

Transboundary ecological networks as an adaptation strategy to climate change: The example of the Dutch – German border



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Received 11 January 2014; accepted 27 September 2014
Available online 6 October 2014

Abstract

Establishing ecological networks across national boundaries is essential for species to adapt to shifts in future suitable climate zones. This paper presents a method to assess whether the existing ecological network in the Dutch – German border region is “climate proof”. Using distribution data and climate envelope models for 846 species in Europe (mammals, birds, reptiles, amphibians and butterflies) we identified 216 species with climate-induced range shifts in the border region. A range expansion is predicted for 99 species and the ranges of 117 species are predicted to contract. The spatial cohesion of the ecological network was analysed for selected species that vary in habitat requirements and colonisation ability (forest species: *Brenthis daphne*, *Dendrocopos medius*; wetland species: *Maculinea teleius*, *Lutra lutra*). The assessment shows that optimising transboundary networks and developing corridors seems a suitable adaptation strategy for the forest species and for *L. lutra*. For the immobile butterfly *M. teleius*, the present habitat network is too weak and translocation into future suitable climate space seems to be a more appropriate adaptation measure. Our results underline that due to climate change landscape planning and management should not only focus on areas where target species occur today. The presented method can identify strongholds and bottlenecks in transboundary ecological networks and incorporate demands of climate adaptation into spatial planning which forms the basis for taking measures at a more detailed level.

Zusammenfassung

Der Biotopverbund gilt als eine zentrale Anpassungsstrategie des Naturschutzes an die Folgen des Klimawandels. In der vorliegenden Arbeit wurde untersucht, welchen Beitrag Biotopverbundsysteme zwischen Deutschland und den Niederlanden zur Anpassung von klimawandelbedingten Arealverschiebungen von Arten leisten können. Durch eine vergleichende Analyse von Verbreitungsdaten und Klimahüllen-Modellen von 846 Tierarten (Säugetiere, Vögel, Reptilien, Amphibien und Tagfalter) wurden 216 Arten identifiziert, die in Zukunft potenziell grenzüberschreitende Arealverschiebungen aufgrund von Gewinnen (99 Arten) oder Verlusten (117 Arten) von klimatisch geeigneten Gebieten erfahren werden. Für ausgewählte Arten der Wälder (*Brenthis daphne*, *Dendrocopos medius*) sowie der Gewässer- und Feuchtlebensräume (*Maculinea teleius*, *Lutra lutra*) wurde die funktionale Kohärenz der vorhandenen Biotopverbundsysteme modelliert und vor dem Hintergrund der Arealverschiebungen bewertet. Dadurch, dass Wanderungskorridore und Kernlebensräume erhalten, entwickelt und neu geschaffen werden, können die Arten der Wälder und *Lutra lutra* potenziell bei der Realisierung der Arealverschiebungen unterstützt werden. Die für

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den Biotopverbund relevanten Bereiche wurden grenzüberschreitend räumlich dargestellt. Für die wenig mobile Tagfalterart *Maculinea teleius* ist die Kohärenz des Netzwerkes vermutlich zu gering, so dass eine Umsiedlung in klimatisch geeignete Lebensräume als Anpassungsmaßnahme vorgeschlagen wird. Die Ergebnisse verdeutlichen, dass sich Biotopverbundplanungen in Zeiten des Klimawandels nicht nur auf die Gebiete konzentrieren sollten, in denen Zielarten bereits heute vorkommen. Mit der vorgestellten Methode können die potenziellen Auswirkungen von Klimaänderungen mit Relevanz für den grenzüberschreitenden Biotopverbund ermittelt werden, so dass eine Grundlage für Maßnahmenkonzepte auf regionaler und lokaler Ebene zur Verfügung steht.

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Keywords: Range shift; Climate envelope; Habitat network; Spatial cohesion; Connectivity; Spatial planning; Marbled fritillary; Middle spotted woodpecker; Scarce large blue; European otter

Introduction

It is widely recognised that climate change is an important factor driving shifts in species geographical distributions (Root et al. 2003; Gaston 2006). Range shifts occur when a species range contracts or a species goes extinct at the range boundary where the climate is no longer suitable. These shifts also occur as species expand towards the poles and towards higher elevations where climatic conditions have recently become suitable (Opdam & Wascher 2004). Such climate-induced shifts have already been documented for many species groups, for example, plants, butterflies and birds (e.g. Parmesan et al. 1999; Hickling, Roy, Hill, Fox, & Thomas 2006; Lenoir, Gégout, Marquet, Ruffray, & Brisse 2008) and shifts in species ranges are expected to continue in the coming centuries (Hughes 2000). A common method for predicting future ranges of species in response to global warming are climate envelope models (Berry, Jones, Nicholls, & Vos 2007). These models forecast shifts in distribution ranges of hundreds of kilometres for many species (e.g. Araújo, Thuiller, & Pearson 2006; Settele et al. 2008). Whether species will be able to migrate into suitable climate zones depends on both species characteristics and landscape patterns (Wilson, Davies, & Thomas 2010). Species with low dispersal capacity and reproductive potential will require more time to expand their range (Clobert, Ims, & Rousset 2004). Habitat generalists might adapt their distribution pattern and range along climate gradients more easily than habitat specialists (Warren et al. 2001). Habitat loss and fragmentation affect the migration of species and might hamper colonisation of a habitat that has become suitable because of climate change (Anderson et al. 2009). When the range expansion of species is blocked or too slow to adapt to the rate of changing habitat suitability, species may go extinct (Thomas, Franco, & Hill 2006).

