

# Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation

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## Abstract

Climate change and habitat fragmentation are considered key pressures on biodiversity. In this paper we explore the potential synergetic effects between these factors. We argue that processes at two levels of spatial scale interact: the metapopulation level and the species range level. Current concepts of spatially dynamic metapopulations and species ranges are consistent, and integration improves our understanding of the interaction of landscape level and geographical range level processes. In landscape zones in which the degree of habitat fragmentation allows persistence, the shifting of ranges is inhibited, but not blocked. In areas where the spatial cohesion of the habitat is below the critical level of metapopulation persistence, the expansion of ranges will be blocked. An increased frequency of large-scale disturbances caused by extreme weather events will cause increasing gaps and an overall contraction of the distribution range, particularly in areas with relatively low levels of spatial cohesion. Taking into account the effects of climate change on metapopulations, habitat distribution and land use changes, future biodiversity research and conservation strategies are facing the challenge to re-orient their focus and scope by integrating spatially and conceptually more dynamic aspects at the landscape level.

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## 1. Introduction

A notable man-induced change of climate seems inevitable. The Intergovernmental Panel for Climate Change (IPCC, 2001a) concluded that by increasing the concentration of greenhouse gasses, man has a discernible influence on climate, expected to be a long-term phenomenon affecting the environment in the forthcoming decades or even centuries. Since climate is a key driving force, climate change is likely to exert considerable effects on current biodiversity conservation goals of countries and NGO's. Indications for impacts were found in many species over a wide range of taxa (Parmesan and Yohe, 2003). Such impacts may influence the return on current investments in biodiversity conservation.

Do species respond to climate change by genetic or physiological adaptations, or do they respond by find-

ing a better place? Quite some papers reported a correlation between the past or current geographical distribution of a species and some climate variable, and used this to extrapolate a future distribution on the basis of some climate change scenario (e.g. Sykes and Prentice, 1996; Currie, 2001; Davis and Shaw, 2001). One characteristic assumption of such studies is that species distributions always mirror climatic limitations. Alternatively, species may respond to shifting climate conditions by a shift in the realised niche (Lavorel, 1999). Acknowledging the shortcomings in our knowledge on this subject (Parmesan and Yohe, 2003), and stressing that at this point we do explore risks rather than give predictions, we focus on demographical rather than physiological responses. We feel supported by Davis and Shaw (2001) concluding that genetic constraints on adaptation, together with land cover changes that impede gene flow, are likely to reduce the rate of adaptation well below the pace required with the expected change in climate. So we assume that many species responses to climate change will be influenced by the spatial configuration of habitat in the landscape.

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Studies exploring spatial responses to climate change often disregarded the role of the landscape pattern (Ellis et al., 1997; Hill et al., 1999; Parmesan et al., 1999; Roy et al., 2001; Conrad et al., 2002). Although in some literature range expansions driven by climate change were treated in a spatial context (Sykes and Prentice 1996, Lindner et al. 1997, Rupp et al. 2000), little attention was paid to the synergetic effects of habitat fragmentation and climate change. In most studies it is assumed that the habitat is homogeneous, allowing a geographical response only limited by the shift of temperature, and not by the density and the configuration of habitat at the landscape level. However, in a human dominated world, natural or semi-natural ecosystems are embedded in tracts of unsuitable landscape, and populations of species restricted to those habitat types are spatially dissected. Often, such populations show characteristics of a metapopulation structure (Saunders et al., 1991; Opdam, 1991; Fahrig and Merriam, 1994; Villard et al., 1995; Hanski, 1997, 1999; Vos et al. 2001), which is an indicator for a moderate degree of fragmentation (Opdam and Wiens, 2002). The persistence and dynamics of such metapopulations are determined by the spatial cohesion of the habitat networks in such landscapes (Opdam et al., 2003).

By consequence, what is described as a shifting species range is in fact the complex result of extinction of (meta)populations at the warm range limit, and colonisation and growth of (meta)populations into regions that newly came within the cold range limit. So, for understanding the potential risks of climate change to a species, we must consider the dynamics of the populations constituting the geographical range, in connection to the spatial features of the landscapes across the range. Landscapes with a dominant human land use will continue to change due to increasing mobility, economic activity, urbanisation and agricultural development, causing a further decrease of spatial cohesion of habitat for species. We argue that where fragmented landscapes block population responses to climate change, solutions are to be found in adapting the landscape. Therefore, we consider it urgent to link the metapopulation/landscape scale and the species range/climate scale.

In this paper we explore the role of the amount and spatial configuration of habitat at the landscape level for species responding to climate change, and extend the landscape level processes to the scale of the species range. The aim is to explore the risks to biodiversity caused by the synergy of climate change (at the large scale) and habitat fragmentation (at the regional scale). We follow a spatial approach, because human-induced habitat fragmentation has not only an explicit spatial character, but is only to be solved in the context of multifunctional landscape development. Our aim is to answer the following questions:

1. What is the relationship between metapopulation and biogeographical processes and species responses to climate change?
2. What do we know about the potential effects of climate changes on biodiversity in a world where many natural ecosystems have become diminished and fragmented?
3. What are the consequences for biodiversity conservation strategies and landscape development?
4. What does it mean for the research agenda?

The available knowledge is slightly biased to the Northern Hemisphere. This seems acceptable because climate change is more extreme in the Temperate Zone than in the tropics (IPCC, 2001a), and because in the densely populated parts of Europe and North America, habitat fragmentation is most extreme.

