ resolution onto grids of 10-, 5- and 1-km^2 grids (see Supporting Information Appendix S2). A finer resolution of the suitable climate maps had only a relatively small effect on the predictions of climate-proof and non climate-proof networks. Differences mainly occurred where the suitable climate zones were very narrow and dynamic. For these areas, the projection of areas that need adaptation is relatively unsure and depends on small differences in suitable climate boundaries between successive climate zones. A more in-depth investigation of the sensitivity of climate suitability results to various spatial uncertainties (*sensu* the 'modifiable areal unit problem' or MAUP (Jelinski & Wu 1996)) was not possible due to the fixed nature, in terms of the underlying coordinate system, of the baseline bioclimate data and GCM projections.

Generalities about spatial adaptation strategies will greatly improve with an increasing insight into how species respond spatially to climate change. Our results showed that spatial responses to climate change differ widely, and our predictions will become more accurate if this variety of responses can be better captured. We know little about large-scale responses of species to climate change across heterogeneous landscapes. For instance, while the habitat of species becomes less suitable due to climate change, the real pattern of decline may deviate from that projected because of competitive pressure between species (White *et al*. 2001) or altered habitat quality due to climate change or other drivers (e.g. unfavourable microclimatic cooling for butterfly species, due to advanced plant growth, Wallisdevries & Van Swaay 2006). Additionally, the influence of increased weather extremes on local extinctions (Easterling *et al*. 2000) and of decreased habitat quality on dispersal probability or reproduction success (Lurz, Garson & Wauters 1997; Haas 1998) may be important mechanisms determining whether species will be able to track future climate space. Also, many factors might constrain the establishment of populations in new climate zones, like the lack of the required natural resources or antagonistic interactions among species (Hulme 2005). Large-scale monitoring of species responses is needed to better tune model projections.

Our results suggest that to prevent loss of biodiversity due to global warming, two spatial adaptation strategies might be considered. The most important one is to increase the connectivity between ecosystem networks on a large spatial scale. With our method, the European Union can identify where isolated ecosystem networks require improved connectivity to climate-proof networks. There is growing support for improved connectivity as a sensible adaptation measure (e.g. Opdam & Wascher 2004; Da Fonseca, Sechrest & Oglethorpe 2005; Hannah & Hansen 2005). This strategy entails both the creation of new ecosystem sites as well as adaptive landscape management to achieve sufficient permeability between protected areas (Lovejoy 2005). Our method allows regions to be prioritized on the basis of where improvement of connectivity is most urgent or potential gain is highest, thus identifying the best locations for European climate corridors. Any consideration of starting adaptation measures will have to balance any risk that measures will be taken at the wrong place against the chance that adaptation will be too late for accommodating biodiversity responses to climate change. For forest ecosystems, for example, development time is very long, and any measures will not be effective within 50 years. We suggest our method should be used to identify focal points for European-wide adaptation policies of forest ecosystem patterns, in combination with opportunities for improving other ecosystem services, for example, the carbon fixation and water regulation capacities of broad-leaved forests.

A second important adaptation measure is increasing the area and density of ecosystem networks in regions where dispersal sources are small and widely distributed. Increasing the dispersal flow will speed up colonization of new climate spaces. We suggest that this adaptation strategy is most urgent in wetland ecosystems, specifically marshland, because these are small, isolated and poorly represented within Natura 2000 sites. The effect of this fragmentation is aggravated by climate change, as illustrated by the projections for the bittern. Wetland restoration may also help to prevent flooding after extreme rainfall and summer drought damage in agricultural crops. Wetland restoration should be initiated in regions where multiple ecosystem services can be achieved, for example, by developing regulated flooding areas and broader, more natural, river systems.

Protection of sites may be most cost-effective in parts of a species' range where the climate is predicted to remain suitable over time. From these sites, the species might expand if and when conditions become more favourable. Our method allows the identification of ecosystem hotspots (where climate refugia for a significant set of species coincide), and these sites could become focal points in developing the Natura 2000 conservation network across Europe.

A major challenge is how to implement such European-level priorities at the regional level. Currently, there is no European spatial policy, and decision-making on landscape change takes place at a regional level (Opdam, Steingröver & Van Rooij 2006). Our method cannot be applied to guide decisions at this detailed scale, but can support communication between local regions and national governments to ensure common and compatible policies (Adger, Arnell & Tompkins 2005; Da Fonseca *et al*. 2005).

In this study, we analysed spatial cohesion of ecosystem networks in the context of climate change and fragmentation across northwest Europe. We see no limitations to applying the method elsewhere, except for the availability of adequate habitat maps. In regions where ecosystem fragmentation is not a limiting factor in biodiversity responses to climate change, the approach needs to be adjusted.

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Supporting Information

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

Appendix S1. Additional information on the models and simulation results.

Appendix S2. Sensitivity analysis on the impact of differences in resolution between climate and habitat data.