Ecological networks are proclaimed to be an adaptation strategy to help species and ecosystems adjust to climate change (Heller & Zavaleta 2009), facilitating range expansions (Vos et al. 2008). However, most existing ecological networks in Europe aim to create spatial cohesion on a regional or national level within the present distribution (Haaren & Reich 2006). There is an increased interest in

transboundary cooperation and management of ecological networks (Leibenath, Blum, & Stutzriemer 2010), but large-scale shifts in species distribution ranges caused by climate change have rarely been taken into account (Hole et al. 2009). Although some natural links between national networks already exist, for instance, through river basins as parts of the NATURA 2000 European wide network of protected areas, it is unknown whether these links are sufficient to facilitate predicted range expansions of species of different habitats and colonisation ability. Thus comprehensive methods for the assessment of international connectivity under climate change are required (Beier, Spencer, Baldwin, & McRae 2011).

In this paper we present an approach to assess whether the ecological network in the Dutch – German border region is “climate proof”. First we explore the extend of the problem by identifying which fraction of species have predicted range shifts in the border region, using climate envelope data for a variety of taxa. Next, we analyse the spatial cohesion of the ecological network for selected species that vary in their habitat requirements and colonisation ability. This assessment identifies strongholds and bottlenecks in the transboundary ecological networks on regional level and identifies locations where adaptive measures should be developed on local level.

Materials and methods

Study area

The study area covers the Netherlands and the federal states of Schleswig-Holstein, Lower Saxony and North Rhine-Westphalia in the north-west of Germany. The whole region stretches over an area of 133,000 km². Agriculture is the dominating land use (49% arable land, 20% pastures and meadows). Forests cover about 17% of the study area, predominantly in the central part of the Netherlands and in the southern and eastern parts of the German border region. Water bodies, coastal mudflats and swamps account for 3% of the study area. Artificial surfaces, such as urban areas, cover 11%.

Analysis of transboundary range shifts

Potential transboundary range shifts of species were determined by a comparative spatial analysis of the present species distribution and future range projections based on climate envelope models. The analysis was carried out on 846 species from five taxonomic groups: mammals, birds, reptiles, amphibians and butterflies. European distributions were available from published data (see Appendix A: Table 1). We estimated changes in suitable climate space based on the climate envelope model SPECIES (Berry et al. 2007), ALARM (Araújo et al. 2006; Settele et al. 2008) and the Climatic Atlas of European Breeding Birds (Huntley, Green, Collingham, & Willis 2007). Predicted future distributions were based on highest SRES emission scenarios (corresponding to the highest rates of projected global average surface warming) and maximum time period available for each species (see Appendix A: Table 1).

The grid cell resolution of climate envelopes was 50×50 km, except for data on amphibians and reptiles where future potential distributions were projected at $10 \times 10'$ resolution (ca. 16×16 km). Data from more than one grid cell has been recommended by other studies assessing climate change impacts at the regional level (Rannow, Loibl, Greiving, Gruehn, & Meyer 2010). Therefore, a 50-km buffer zone was chosen to delineate the Dutch – German border region. We compared the present and predicted distribution of species within this zone and classified the potential distribution of each species in the border region into the following categories: remaining constant, expanding, contracting or being absent (Fig. 1).

We categorised the preferred habitat types of the species to identify potential requirements for ecological networks. Habitat preferences were grouped into the categories forests, waterbodies, wetlands and dry open landscapes according to the literature (see Appendix A: Table 1). If a species could inhabit different habitat types (e.g. for reproduction, feeding), it was included in several categories.

Analysis of transboundary ecological networks

LARCH

The spatial cohesion of habitats was analysed with the habitat network assessment tool LARCH (Verboom & Pouwels 2004). The model is based on metapopulation theory (Hanski 1999) but it does not model reproduction and mortality processes like other models. The network analysis uses species-specific habitats (amount of habitat required for one reproductive unit), dispersal characteristics (maximum distance between habitat sites), as well as the permeability of the landscape matrix between habitat sites (sensitivity to barriers) (see Groot Bruinderink, Sluis, Lammertsma, Opdam, & Pouwels 2003 and Verboom & Pouwels 2004 for a detailed description of the model). The LARCH-SCAN function determines the connectivity of each individual habitat grid cell by weighting the carrying capacity of all grid cells within the potential dispersal distance (see Appendix A: Formula 1).

A species-specific map of spatial cohesion was produced at 100×100 m resolution, which shows whether the available habitat is connected or consists of separate networks. Each habitat network was categorised as potentially sufficient to maintain (1) a key population, (2) a sustainable network or (3) a highly sustainable network. A key population is defined as a relatively stable and large local population in a network, which persists under the conditions of one immigrant per generation (Verboom, Foppen, Chardon, Opdam, & Luttikhuisen 2001). A habitat network is sustainable if it is large enough to support a minimum viable metapopulation (with an extinction probability of $<5\%$ in a period of 100 years, Opdam, Verboom, & Pouwels 2003). A habitat network is highly sustainable when the size is at least five times larger than the size of a suitable network.

Selected species and parameters

We selected four species which cover two ecosystem types in the study area: forest and wetland. For each ecosystem type

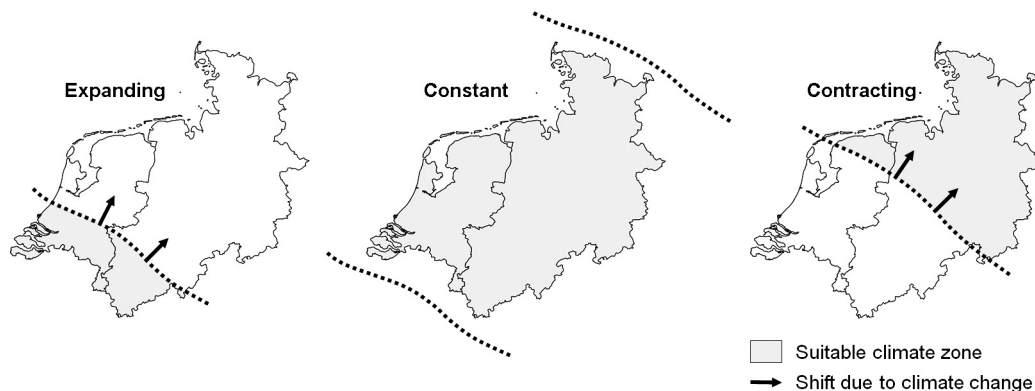


Fig. 1. Schematic overview of potential shifts in suitable climate zones in the Dutch – German border region due to climate change. Expanding: species with northern limit of present distribution south of the border region are predicted to expand their range further north; Constant: overlap of present distribution and predicted future suitable climate zone; Contracting: the ranges of species with present distribution in the border region are predicted to contract.

