Consequences of correlations between habitat modifications and negative impact of climate change for regional species survival

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ABSTRACT

While several empirical and theoretical studies have clearly shown the negative effects of climate or landscape changes on population and species survival only few of them addressed combined and correlated consequences of these key environmental drivers. This also includes positive landscape changes such as active habitat management and restoration to buffer the negative effects of deteriorating climatic conditions. In this study, we apply a conceptual spatial modelling approach based on functional types to explore the effects of both positive and negative correlations between changes in habitat and climate conditions on the survival of spatially structured populations. We test the effect of different climate and landscape change scenarios on four different functional types that represent a broad spectrum of species characterised by their landscape level carrying capacity, the local population turnover rates at the patch level (K-strategies vs. r-strategies) and dispersal characteristics. As expected, simulation results show that correlated landscape and climatic changes can accelerate (in case of habitat loss or degradation) or slow down (in case of habitat gain or improvement) regional species extinction. However, the strength of the combined changes depends on local turnover at the patch level, the overall landscape capacity of the species, and its specific dispersal characteristics. Under all scenarios of correlated changes in habitat and climate conditions we found the highest sensitivity for functional types representing species with a low landscape capacity but a high population growth rate and a strong density regulation causing a high turnover at the local patch level.

The relative importance of habitat loss or habitat degradation, in combination with climate deterioration, differed among the functional types. However, an increase in regional capacity revealed a similar response pattern: For all types, habitat improvement led to higher survival times than habitat gain, i.e. the establishment of new habitat patches. This suggests that improving local habitat quality at a regional scale is a more promising conservation strategy under climate change than implementing new habitat patches. This conceptual modelling study provides a general framework to better understand and support the management of populations prone to complex environmental changes.

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1. Introduction

Climatic and landscape changes are considered to be major drivers of biodiversity loss in terrestrial ecosystems (Opdam and Wascher, 2004; Thomas et al., 2004; Fischer and Lindenmayer, 2007). Several empirical and theoretical studies have clearly shown the negative effects of past, current, and predicted changes in climate regimes on population and species survival. This is due to changes in the mean and spatiotemporal patterns of temperatures and precipitation as well as an increase in the frequency and intensity of weather-related catastrophic events (e.g. Saether et al., 2000; Roy et al., 2001; Hannah et al., 2002; Walther et al., 2002; Thomas et al., 2004; Thuiller et al., 2005; Schwager et al., 2006; Blaum and Wichmann, 2007). Likewise, the negative consequences of ongoing landscape changes, including habitat loss, degradation and fragmentation, have been explored and demonstrated in a multitude of studies (e.g. Debinski and Holt, 2000; Hanski and Ovaskainen, 2000; Fahrig, 2002; Johnst et al., 2002; Henle et al., 2004a; Ewers and Didham, 2006; Körner and Jeltsch, 2008). While all of these studies point to important threats imposed by different aspects of environmental change, it is often overlooked that climatic and landscape changes are not independent of each other (Dale, 1997; Pearson et al., 2004). For example, synergistic interactions of climate change...
coupled with fragmentation may magnify the impacts of climate changes alone (Travis, 2003; Bomhardt et al., 2005; Ewers and Didham, 2006). While climate change will have a direct impact on the performance of many species, there will be additional indirect effects that result from changes in the spatiotemporal availability of habitat and natural resources (Hulme, 2005). These indirect effects are not only caused by the ‘natural’ response of the biotic environment to climate shifts (e.g., changes in structural diversity of habitat forming vegetation – Tews et al., 2004, 2006), but may also result from human imposed modifications to land use type, patterns and intensities (Dale, 1997; Hulme, 2005; Pearson and Dawson, 2005; Ewers and Didham, 2006). For example, when populations are isolated by habitat fragmentation and loss, range expansion, which would have occurred in response to climatic shifts, is restricted. Consequently populations may become more vulnerable to the effects of climate change and extreme weather events (Travis, 2003; Pearson and Dawson, 2005, Ewers and Didham, 2006; Best et al., 2007). Hill et al. (2002) report that in the U.K., the synergistic effects of fragmentation and recent climate change have led to reduced geographic range sizes in 30 out of 35 butterfly species over the last 30 years (see also Warren et al., 2001). On a more local scale, climate change may significantly reduce habitat suitability leading to smaller (sub-) populations that will suffer from higher extinction risks due to environmental or demographic stochasticity, reduced genetic variation, inbreeding depression, and reduced potential for evolutionary adjustments (e.g. Matthies et al., 2004; Bruna and Oli, 2005; Willi et al., 2006; Berec et al., 2007).

Although landscape change may have negative effects correlated to the negative effects of climatic change, other anthropogenic changes to the landscape may be beneficial. For example, habitat restoration, including (re-)afforestation and rehabilitation of degraded land, has been discussed as one of an array of potential human responses to climate change (Donald and Evans, 2006; Harris et al., 2006). Management measures to improve local habitat conditions, to create new habitats or to increase landscape connectivity may buffer the negative effects of deteriorating climatic conditions (Hulme, 2005; Pearson and Dawson, 2005). Although considerable international research has focused on the impacts of climate change, relatively little work has explored management strategies for adapting to climate change (Ormerod et al., 2003; Hulme, 2005).