## 2. Predicted effects of changing climate on ecosystems and species

Records show that atmospheric concentrations of the greenhouse gases (GHG) have grown significantly since the 18th century (IPCC, 1996). Models project an increase in global mean surface temperature relative to 1990 of about 1–3.5 °C by 2100. The Third Assessment Report on Climate Change (IPCC, 2001b) predicts a global temperature increase of maximally 5.2 °C—with regional peaks of more than 8 °C. This change of climate is thought to lead to an increase in average global temperature, changes in the frequency and distribution of precipitation, and changes in the pattern and occurrence of droughts and floods (Parry and Swaminathan, 1992). For Europe, Parry (2000) predicted that the annual temperature warms up at a rate of 0.1–0.4 °C/decade. Also, hot summers are predicted to become much more frequent, annual precipitation in northern Europe to increase 1–2%/decade, most of Europe to get wetter in the winter season and global mean sea level to rise 13–68 cm around the middle of the 21st century.

The key implications of these predictions are shifts and fluctuations of habitats and habitat conditions, even without land use changes due to human response to climate change (Parry, 2000). Ecosystems may shift geographically, or change in species composition. Net productivity in ecosystems is likely to increase. Native pinewoods, calcareous grassland, mesotrophic lakes, riverine and wetland ecosystems have been identified as particularly vulnerable (Van Ierland et al., 2001). Still, there is large uncertainty about the magnitude and concrete impact patterns that have to be expected (Hossel et al., 2000). This is even more so because climate change will not occur in isolation but is going to be part of a series of synergetic processes, involving hydrological, pedogenic as well as land use processes.

Climate change affects land-use as well, and this may either augment or mitigate fragmentation. For example, a doubling of CO<sub>2</sub> concentration can lead to a production increase of 15–50%, depending on crop and weather conditions, which would have major effects on the area needed for farming (Schapendonk et al., 1998; Van Ierland et al., 2001). Where land will be abandoned depends on interactions between landscape conditions, change in weather variability, adaptations in farming, increase in productivity, and the world food market. Flood magnitude and frequency is expected to increase due to more frequent heavy rains, resulting in increased runoff and, in floodplains, groundwater recharge. River flood hazards will increase across much of Europe (IPCC, 2001b). Due to higher temperature, evaporation is likely to increase, causing reduced stream flows during dry seasons with negative effects on water habitat quality.

In terms of potential risks to biodiversity, these changes can be classified under two headings: rise in average temperature, and an increased fluctuation of weather conditions, leading to increased perturbations in ecosystems. While temperature rise is affecting all ecosystem types, weather fluctuations (extreme rainfall, dry and hot summers) may be particularly important in wet ecosystems, in the lower parts of catchment areas and in river deltas, but also in open dry ecosystems.

### 3. Linking the landscape and biogeographical scale

#### 3.1. A conceptual model

We consider the landscape as the unit of spatial planning, where humans change landscape patterns to adapt

the functions of the landscape, and the (often spatially structured) population in the landscape as the unit of conservation. So we focus on population rather than on individual responses. At a higher spatial scale, the geographical range is imagined as a spatially organised set of landscapes with a variable spatial cohesion (Fig. 1). These landscapes support regional populations (or metapopulations), but also they may fall below the critical spatial cohesion threshold for persistence. Long distance dispersal plays a key role in linking regional populations. The result is a mosaic of landscapes with populations alternated by parts of the range where the species is absent. Hence, this “network of habitat networks with interacting regional populations” includes two levels of spatial scale. Of course this network is dynamic over time, due to large- and small-scale (environmental) disturbances, causing regional extinction and reestablishment.

According to this conceptual model (Fig. 2), climatic change affects the interaction between the two levels of spatial scale in two different ways. Firstly, temperature rise leads to a shift in environmental conditions. The change in distribution range is mediated by landscape cohesion affecting metapopulation extinction rate in regions that became unsuitable, and affecting the establishing rate in newly emerging habitat. Secondly, an increased frequency of weather extremes is affecting the distribution range by the interaction of large-scale disturbances and landscape cohesion. [Indirectly, climate change may affect landscape cohesion (either positively or negatively) if humans adapt the use of land, but this is not considered here.] Hence, our model inserts the landscape level in the response chain between climate change and the species range. This is necessary to

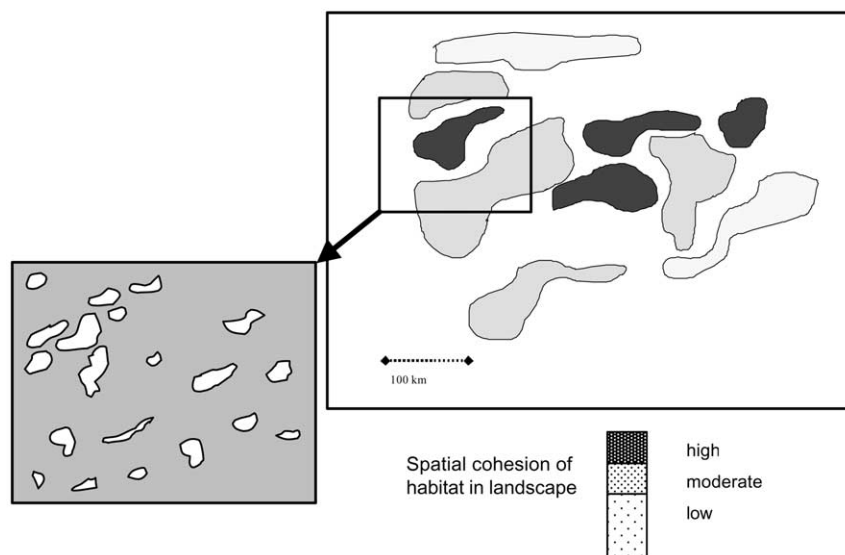


Fig. 1. Patterns at two spatial scale levels. The map shows a virtual representation of a species range, encompassing landscapes with a varying spatial cohesion of habitat. It is assumed that highly cohesive landscape areas support the highest densities of the species per area of habitat. The detailed map illustrates the assumed variation in the density of habitat.