Table 1. Selected species for LARCH-SCAN analysis and parameters. The species' minimum number of reproductive units (RU) needed to form a key population (KP), carrying capacity for a species in its optimal habitat (CC), species dispersal capacity (DC) and barrier sensitivity (BS) (– not sensitive, + sensitive, ++ highly sensitive). The calculation $KP^* (100/CC)$ gives the minimum area in hectares needed to form a key population. Alpha indicates the distance over which potential source patches can still deliver immigrating individuals.

Ecosystem type and species	Alpha (km ⁻¹)	KP (RU)	CC (RU/100 ha)	DC (km)	BS
Forest					
Marbled fritillary (<i>Brenthis daphne</i>)	0.58	500	1000	4	+
Middle spotted woodpecker (<i>Dendrocopos medius</i>)	0.15	40	5	15	–
Wetland					
Scarce large blue (<i>Maculinea teleius</i>)	2.30	1000	1000	1	+
European otter (<i>Lutra lutra</i>)	0.12	40	0.1	20	++

two species were chosen that are predicted to show potential range shifts within the border region. The species differed in terms of dispersal capacity, preferred habitat (habitat type and area requirements), as well as sensitivity towards barriers in the landscape (Table 1).

The marbled fritillary (*Brenthis daphne*), a nymphalid butterfly, and the middle spotted woodpecker (*Dendrocopos medius*) are found in broadleaved and mixed forest ecosystems. The marbled fritillary especially occurs at forest edges and feeds on rough growth vegetation (e.g. *Cirsium*). The eggs are mainly deposited on plants of the genus *Rubus* (Tolman & Lewington 2009). We assumed a maximum dispersal distance of 4 km referring to recorded data for the morphologically similar lesser marbled fritillary (*Brenthis ino*) (Zimmermann, Fric, Filipová, & Konvicka 2005). The middle spotted woodpecker prefers forests with old and rough-barked trees (Pasinelli 2007). It has a specific preference for old oak trees to nest, especially dead trees or those which have fungus attached to their bark (Kosiński & Winiecki 2005), but this species can also be found in other broadleaved and mixed forests, if enough old trees are present.

The scarce large blue (*Maculinea teleius*), a lycaenid butterfly, and the European otter (*Lutra lutra*) were selected as representative species for wetlands. The scarce large blue lives in marshes and wet meadows and oviposits in the flowerheads of its foodplant, great burnet (*Sanguisorba officinalis*). During a part of its life cycle it parasitises the nests of *Myrmica* ants (Dierks & Fischer 2009). Recorded dispersal distances reached up to 2–4 km, but such long-distance movements are very rare (Nowicki, Witek, Skórka, Settele, & Woyciechowski 2005). The species is known to be sedentary and sensitive to barriers like forests or settlements (Nowicki et al. 2007). The European otter inhabits a variety of wetland and aquatic habitats, including rivers, streams and lakes with bank side vegetation, as well as marshes, swamp forests and coastal areas (Mason & Macdonald 1986). In Europe, the species is found from sea level up to 1000 m above sea level in the Alps (Reuther 2004). Although otters have a high dispersal capacity, observed dispersal distances reach up to 15–30 km (Sjöåsen 1997), the species is highly sensitive to barriers in the landscape such as motorways and urban areas (Robitaille & Laurence 2002).

For each species, patches of potential suitable reproduction habitat as well as potential dispersal barriers were identified using the Dutch and German national habitat maps (in Germany habitat maps of the federal states of Schleswig-Holstein, Lower Saxony and North Rhine-Westphalia), the national stream network, road maps and CORINE Land cover data. Using this information, we created a species-specific reproduction habitat map and a barrier map for dispersal. Note that in the case of the European otter main core areas of the existing habitat network are located just beyond the eastern borders of the study area. These core areas were included in the analysis as they have a large impact on the spatial cohesion of the network in this part of the study area. Parameters for suitable habitats, barriers, dispersal capacity and area needed to form a key population were derived from the literature or estimated by expert knowledge (see Appendix A: Tables 2–5).

Assessment of climate proof ecological networks

We compared the modelled spatial cohesion of a species' habitat network with data of the present distribution and the predicted future climate envelope to locate where the spatial cohesion would allow range expansion between present and future distribution and where bottlenecks might occur. We used projections of future climate under the A2 SRES scenario to evaluate changes in potential suitable climate zones for two time periods (2050 and 2080). The A2 scenario falls along the upper ranges of projected climate change in Europe. Annual mean temperature is expected to increase between 1.3 °C in northern Europe and 7.2 °C in southern Europe until 2080 (European-average increase by 4.2 °C). Substantial decreases in summer precipitation up to –50 mm/month are predicted in central Europe (Berry et al. 2007).