In this study, we apply a conceptual spatial modelling approach to explore the effects of both positive and negative correlations between changes in habitat and climate conditions on the survival of spatially structured populations. Positive correlations here mean that both types of environmental change, i.e., climate and landscape change, lead to deteriorated living conditions for species, whereas negative correlations between these key drivers imply that, although climate change leads to deteriorated conditions for populations, suitable habitat increases or habitat conditions improve. For both circumstances, we differentiate between two principal types of landscape change: (i) habitat degradation vs. improvement, i.e., a change in the quality of local habitats leads to a change in the carrying capacity in the habitat and (ii) habitat loss vs. gain, i.e., a change in the number of suitable habitat patches in a fragmented landscape. We test the effect of these different landscapes scenarios on four different functional types that differ in their overall abundance, rate of species turnover (K-strategies vs. r-strategies) and type of density dependence, and for different dispersal scenarios.

We use a model system combining a modified version of a well-established, local population model (Maynard Smith and Slatkin, 1973; Bellows, 1981; Johst and Dreschers, 2003; Wichmann et al., 2005) with spatially explicit, individual-based dispersal in differentially fragmented landscapes to examine the effects of the climate by landscape interaction. Two contrasting levels of fragmentation (high vs. low) were explored with a sufficiently high number of landscape repetitions to allow for a systematic investigation. Our key research question is: (i) to what degree does a change in the landscape modify the effects of climate change on population survival? More specifically, we ask: (ii) how do the combined effects of climate and landscape change differ among functional types and dispersal scenarios? (iii) are these effects related to the level of landscape fragmentation? (iv) is habitat degradation more critical than habitat loss for species extinction when correlated with negative impact of climate change? and, with regard to restoration: (v) does the improvement of local habitat conditions have a higher potential to buffer the negative effects of climate change than the establishment of new habitats?

2. Methods

2.1. Model description

2.1.1. General model structure

We simulated regional population dynamics in a spatially explicit landscape context linking local (sub-) population dynamics in suitable habitat patches by dispersal. The spatial extension of the grid-based model represents the regional distribution of one species and is divided into 129 × 129 grid cells (a grid size that is related to the landscape generating algorithm – see below). Cells are either unsuitable for the species or represent potentially suitable habitat patches. Potentially suitable habitat patches (i.e., grid cells) can accommodate one local population, but patches differ in habitat quality, i.e., local carrying capacity. We used periodic boundary conditions leading to a torus-like structure of the simulated landscape to avoid artefacts resulting from limited grid extent.

Climatic changes were simulated to directly affect local populations by reducing effective population growth rates over time. Landscape changes were produced through habitat degradation or improvement by changing local patch carrying capacities or through habitat loss or gain by increasing or decreasing the number of cells of suitable habitat. All simulation experiments were conducted in two contrasting types of landscapes, i.e. those with a high vs. a low level of fragmentation. Landscape changes were positively correlated, negatively correlated or uncorrelated with respect to declining climatic conditions.

Fig. 1 depicts a flow chart of the model and example landscape realisations. In the following, the individual model steps are described in detail.

2.1.2. Landscape generation and change scenarios

We used the midpoint displacement algorithm (Saupe, 1988; With, 1997; Moloney and Levin, 1996; With and King, 2004; Körner and Jeltsch, 2008) to generate fractal landscape patterns with contrasting degrees of fragmentation. This well-documented and tested algorithm (e.g. Hargrove et al., 2002; Körner and Jeltsch, 2008) produces realistic ‘neutral’ landscapes (With, 1997; With and King, 2004) with a three-dimensional fractal surface that is characterized by only two parameters, the Hurst-factor $H$ (spatial dependence of points) and $\sigma^2$ (variance in displacement of points). Moving $H$ from 0 to 1 increases the level of aggregation (i.e., spatial correlation) and determines the fractal dimension and thus the level of fragmentation. We here compare landscapes with two contrasting but still realistic fragmentation levels, i.e. $H = 0.1$ (high fragmentation, see Fig. 1) and $H = 0.7$ (low fragmentation, see Fig. 1) ($\sigma^2 = 30$ for both levels). For our purposes we let landscape elevation (i.e., the third dimension of the fractal landscapes) represent a relative measure for local habitat quality. We first limited the initial overall percentage of suitable habitats $S$ to 15% of the landscape by sectioning the three dimensional fractal surface at the
For all simulation experiments of landscape and climate change, we generated 100 replicate landscapes characterized by the same statistical properties. Starting with these landscapes, we systematically investigated five scenarios (Table 1): one in which (i) landscapes did not change and four with deteriorating climatic conditions over time. The latter four scenarios were characterized by different forms of habitat change over time: (ii) landscapes with habitat degradation produced by a linear decrease in local patch capacity $K_i$ over time; (iii) landscapes with improving habitat conditions, produced by a linear increase in local capacities $K_i$ over time; (iv) habitat loss produced by a linear decrease of the percentage of suitable patches $S_i$ over time; and (v) habitat gain produced by a linear increase of the percentage of suitable patches $S_i$ over time. For the latter two scenarios, habitat loss and gain, we removed or added habitat with the highest currently existing habitat capacity to see the strongest possible effect. The local carrying capacities $K_i$ of suitable habitats remained unchanged in these scenarios. All scenarios of landscape change were spatially implemented in such a way that the given fractal landscape dimension remained unchanged over time.