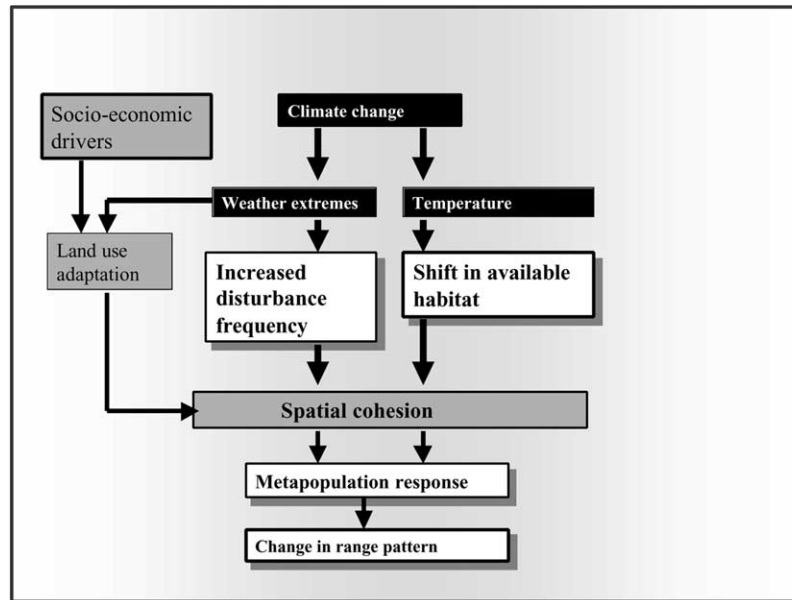


Fig. 2. The response chain from climate change to distribution pattern is mediated by landscape cohesion. Two levels of spatial scale interact. The response is established by two mechanisms: increased disturbance and increased temperature. Spatial cohesion is also affected by land use, partly in response to climate change.

understand the impact of the interacting pressures of habitat fragmentation and climate change on biodiversity. In the next sections we will review current knowledge for supporting evidence.

### 3.2. The landscape scale: metapopulation dynamics

Habitat loss and habitat fragmentation are sometimes distinguished, the latter defined as the configuration of habitat in space (Fahrig, 2001a). In the context of this review, we consider the two processes as correlated in space and time. Relevant is though that above a certain amount of habitat, spatial configuration does not play a significant role. This fragmentation threshold is species specific, and therefore scale dependent (Andr n, 1996; Fahrig, 2001b; Opdam et al., 2003). Assuming that in many regions in the Northern Temperate Zone, the degree of fragmentation of natural ecosystems is considerable (Opdam, 2002), we take the habitat network as the conceptual basis for conservation and landscape development.

Given enough habitat of good quality, the spatial pattern of the habitat network (Opdam, 2002) and the landscape matrix in which the network is embedded are crucial for the long term conservation of many species (Tilman and Kareiva, 1997; Opdam et al., 1995; Collinge, 2001; Hanski, 2001; Opdam and Wiens, 2002; Geertsema et al., 2002). The structure of the landscape matrix, the non-habitat part of the landscape in which the habitat network is embedded, affects the direction and density of the stream of dispersing individuals or seeds between the habitat sites (Schumaker, 1996; Beier

and Noss, 1998; Harvey, 2000; Vos et al., 2002). Empirical studies in human-dominated landscapes showed that the configuration of habitat determined the spatial distribution for a variety of plant and animal species (e.g. Van Dorp and Opdam, 1987; Verboom et al., 1991; Quintana-Ascencio and Menges, 1995; Thomas and Hanski, 1997; Bastin and Thomas, 1999; Villard et al., 1999; Biedermann, 2000; Vos et al., 2000; Foppen et al., 2000; Geertsema and Spangers, 2002). Several authors also pointed out the role of history and the disturbance regime in the effect of habitat fragmentation, in particular in relation to plants (Grashof-Bokdam and Geertsema, 1998; Ross et al., 2002).

With ongoing intensity of land use for economic productivity and urban dwellings, the spatial density of habitat decreases, the pieces of habitat become smaller and more widely scattered and the landscape matrix becomes increasingly impermeable for dispersing organisms. Model simulations (Andr n, 1994, 1996; With et al., 1996; With and King, 1999; Vos et al., 2001; Fahrig, 2001a) indicate that this is a non-linear relationship, which means that there is a critical viability threshold in the response of species to ongoing habitat loss. Beyond the critical threshold the fragmented population is not viable. Above this threshold the landscape is moderately fragmented, allowing persistence in a metapopulation structure.