The following procedure was used to determine if and where adaptation measures were required to improve the adaptive capacity of the habitat network (Vos, Hoek, & Vonk 2010). If the network consisted of one sustainable network, without bottlenecks in connectivity between present and predicted future distribution, no adaptation measures were required. If the habitat consisted of separate networks, with bottlenecks between present and predicted future distribution, the strongest networks were identified. Sustainable networks or (if sustainable networks were not present)

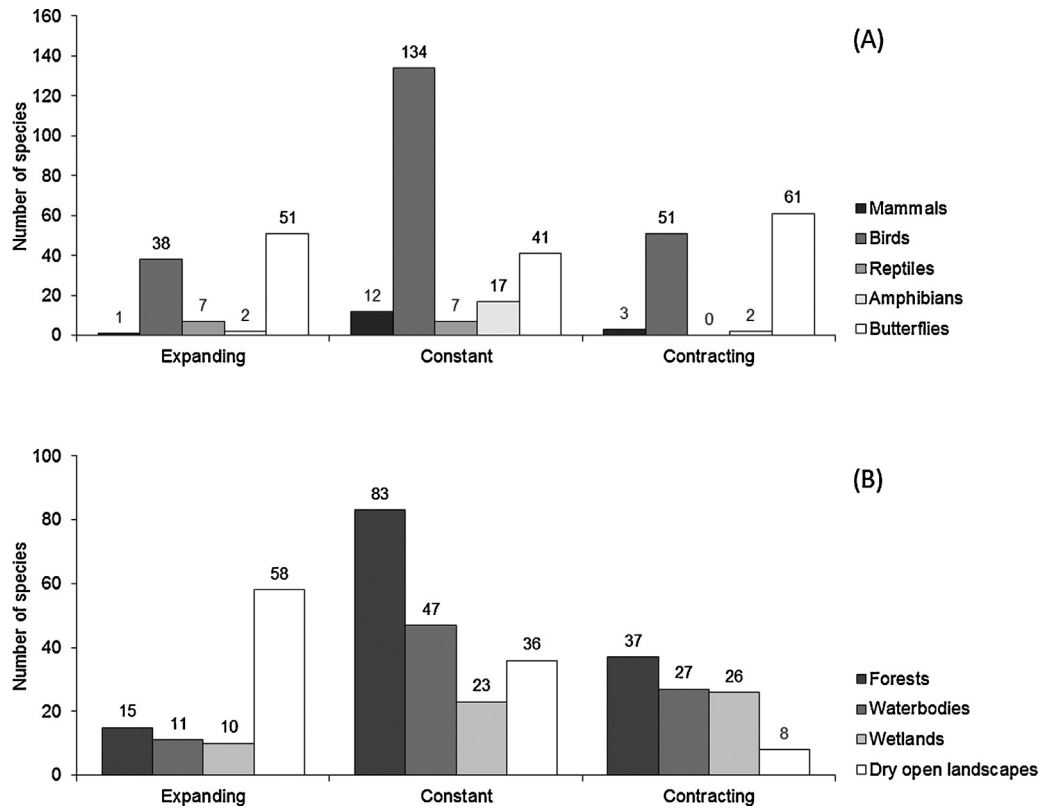


Fig. 2. Species numbers for the different categories of potential shifts in suitable climate zones in relation to (A) taxonomic groups and (B) habitat requirements of the species.

networks containing a key population and corridor zones were identified for the connection of these networks. For example, when core areas were located in newly suitable climate space, but were not connected to the habitat network within the observed present distribution, they were connected using the shortest route via suitable habitats. If the habitat network was weak and void of core areas, locations were identified with highest potential to enlarge existing habitat patches. The identified or potential core areas and corridors were illustrated as circles and straight line arrows in habitat network maps for each species. Thus, regions were identified where forest and wetland ecological networks should be improved.

Results

Analysis of transboundary range shifts

For 427 of the 846 analysed species, either the present or the predicted future climate envelope showed an overlap with the border region. Of these 427 species, the number of species with potential range shifts was considerable. For 117 species (27%) the potential suitable climate zone located in the border region is predicted to contract. 99 species (23%) were classified as potentially expanding, whereas for 211 species (50%), the suitable climate zone is predicted to remain stable

(Fig. 2A). For the butterfly species ($n = 153$) the percentages are approximately similar for all three categories of potential shifts in suitable climate zones. High percentages of species with potentially constant climate suitability were predicted for birds (60%, $n = 223$), for mammals (75%, $n = 16$) and for amphibians (81%, $n = 21$). The reptiles are the taxonomic group with the highest percentage of species that are expected to expand their range (50%, $n = 14$) and no reptiles were classified as potentially contracting (Fig. 2A). Substantial parts of the species with potential expanding ranges occur in dry open landscapes. In contrast, most species with predicted decrease in climate suitability inhabit forests, wetlands and waterbodies (Fig. 2B).

Assessment of climate proof ecological networks

Forest species

For the marbled fritillary the climate envelope models for 2050 and 2080 showed considerable gain in projected climatic niche space in the whole Dutch – German border region (Fig. 3). Indeed, the butterfly has recently expanded its range in neighbouring regions such as northern France and Belgium (Fichefet et al. 2008). In Germany it has spread progressively in the federal states of Saarland and Rhineland-Palatinate, especially along the Mosel river valley (Schmitt 2011). Furthermore, in 2011 the species was recorded in South Limburg

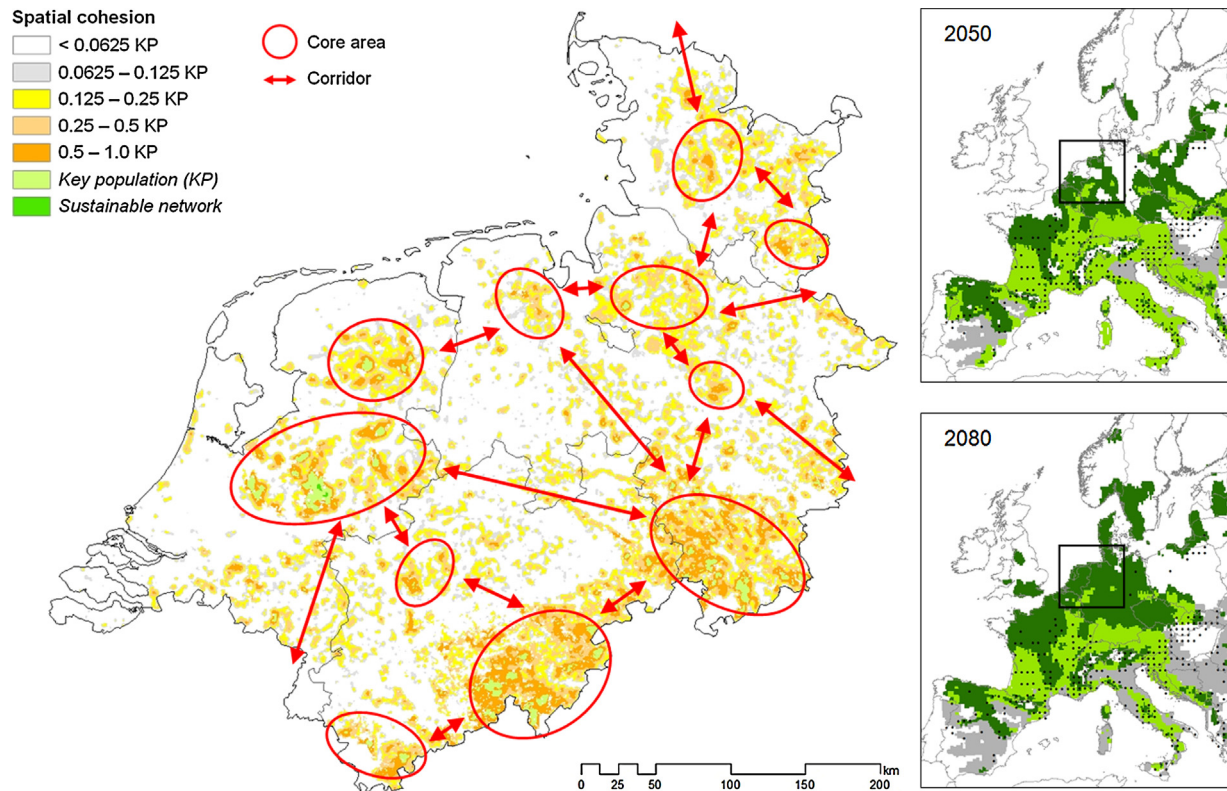


Fig. 3. Habitat network map for the marbled fritillary (*Brenthis daphne*). The map gives an indication for the possible locations of core areas and potential corridors in the Dutch – German border region. The maps on the right show the observed present distribution (black dots) and the projected climatic niche space distribution of the species in Europe under the scenario BAMBU (A2) for the years 2050 and 2080: (a) remains stable (light green), (b) is lost (grey) and (c) is gained (dark green) (based on Settele et al. 2008).

(Netherlands) for the first time (Dutch Butterfly Conservation 2011). The LARCH analysis shows that the present habitat network is not sustainable and several bottlenecks of poor connectivity exist for this species. There are several relative strongholds in the habitat network which could be enlarged and strengthened as future core areas in the network, such as the forested uplands in North-Rhine Westphalia. Forested areas in the Netherlands and in Germany are too isolated to allow cross-border dispersal for the butterfly. Thus, corridors were identified where the connectivity between the potential core areas should be improved as displayed in Fig. 3 to allow further range expansion of the marbled fritillary.

The LARCH analysis for the middle spotted woodpecker showed large areas of well-connected forest habitat, already indicating a highly sustainable network (Fig. 4). Today, the bird has a continuous distribution in Germany, ranging eastwards to European Russia and from the Baltic states southwards to the Balkans. In the Netherlands, the species has colonised the southern and eastern parts of the country in recent years (Dutch Centre for Field Ornithology 2012). For the future, climate envelope models predict discontinuous climate suitability in the Dutch – German border region. Whereas in 2050, the species will probably gain suitable

climate niche space, it disappears already in 2080 (Fig. 4). By 2080, many areas with present distribution in Europe are predicted to become unsuitable (e.g. parts of France, Germany, Poland and the Balkan states). This indicates that for the survival of the middle spotted woodpecker in Europe, the species needs to expand its range northwards with considerable speed.

Wetland species

The scarce large blue butterfly shows significant loss of suitable climate space in 2050 and 2080, especially in Southern and Eastern Europe and potential range shifts towards Scandinavia, where climate is predicted to become suitable between 2050 and 2080 (Fig. 5). Hence, the Dutch – German border area plays an important role in connecting present and future ranges. However, the LARCH analysis shows that habitat areas are too scarce and isolated to allow these long-distance range shifts. Additionally, the mobility of this butterfly is low, so that the capacity to colonise new climate space in the border region is very limited. Due to this unfavourable combination of insufficient habitat and limited colonisation ability, the development of a well-connected international network, may not be a good or even a