The following effects of habitat fragmentation on populations are known:

- Population decline and extinction (Donovan and Flather, 2002)

- Loss of genetic diversity (Gibbs, 2001)
- As little as 50% of patches in a sustainable habitat network may yearly be occupied (Vos et al., 2001).
- Lower densities due to less effective distribution of individuals over habitat network (Haddad and Baum, 1999; Gonzales et al., 1998)
- Effects of large-scale disturbances stronger in more fragmented habitat, causing temporary extinction at the regional level (Foppen et al., 1999, Fig. 3).
- Reduced growth rate causing recovery time from large-scale disturbances to be extended (Foppen et al., 1999).
- Disruption of biotic interactions, reducing seed setting and rates of parasitism (Kruess and Tscharnke, 2000)

Hence, smaller densities and lower percentage of habitat occupation all decrease the resilience of populations to increased environmental disturbance, including climate change. Also, because the extinction/recolonisation processes cause a less effective distribution over habitat, and because dispersal mortality is high, metapopulation recovery time is extended compared to homogeneous populations.

The impact of fragmentation will however vary among ecosystem types. Under natural conditions, fragmentation of habitat is caused by natural disturbances (Opdam and Wiens, 2002). Species have adapted to unpredictable habitat availability in space and time by developing a high mobility, and consequently are less susceptible to human-induced fragmentation, for example species from coastal habitats and early succession stages of ecosystems. In reverse, species of systems with low natural dynamics, like forest, have evolved under fairly predictable conditions in a more or less continuous habitat. Marshland and heath species are intermediate. Moreover, forests, fresh water marshland and unimproved grasslands often have become

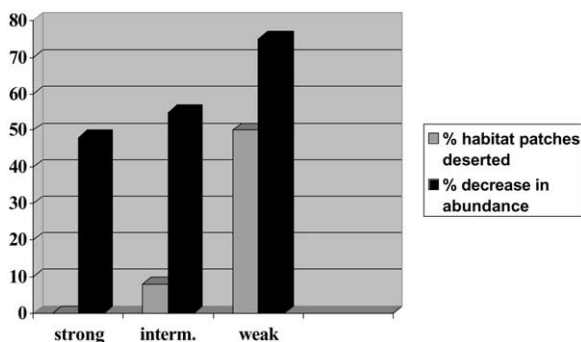


Fig. 3. Sedge warbler population decline after extreme drought in African winter quarters. The decrease in abundance and occurrence is highest in regions with the weakest spatial cohesion (based on Foppen et al., 1999).

highly fragmented. We postulate that species in these ecosystems, when responding to climate change, are most limited by the amount and spatial configuration of habitat. Agricultural systems therefore are regarded here less vulnerable.

Critical thresholds in the amount of habitat below which the above mentioned phenomena may occur also vary among species of the same ecosystem type. Metapopulations were reported to exist at varying amounts of habitat coverage (1–40%, Andr en, 1994, 1996; Villard et al., 1999; Vos et al., 2001). The variation is due to differences in habitat choice, in the influence of landscape type and structure on movements between habitat patches, and in the ecologically relevant scale of factors determining metapopulation processes.

The effects of large scale environmental disturbances, which hit all the local populations at once, is largely missing from metapopulation literature (Hanski, 2001). Ak akaya and Baur (1996) pointed out that metapopulation extinction time is shortened by spatially correlated disturbances. In a modelling experiment, using a metapopulation model of a Leadbeater's possum *Gymnobilideus leadbeateri*, McCarthy and Lindenmayer (2001) demonstrated that spatially correlated disturbances (in their case: fires) elevated the risk of regional extinction. Empirical research rarely highlights the role of climate perturbations in fragmented populations. To explain the dramatic decline of the green salamander *Aneides aeneus*, a species with a highly fragmented habitat, in the southern Appalachians in the US, Corser (2001) suggested that the increase in the July temperature and greater fluctuations in the January temperature since 1970 could have caused the observed trend. McLaughlin et al. (2002) showed that changes in precipitation amplified fluctuations in (isolated?) populations of Bay checkerspot butterflies *Euphydryas editha*, leading to more extinction. Foppen et al. (1999) showed that sedge warblers *Acrocephalus schoenobaenus* in heavily fragmented habitat networks in the Netherlands almost got extinct during periods of population crashes caused by droughts in African wintering areas. In less fragmented regions, the decrease was much smaller, and the recovery much faster. (Fig. 3). The explanation for this may be that in a fragmented habitat network the individuals are not able to locate all the best quality habitat sites (a considerable number remains unoccupied yearly), and the mortality loss during dispersal is much higher due to longer searching through unfavourable landscape. Also, smaller patches may have a lower habitat quality, with less reproduction. Paradis et al. (1999) pointed out the potential role of dispersal in increasing synchrony in fluctuating populations of wetland birds.

Spatial heterogeneity in habitat quality may dampen the effects of local disturbances. In heterogeneous habitat some parts may allow a positive growth rate,

whereas other parts may be suitable for individuals to live, but not to reproduce. This pattern may be reversed due to temporal variation in weather conditions, as was shown for a spatially structured population living in a heathland with dry and wet patches by [Den Boer \(1986\)](#). A modelling study of the effect of spatially correlated fires on a metapopulation of Leadbeater's possums in a fragmented woodland landscape by [McCarthy and Lindenmayer \(2002\)](#) confirmed that the effect of large-scale disturbances is mitigated by spatial heterogeneity of patches. The role of heterogeneity among patches in metapopulation resilience to large-scale disturbances is unknown ([Hanski, 2001](#)).