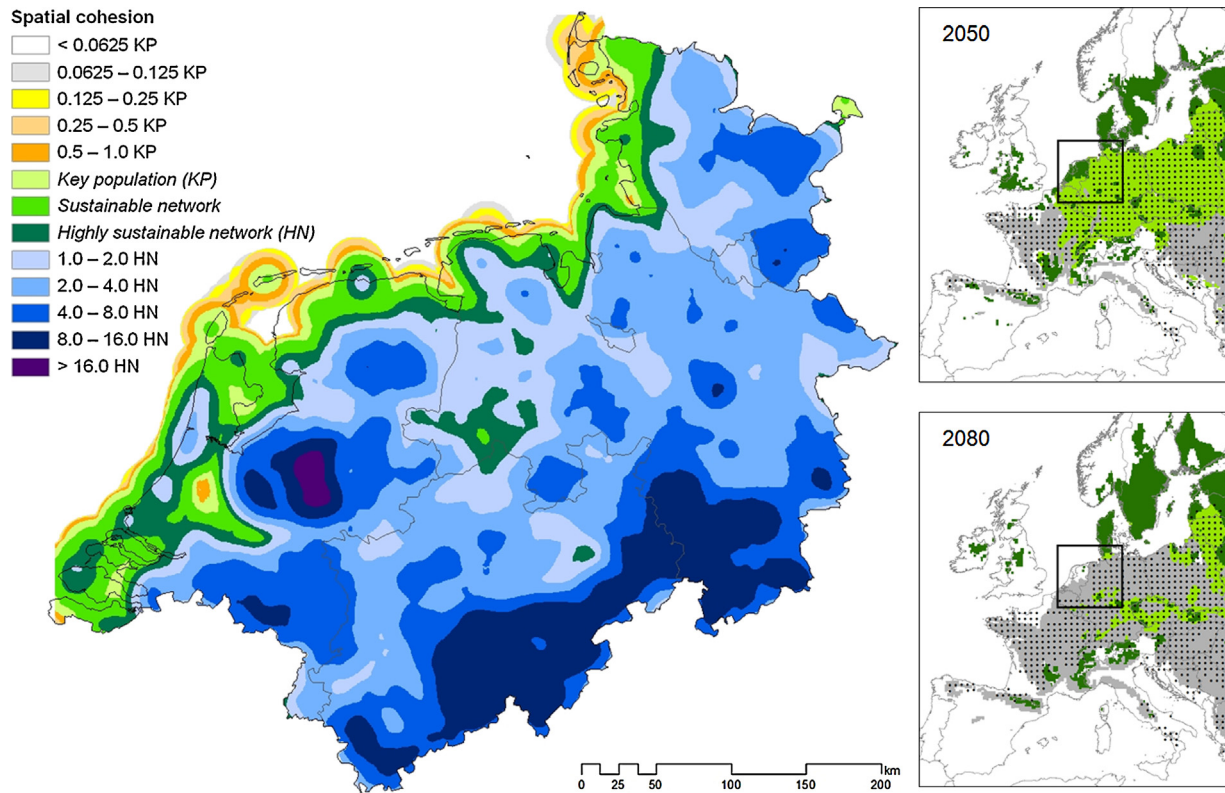


Fig. 4. Habitat network map for the middle spotted woodpecker (*Dendrocopos medius*). Maps on the right: observed present distribution (based on Huntley et al. 2007) and projected climatic niche space distribution in Europe (A2, 2050 and 2080; based on Berry et al. 2007). See Fig. 3 for legend explanation.

feasible adaptation strategy. It could be an option to consider the introduction of the scarce large blue. Introduction of this myrmecophilous species is possible, since the host plant and ant species are abundant. In the Netherlands, the butterfly was already successfully introduced in 1990 to the area that forms its present northern range boundary (Wynhoff 1998). As a climate adaptation strategy, the butterfly might be introduced to the potential core areas where the climate is predicted to become suitable in the future, such as in the north of Lower Saxony (dotted circles, Fig. 5). Before introduction, these potential core areas should be strengthened by improving their quality or enlarging their size. In addition the connectivity between the core areas needs to be improved in the indicated corridors, to facilitate range expansions from these starting points towards the north.

Climate envelope models for the European otter show considerable range expansion in the study area by 2050 and 2080, emphasising the significance of a well-connected network in this region. The LARCH analysis showed that some parts of the habitat networks are already highly sustainable (Fig. 6). Examples of these strongholds where the European otter already occurs are, for instance, the peat marshes in the provinces Overijssel and Friesland in the Netherlands and the area in the north of Lower Saxony, Germany. To facilitate range expansion several bottlenecks of low connectivity need

to be solved in the transboundary network. There are some isolated patches, especially in the northeast of the Netherlands in the province of Groningen, which need to be enlarged to increase colonisation capacity. In addition, the connectivity needs to be increased in the indicated corridors (Fig. 6). Corridors should be situated along streams and rivers in the lowlands, adding mitigating measures at roads.

Discussion

We analysed whether the spatial cohesion of the ecological networks in the Dutch – German border region would be sufficient to facilitate potential range expansion as a response to climate change and how these networks could best be strengthened through landscape planning. The need for transboundary spatial coherent networks was illustrated by the analysis of predicted shifts of suitable climate envelopes under climate change. Either a range expansion or a contraction through the Dutch – German border zone was predicted for a considerable number of species for which the present or future climate in the border region was predicted to be suitable.

The analysis for the forest ecosystems showed that along the Dutch – German border there are poorly connected landscapes, especially for less mobile and barrier sensitive

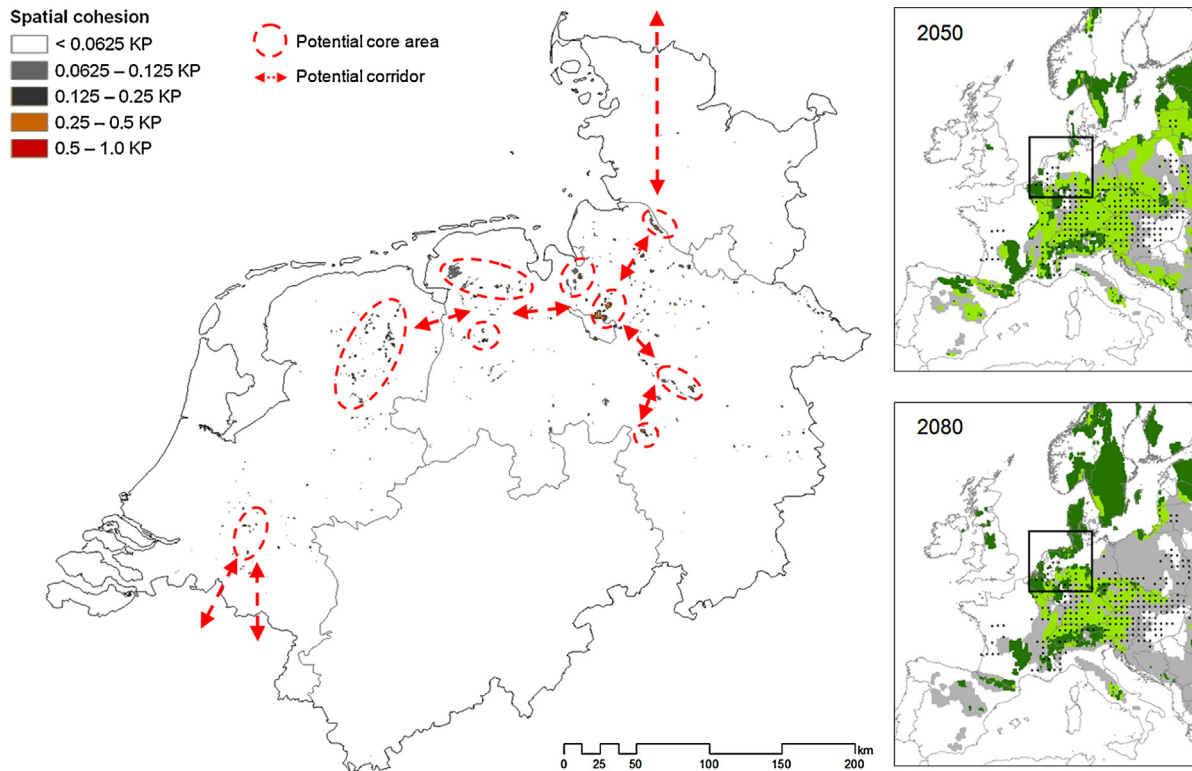


Fig. 5. Habitat network map for the scarce large blue (*Maculinea teleius*). The butterfly could be introduced to the potential core areas shown as dotted circles. Maps on the right: observed present distribution and projected climatic niche space distribution in Europe (BAMBU (A2), 2050 and 2080; based on Settele et al. 2008). See Fig. 3 for legend explanation.

species like the marbled fritillary (Fig. 3; west of the line Hamburg-Cologne). The corridors show where adaptation was recommended to improve connectivity for this butterfly, as a representative for forest species with low mobility. Enlarging patch size through habitat restoration and improving patch quality will increase the carrying capacity and, therefore, population survival. This adaptation measure is especially recommended for populations at the leading edge of expansion, to accelerate colonisation of new climate space (Vos et al. 2008). The effectiveness of this measure is illustrated by the results from Lawson, Bennie, Thomas, Hodgson, and Wilson (2012) for the silver-spotted skipper (*Hesperia comma*) where population survival of the butterfly on the edge of its range was an important factor for range expansion.

For the middle spotted woodpecker the spatial cohesion of the ecological network seems sufficient to facilitate range expansion. One might argue, however, that habitat quality was overestimated for this species and that management focussed on the development of forest with old trees and dead wood should be stimulated. In addition, the species needs to expand with considerable speed, and, therefore, requires a well-connected network with a high carrying capacity to be able to keep up with the predicted movement rate of its suitable climate zone (Schippers, Verboom, Vos, & Jochem 2011).

For wetland species the assessment showed that improving connectivity seems to be a good solution for species with high dispersal capacity like the European otter. Ecological networks should also include links to adjacent populations in the East (Germany, Poland) and to the South (Belgium), because range shifts will probably follow this direction.

In the case of highly fragmented habitat and species with limited dispersal and number of remnant populations, translocation to suitable, unoccupied sites that have a low probability of short-term colonisation (Maes, Vanreusel, Talloen, & Van Dyck 2004) is a reasonable adaptation strategy (Brooker, Britton, Gimona, Lennon, & Littlewood 2011). In the Dutch – German border region, this strategy seems an appropriate measure for the sedentary scarce large blue butterfly during climate change.

The recommendations presented in this study were based on a limited number of forest and wetland species that differ in their spatial functioning. This number should be extended in further studies to get a more balanced set of species (or eco-profiles, Opdam, Pouwels, Rooij, Steingröver, & Vos 2008) that are representative for the existing variation in habitat choice, area requirements and dispersal capacity. Additionally, the number of ecosystem types needs to be extended to, for instance, dry open landscapes which may be important to reptiles and butterflies showing potential range expansion