### 3.3. *The geographical scale: range dynamics*

Range limits may be caused by environmental factors that push the population into a domain where death rate exceeds birth rate. For example, winter temperatures in North America could be related to breeding bird distributions ([Brown et al., 1995](#); [Mehlman, 1997](#)). Apart from temperature, biotic interactions may also contribute to range boundaries, for instance in the case of strongly competing species ([Brown, 1984](#)). Moreover, habitat fragmentation may limit the distribution range, if local extinction exceeds re-colonisation ([Holt and Keitt, 2000](#)). [Keitt et al., 2001](#) showed by simple mechanistic models that range borders may be established where the population density becomes so thin that growth becomes negative (due to individuals have difficulty in finding mates and establish pairs on good habitat). This can be expected at high levels of habitat fragmentation. Because of long-range dispersal, individuals may incidentally settle beyond this limit, particularly in periods of favourable weather. Breeding bird atlases comparing distribution patterns from different decades, always include a number of species showing such a pattern, e.g. in The Netherlands *Aegolius funereus*, *Carpodacus erythrinus*, *Locustella fluviatilis*, with an eastern distribution, or *Cettia cetti*, *Cisticola jucidis*, expanding temporally from the south ([SOVON, 2002](#)). Such observations, although circumstantial, illustrate the role of long distance dispersal. Often, such new settlements disappear after some years. The potential to expand a range limit varies among species. A systematic study of such patterns by [Gaston and Blackburn \(2002\)](#) in the UK showed that species with large dispersal distances were most likely to colonise new areas.

Within the limits, the occurrence patterns of species show variation in space and time. Species have been reported to occur in high densities in the centre of their range, and in low densities in the range margin ([Brown, 1984](#); [Hengeveld, 1990](#); [Rodriguez, 2002](#)). Such patterns can be simulated by assuming that gradients in birth and death rate and dispersal rate are governed by environmental factors that are favourable in the centre

of the range and decline towards the margins ([Maurer and Brown, 1989](#)). For instance, temperature directly affects energy constraints of individual plants, preventing them from growth or reproduction at higher latitudes. For some birds it was shown that in the centre of their ranges the growth rate was higher than in marginal parts of the range (e.g. eastern bluebirds *Sialia sialis*, [Peakall \(1970\)](#), great tit *Parus major*, [Sanz \(1998\)](#)). This pattern should be considered as static. [Hengeveld \(1990\)](#) argued that species ranges reflect the continuous response to changing environmental conditions. He considered climate as the principal component of a species environment. The outcome of species responding to variation in climate is observed as spatial variation in local densities and genetic composition.

[Hengeveld](#) did not elaborate the role of variation in habitat cohesion across the species range. As shown above, habitat fragmentation impedes the growth rate and resilience of populations to large-scale disturbance. Also, we pointed out that many studies indicate a relation between the spatial cohesion of habitat and the density and percentage of habitat occupied. Hence, we propose that the spatial variation in abundance is at least partly controlled by habitat cohesion. This pattern will appear dynamic over time, as a result of the described interaction between spatial cohesion and environmental disturbance regimes. Consequently, regions with highly cohesive landscapes support on average the highest abundance levels, appearing as peaks in the abundance distribution across the range. In support of this, [Brown et al. \(1995\)](#) and [Rodriguez \(2002\)](#) found spatially stable abundance peaks in dynamic species ranges, but did not relate these to variations in landscape pattern. [Brown et al.](#) could also demonstrate that abundance varied at a smaller scale than previously assumed. [Ives and Klopfer \(1997\)](#) showed in a model study that stochastic processes of the type [Hengeveld](#) proposed could be generated by metapopulation processes, which are characteristically stochastic, suggesting that the supposed stochasticity at the range level may be attributed to interacting metapopulations.

Assuming that species distributions are the result of interacting metapopulations, we expect that climate change induced weather perturbations cause temporary absence from moderately to heavily fragmented habitat networks. Since metapopulation growth is retarded as compared to homogeneous populations, an increased disturbance rate implies that recovery in such networks is broken off by repeated perturbations. Therefore, increased weather perturbations will cause permanent retraction in highly fragmented zones of species ranges, causing gaps or increase of gaps in the distribution pattern. Less fragmented regions will show increased oscillations in occupancy and abundance. Where the amount and configuration of habitat limit ranges, the same mechanism will cause a range contraction ([Fig. 4](#)).

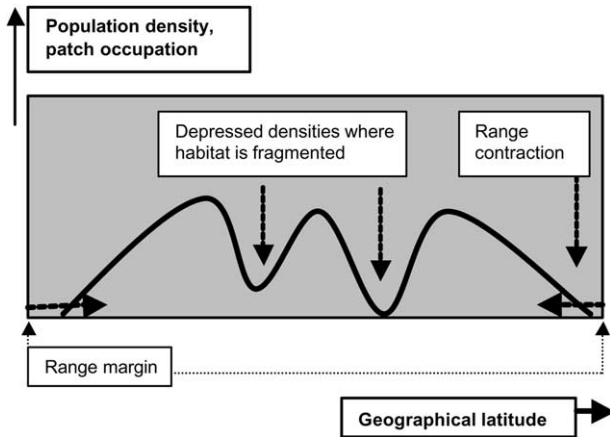


Fig. 4. Cross-section representation of a species range, assuming highest population densities and highest patch occupancy in the range centre. The crosscut passes through two regions with low degree of spatial cohesion, and depressed abundance. In these regions, increased weather variability causes a relatively strong drop in abundance and patch occupation, up to regional extinction.

Landscapes supporting habitat networks with a high spatial cohesion are crucial as sources of recolonisation. During periods with favourable weather conditions, landscapes with few or low quality habitat are colonised from source landscapes.

There is some evidence supporting this vision. Mehlman (1997) analysed counts of American songbirds for oscillations of range patterns. He suggested that environmental disturbances hit hardest in the margins of species ranges. Following a series of harsh winters, the ranges contracted, accompanied with reduced population densities. The marginal zones of the geographical range exerted greater abundance changes than more central parts. The range margin retreated, but not in an equal rate, so that the result was a rougher, more irregular range boundary. There was a great deal of dynamism at the range boundaries, due to a higher frequency of extinction and recolonisation events. The reason for this phenomenon could be twofold. Firstly, species may have lower reproduction and higher mortality rates in parts of the range with less favourable climate, either related to physiological traits or to shifting competitive or predator-prey relationships with other species. Secondly, the habitat may be more fragmented along the edge, because the species accepts less vegetation types as habitat. Mehlman (1997) did not relate the described patterns to any spatial pattern of habitat.

#### 4. Evidence for species responses to climate change in a fragmented landscape

We found no studies exploring the response of species distribution ranges to increased frequency of weather extremes. To our knowledge, all focus is on predicting

responses to temperature increase. Geographical distributions of animals are often regarded to be limited by bioenergetic constraints, meaning that global warming will species allow to expand northwards (Humphries et al., 2002). According to our conceptual model, a shift in range will be the result of newly establishing metapopulations at the northern margin, where a dispersal stream is caused by a positive growth rate. At the same time, at the southern margin metapopulations get extinct (often with a considerable time lag) because death rates exceed birth rates. The extinction rate will be negatively, and colonisation rate positively correlated to spatial cohesion of habitat. Expansion will be fastest in regions where the landscape structure enhances the dispersal stream, and will lag behind in regions where the landscape is fragmented. We found no studies supporting this prediction.

Most studies we found did not address the role of landscape structure, and the majority only demonstrated changes in distribution within the time span of a couple of decades, without explicit correlation to climate change factors (e.g. Ellis et al., 1997). Hill et al. (1999) calculated that the speckled wood butterfly expanded its range northwards in the UK, but not faster than its likely dispersal rate (1 km per generation) following the pattern of temperature rising. These authors predicted that in the UK the butterfly could have colonised all suitable habitat that is predicted under the climate change weather regime. However, they comment that there could be severe restrictions to this expansion due to habitat fragmentation, but did not quantify that effect. Parmesan et al. (1999) analysed changes in the distribution of 35 non-migratory butterfly species (excluding extreme habitat specialists and extremely sedentary species) in Europe. They found that 63% have ranges that have shifted to the north by 35–240 km, and only 3% have shifted southwards. They concluded that this distance was in the order of magnitude of the northward shift of average temperature during the 20th century (0.8 C warmer at given latitude). Conrad et al. (2002) presented data on the distribution of the garden tiger moth *Arctia caja* in the UK, and concluded that the observed decline between 1975 and 1995 is attributable to mild, wet winters with early spring weather. For British breeding birds, Thomas and Lennon (1999) found that 59 bird species moved further north by an average of 19 km over two decades. The only study that suggested a synergy between climate change and habitat pattern we found was Warren et al. (2001), who showed that the butterfly range expansion observed by Parmesan did not occur in the heavily fragmented landscape of the UK. They did not measure the landscape itself, but compared species with small dispersal capacity to mobile species. In spite of the improved climate, 93% of the first category species declined, most expanding species were mobile species.

They concluded that the negative effect of habitat fragmentation is dominant over the positive effect of a warmer climate.

All these empirical studies considered the shift of ranges without taking into account metapopulation processes. In a modelling study on forest expansion, Malanson and Cairns (1997) point out the important role of generation time, that is the number of years after settlement needed before reproduction is possible. Another point that needs more attention is the role of long-distance dispersal. Metapopulation studies focus on the distance covered by the majority of the individuals (because they dominate the metapopulation dynamics), rather than on infrequent long-term dispersal events that are difficult to measure. However, in shifting distribution fronts long-distance propagules may play a key role, because they establish remote source populations, and form bridgeheads from which the surrounding landscape is conquered. Schwartz et al. (2001) found long-distance dispersal largely determining the pace of shifting tree range limits, but also concluded that under the present forest distribution in Ohio, such long-term dispersal events were mostly ineffective to allow tree populations to keep pace with a shifting temperature range. However, if species need a long time to establish new settlements and many colonisation events are not successful, the yearly expansion of the shifting front would be much less than the long distance dispersal range.

The assumed interaction between climate change and fragmentation would result in higher expansion rates in landscapes with a high spatial cohesion. However, such differences might be levelled off if dispersal capacity is enhanced under a selective pressure of habitat fragmentation. Thomas et al. (2001) discussed improved dispersal capacity due to changes in flight morphology in two species of bush crickets. It seems that these insect groups are polymorphic, with the fraction of good dispersers being dominant during population expansion. After settlement in a new area, the fraction of poor dispersers in the local population increases again. In taxa capable of such flexibility, predictions of the effect of climate change on the range extension based on observation in equilibrium could underestimate the potential response (cf. Honnay et al., 2002).