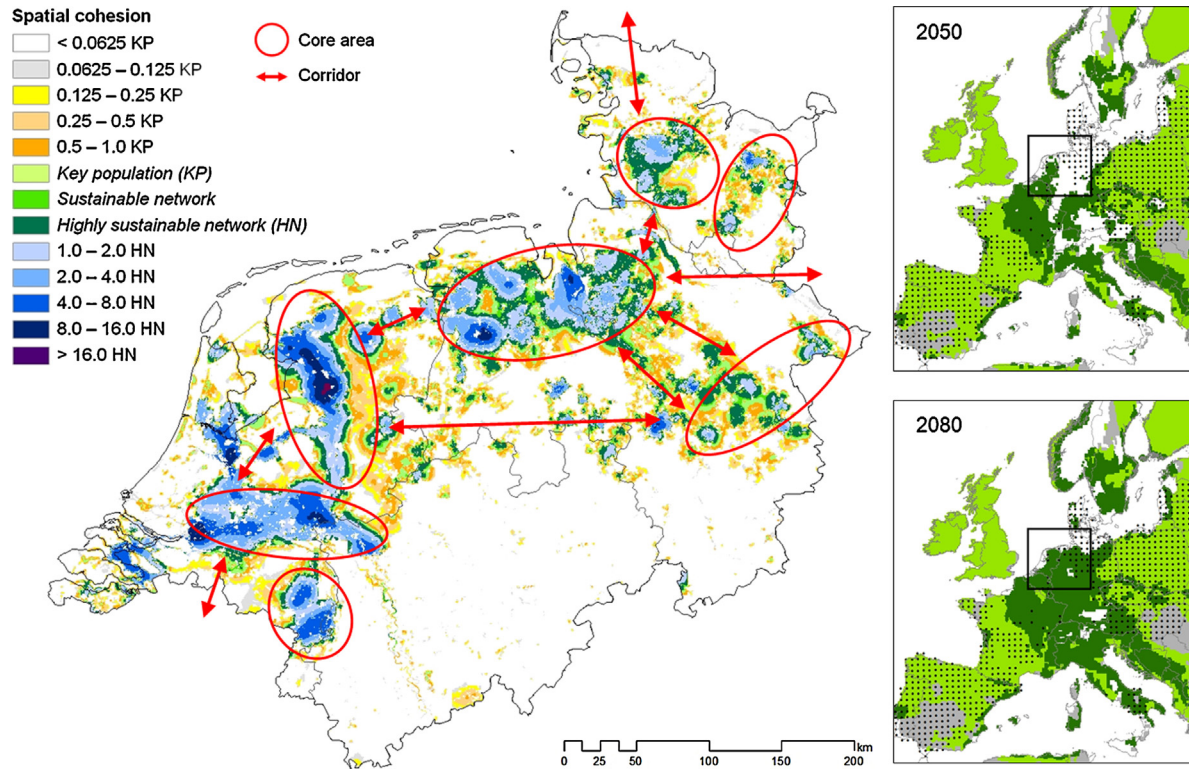


Fig. 6. Habitat network map for the European otter (*Lutra lutra*). The map shows options to connect viable networks and potential core areas. Maps on the right: observed present distribution in Europe (without British Isles, North Scandinavia and South East Europe; based on Reuther 2004) and projected climatic niche space distribution (A2, 2050 and 2080; based on Berry et al. 2007). See Fig. 3 for legend explanation.

in the border region. We focused on wetlands and forests, because both ecosystem types are of special concern for transboundary connectivity in the region today. Both ecosystem types will probably be of special concern for transboundary connectivity under climate change conditions as well since many species from southern and western parts of Europe are supposed to shift their climate zones within the border area. It is worth noting that the results from recent national studies in Germany (Reich et al. 2012) and in the Netherlands (Vos et al. 2010) generally point in the same direction.

Merging national datasets and selection of potential habitats and barriers was possible in GIS, however, differences in the typology of the Dutch and German national habitat maps create a limitation in transboundary network analysis. As a consequence, the available habitat and the spatial cohesion of the network might be overestimated or underestimated. For the middle spotted woodpecker, modelling results depend on the accuracy of selected habitats covering potential breeding trees. This information was available for the Netherlands, while we had to estimate habitat quality for the German part on the basis of relatively coarse habitat classification. Using less precise habitat information may lead to overestimation. In case of the European otter, we assumed that traffic areas and motorways form barriers. However, often individuals will be able to go through tunnels or cross river

valleys. In these cases, actual spatial cohesion will be underestimated in the habitat network map. Model results would be more realistic if input data of potential habitats and barriers were more accurate and if habitat classification was comparable in both European countries (Davies, Moss, & Hill 2004).

Several weaknesses and uncertainties in climate envelope modelling have been extensively discussed elsewhere (e.g. Pearson & Dawson 2003; Thuiller 2004). For instance, these models are criticised as being only a generalisation and not correct in detail. Moreover, the simulations vary greatly depending on different climate parameters, emission scenarios, modelling methods and algorithms (Mbogga, Wang, & Hamann 2010). As models project species' potential climate space in the future, it is not possible to validate modelled events. Additionally, these models cannot account for all factors driving these changes (Araújo, Pearson, Thuiller, & Erhard 2005). While the analysis on the basis of various scenarios, circulation models and climate envelope models should be included to generate relatively robust data, this is unlikely to account for the full uncertainty of climate change (Harrison, Berry, Butt, & New 2006). Although projections for the future should not be relied on completely because they may prove wrong (Thuiller 2004), modelling often remains the only approach for studying the possible consequences of a changing climate on species

distribution (Guisan & Zimmermann 2000). Hence, IPCC SRES emission scenarios and climate envelope models have been widely applied in climate change research (Rannow et al. 2010). Application of climate envelope models may be useful if the range of applications for which the model predictions are suitable is defined (Araújo et al. 2005; Guisan & Zimmermann 2000). We argue that the present level of accuracy and the 50×50 km resolution of the climate envelope models are sufficient to identify the main directions of potential future shifts in climate suitability and can, therefore, be used to identify locations on a regional level where adaptation measures in the ecological network are most needed. Indeed, recent studies confirm that trends in empirical data on the distribution of species are in line with climate envelope model predictions (Devictor et al. 2012), which is encouraging for applications of the models in a management context.

We found that many species will need ecological networks to compensate for potential losses of distribution range with gains in areas adjacent to their current distribution boundaries. Our results underline that conservation planning should not only focus on areas where target species occur today. Efforts should be expanded to areas with high potential for suitable habitats in the future where species have high probabilities of persistence over the long term (Hannah et al. 2007). However, the period of time that would be necessary for this prediction to occur is unknown (Araújo, Cabeza, Thuiller, Hannah, & Williams 2004). Our approach of identifying potential core areas and corridors on the basis of currently suitable habitats is, therefore, more robust than ignoring habitat suitability. But note that our habitat network maps are not meant to be implementable network plans (Beier et al. 2011). Within the identified core areas and corridors on a regional level, many alternatives are possible for designing concrete adaptation measures. The approach presented in this study allows landscape planners and managers on a local level to prioritise species and ecosystem types (Caro, Eadie, & Sih 2005), which may be used to develop habitat networks, taking into account the transboundary scale level as well as additional information, which may exist on the local level (e.g. actual distribution data of species, detailed habitat maps). It offers the chance to incorporate demands from other land-use functions and to integrate them into spatial planning, which is considered to be an instrument with special importance for regional and local adaptation (Rannow et al. 2010). We strongly recommend that the exchange of knowledge between ecological network planning and spatial planning should be strengthened, not only on national, but also on international level (Jongman, Bouwma, Griffioen, Jones-Walters, & Doorn 2011). The method developed in this study can support communication within and between national authorities and stakeholders, like for example regions, NGOs and different sectors (e.g. nature conservation, forestry, hydrology), to provide for common policies and planning concepts, which are greatly needed, as national initiatives often do not include a transboundary planning.

Acknowledgements

We thank Linda van Garderen, Gesa Rode and Marita Wilmes for their assistance in the analysis of climate envelope models. Nana Wix contributed to the preparation of GIS data and illustrations. We thank Martha Graf for proof-reading the manuscript. We are grateful to three anonymous reviewers for their valuable comments on earlier versions of the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baec.2014.09.007>.

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