Understanding the interplay between habitat fragmentation and climate change is further complicated by positive feedback loops, as has been explained by Thomas et al. (1999). They pointed out that a higher temperature might positively affect the microclimate of vegetation types that had been unsuitable before, resulting in patches added to the regional habitat network. The effect is that the spatial cohesion of landscapes may improve. Thomas et al. (1999) demonstrated for ectothermic species that in the northern UK heath contains less suitable sites than in the south, where the

climate is 3–5 °C warmer. For example, only very open, south-exposed heath vegetation offers the microclimate where these species can persist. Thomas et al. (1999) showed by modelling that the silver studded blue butterfly *Plebejus argus* would not be able to persist in the south of England under the northern climatic conditions. In reverse, warming up could increase the extent and cohesion of the habitat network, and by that diminish the effect of fragmentation.

A similar positive loop occurs if a species is capable of widening its habitat choice due to more favourable temperature conditions. This was suggested to occur in the butterfly *Hesperis comma* in the UK (Thomas et al., 2001), which expanded northwards three times faster than expected due to extending its habitat choice from chalk grasslands to a wider array of vegetation types. A similar change was recorded in the brown argus butterfly *Aricia agrestis*. By including *Geranium molle* plants in its habitat profile, this species could cover 14-km gaps in the distribution of its original host plant, a distance impossible to cross directly. It is not clear whether this change also involved evolutionary changes in habitat choice. However, *Geranium molle* is already used elsewhere in the species range, so that a purely physiological and behavioural explanation (e.g. by imprinting on habitat type) might suffice.

## 5. Implications for conservation strategies

We conclude that the integration of metapopulation and range ecology in a climate change context demonstrates that fragmentation multiplies the impact of climate change through several mechanisms (Fig. 2). Firstly, the shifting of ranges is inhibited in landscape zones in which the degree of habitat fragmentation allows persistent metapopulations, and blocked in areas where the spatial cohesion of the habitat is below the critical level of metapopulation persistence. Secondly, an increased frequency of large-scale disturbances caused by extreme weather events will cause increasing gaps and an overall contraction of the distribution range, particularly in areas with relatively low levels of spatial cohesion.

This picture is complicated by interactions between climate change and the availability of habitat in existing networks. If more vegetation types become suitable, spatial cohesion will increase allowing the metapopulation to respond quicker to climate change. Further complications emerge if climate change interferes with inter-specific relations (Harrington et al., 1999).

Our conceptual model assumes that the spatial cohesion of a habitat network has a minimum threshold critical to the survival of the metapopulation. The assumption that species occur in metapopulations at the landscape scale may not be realistic to species with very



limited dispersal, as pointed out by Watkinson et al. (2000) after an analysis of local and regional population dynamics of the grass *Vulpia ciliata*. Freckleton and Watkinson (2002) conclude that some plant species occur in regional ensembles of local populations with virtually no contact, if at all (like *Vulpia*), while others constitute (at the regional scale) spatially interacting populations in which local extinction and spatially dependent colonisation are common features (e.g. *Silene alba*). Under a changing climate, the former category has only one real strategy for survival in a fragmented landscape: local adaptation. For example, increased seed longevity in the seed bank may be an adaptation to increased weather extremes. Increased weather perturbations may increase local extinction rates in plants, increasing the dependency of metapopulations on (re)colonisation events. The described regional dynamics due to increased weather perturbations can only occur if local populations interact in regional ensembles, and may be more frequent in species with good dispersal capacities. Spatial extension of geographical ranges depends on dispersal capacity as well, and is not to be expected in species with very local dispersal. However, the role of long-distance dispersal in this process remains largely unknown.

What are the implications for biodiversity conservation? Admitting that our knowledge does not permit predictions on population changes and species distributions under the combined regime of climate and landscape change, we propose three major shifts in conservation strategies. Firstly, a species-oriented focus should be replaced by a focus on landscape conditions for biodiversity. These conditions should allow populations to respond to large-scale disturbances. If species distributions become more and more dynamic in space and time, local conservation management for single species will be less effective, if not a waste of money. We must accept that nature is much more dynamic and unpredictable than we may wish, and that our local flagship species may disappear in spite of much effort. We must envisage a landscape that allows species to respond to temperature shift, to respond to increased weather perturbations, and to adapt genetically to changing environments. Secondly, we propose to shift in strategy from protected areas towards landscape networks including protected areas, connecting zones and intermediate landscapes. To invest all our conservation money in protected areas will not be effective if nature is changing at a spatial scale far exceeding the scale of single reserves. Thirdly, we propose a shift from a defensive conservation strategy towards a landscape development strategy. A static approach of establishing isolated reserves surrounded by a highly unnatural landscape is not an effective strategy under a climate change scenario. We must accept that conservation of biodiversity is only effective if we integrate it in the

dynamic development of the landscape, and develop an offensive strategy based on coalitions with other functions.

All this implies a shift in conservation focus from the local level towards the regional and international level. The basis of all regional landscape development should be a spatially explicit vision on the required development of the future landscape network over a large geographical region. Such a vision integrates three components:

1. *Stabilising key areas*. Ecosystems most vulnerable to the combined stress of climate change and fragmentation are developed as a spatial network, including large nature areas as well as landscape regions with a high density of nature coverage. Such 'nodes' lower the risk of regional extinction under extreme weather perturbations and serve as sources of regional recovery.
2. *Heterogeneity*. Increasing the spatial variation of habitat quality in large nature areas and landscapes could make local populations and metapopulations less vulnerable to weather variability.
3. *Permeability of the landscape*, by developing bold connectivity zones, networks of narrow corridors, landscapes with a high density of small semi-natural landscape elements, and wildlife passages in infrastructure barriers.

## 6. Research priorities

Range ecology is evolving towards a more dynamic approach, but still largely neglects the underlying landscape pattern as a driving force of range structure and dynamics. Climate change ecology has been treating potential range shifts as a deterministic process, not bothering too much about the underlying landscape patterns and resulting metapopulation dynamics. Very little attention was paid to the impact of increased weather perturbations. On the whole, there is little empirical evidence, mostly based on butterflies. Metapopulation ecology thus far neglected the effect of large-scale disturbances on metapopulation extinction. While all these missing links are understandable simplifications in complex fields of research, solving the conservation problem we face requires an integrated approach of climate change ecology, dynamic biogeography and metapopulation ecology within a spatially explicit context of a dynamic landscape.

### 6.1. Research at the metapopulation level

Most metapopulation studies thus far have assumed habitat networks be stable (Hanski, 2001). In changing networks, either due to human land use or to a shifting

temperature range, metapopulation persistence will require a higher degree of habitat cohesion (Opdam et al., 2003). Can we quantify this in terms of how much extra area, patches or connecting elements are needed? What is the importance of key patches (Verboom et al., 2001) and dense clusters of smaller patches in networks for the resilience of metapopulations to large-scale disturbances, and can we quantify this contribution in terms of a minimally required key patch area in relation to the network size? In particular, the relation between the spatial distribution of habitat and the synchrony in population fluctuations, with dispersal as the key process, should receive much more emphasis (Paradis et al., 1999). Little attention is given to the time lag in metapopulation response to changing landscapes (Nagelkerke et al., 2002). We should know more about the metapopulation recovery after a regional disturbance with varying degrees of habitat cohesion, and for species with different life strategies.

### 6.2. Research at the range level

Little is known on how metapopulation dynamics determines the variation of presence/absence and abundance across ranges in time and space, how metapopulation dynamics varies between range centre and margins, particularly in shifting ranges, and how landscape characteristics are related to these processes. We should know more about the role of fragmentation in limiting ranges, and the contribution of stochastic metapopulation dynamics to the type of range stochasticity suggested by Hengeveld (1990), Brown et al. (1995) and Ives and Klopfer (1997). Experiments with linked metapopulation models may clarify the spatio-temporal behaviour of networks of metapopulations, and large-scale monitoring data are useful to test the results.

### 6.3. Research at range limits

Knowing more about how fast species can invade new habitat outside the original range is extremely important. Priority topics are to develop more realistic estimates of dispersal rates, which not only accounts for habitat coverage, but also for the time lag due to building up metapopulation equilibrium. We raised questions about the importance of long-distance dispersal at invasion fronts in relation to habitat cohesion and time lags in metapopulations. Such questions can be addressed by a combination of modelling and monitoring on different levels of scale. All this should be explored for various ecological profiles (Vos et al., 2001).

### 6.4. Towards landscape indicators

Because landscapes are not planned for single species, and planners are no ecological experts, we must develop

simple indicators for landscape diagnosis, planning guidelines and design rules (Opdam et al., 2002). This requires that we can scan the landscape pattern across a geographical range, and assess the contribution of landscape areas to the range dynamics. For example, we could distinguish key regions, in analogy to key patches in habitat networks (Verboom et al., 2001). Such key regions have strong, relatively stable networks, which support populations even after a heavy disturbance, and may act as sources for surrounding weaker networks in a post-disturbance recovery phase. Such an approach could be theoretically based on the Allee effect (Keitt et al., 2001). This will allow us to infer, from a GIS-landscape, regions where the spatial cohesion is so poor that recovery from a disturbance is not likely, given the frequency of disturbance events. We might even search for minimal patch occupancy thresholds (analogous to the 50% patch occupancy threshold suggested by Vos et al., 2001).

### 6.5. Application for landscape development

Any of the suggested strategies for landscape development is still hypothetical and its effectiveness and applicability should be tested for different ecosystem types, as suggested above. After that, we suggest the following steps based on applied GIS-modelling.

- Find bottlenecks regions in the spatial cohesion of large areas, where mitigation measures are taken most effectively. Bottlenecks could be either regions where the spatial cohesion is not good enough to allow northward expansion, or where the spatial cohesion is at a level at which increased perturbations will cause regional extinction
- Explore possible solutions to increase spatial cohesion above the critical thresholds of species under stress of climatic change. This could entail developing regional landscapes to serve as corridor zones, or conservation of nature areas that may function as key areas during perturbations.
- Develop a knowledge base, which help politicians and stakeholders to select the best solutions in different situations, and support them implementing solutions in a multifunctional landscape context.

It is important that ecologists transfer their knowledge appropriately to the different levels of decision-makers and stakeholders. Awareness of the problem, maps of bottleneck areas and general strategies should be developed at the European and national levels. At the regional level, the development of the landscape, often with a multifunctional purpose, the strategies should be adequately transformed into a regionally effective and acceptable landscape plan.

Time does not allow waiting with the applied steps until we have answered all the more theoretical questions. It is important to design research programmes that combine and let interact applied and basic research, so that the delivering of results is properly tuned with the planning process needed to adapt the landscape for biodiversity in fragmented ecosystem networks to respond to climate change.

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