### 2.1.3. Local population dynamics and climate change

We used a well-established population model, introduced by Maynard Smith and Slatkin (1973), as a basis for simulating the basic dynamics of populations on a single patch (see also Josth and Drechsler, 2003; Wichmann et al., 2005; Schwager et al., 2006). One reason for the choice of this particular model is that it has been successful in describing a wide range of empirical data on density dependence (Bellows, 1981). The basic population dynamics are given by:

$$N_{i,t+1} = \frac{N_{i,t}R_0}{1+(R_0-1)(N_{i,t}/K_{i,t})^d}$$

where $N_{i,t}$ is the local population size at time $t$ in patch $i$, $R_0$ is the maximum rate of increase, and $b$ is a parameter controlling the effects of density dependence on population growth, ranging through undercompensatory ($b < 1$), compensatory ($b = 1$) to over-compensatory ($b > 1$). $K_{i,t}$ is the carrying capacity of the local patch. To allow for demographic stochasticity, the actual population size was drawn from a Poisson-distribution with mean $N_{i,t}$. Furthermore, population size was set equal to 0 when $N_{i,t} < 2$, to account for Allee effects (compare Münkemüller and Josth, 2006). In addition, we introduced local stochastic disturbances that could lead to the extinction of local populations with the spatially and temporally uncorrelated probability $p_{st}$. Habitats that suffered from disturbance can be recolonized in the following timesteps.

To introduce climatic changes and environmental stochasticity caused by yearly climatic variation and other factors, we modified the basic model described above by multiplying the right hand term by $f(t)\delta(t_1)$, where $f(t)$ is a function that describes the temporal

### Table 1
Summary of landscape change scenarios correlated with climatic changes.

<table>
<thead>
<tr>
<th>Scale of change</th>
<th>Type of change</th>
<th>+ Correlated with climate change</th>
<th>Neutral (no change)</th>
<th>− Correlated with climate change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local</td>
<td>Habitat degradation or improvement, i.e. local carrying capacity $K_i$ increases or decreases</td>
<td>$K_{i,t} = g_{i,t} \times K_{i_0}$ with $g_{i,t} = 1 + \delta (t;T)$; the degradation rate $\delta$ is varied systematically between $[-1$ and $0]$</td>
<td>$K_{i,t} = K_{i_0}$</td>
<td>$K_{i,t} = g_{i,t} \times K_{i_0}$ with $g_{i,t} = 1 + \delta (t;T)$; the degradation rate $\delta$ is varied systematically between $[0$ and $1]$</td>
</tr>
<tr>
<td>Landscape</td>
<td>Habitat loss or gain, i.e. the % of suitable habitats $S_i$ increases or decreases: − loss of best habitats first, − gain of best habitats</td>
<td>$S_i = h_{i_1} \times S_{i_0}$ with $h_{i_1} = 1 + \psi (t;T)$; the rate of habitat loss $\psi$ is varied systematically between $[-1$ and $0]$</td>
<td>$S_i = S_{i_0}$</td>
<td>$S_i = h_{i_1} \times S_{i_0}$ with $h_{i_1} = 1 + \psi (t;T)$; the rate of habitat loss $\psi$ is varied systematically between $[0$ and $1]$</td>
</tr>
</tbody>
</table>

Climate and landscape changes start after an initial phase of 100 years. Changes at the landscape level (habitat loss or gain) do not change the level of fragmentation. The default value of suitable habitats $S_i$ is 15% (of all grid cells), $T=1000$ for all scenarios. Habitat changes (i.e. degradation, improvement, loss or gain) proceed with simulation time at constant rates (i.e. degradation rates $\delta$ and rates of habitat loss $\psi$ remained constant within single simulation runs).
degradation of climatic conditions:
\[ f(t) = 1 - \frac{t}{T} \]  

(2)  

\( T \) determines the velocity of the degradation of climatic conditions. The term \( \epsilon_t \) models yearly climatic variation and is a noise term (‘white’ noise) drawn from a uniform distribution between \((0.5 \text{ and } 1.5)\) and applies to all patches within a time step. In contrast \( \tau_{it} \), represents additional local variability in environmental effects, which are also drawn from a uniform distribution between \((0.5 \text{ and } 1.5)\). In our approach climatic changes were modelled as having a direct influence on the number of individuals (or the effective reproductive rate) occurring at a site. This was realised through the influence of weather conditions on survival and reproduction of individuals instead of through an effect on the availability of resources (i.e., \( K_{it} \)). In contrast, \( K_{it} \), the local patch carrying capacity, depends on landscape pattern and the climate-habitat-correlation scenarios (see Section 2.1.2). This leads to:

\[ N_{it+1} = N_{it} R_0 (1 - \tau_{it}) \frac{t}{T} + (R_0 - 1) \left( \frac{N_{it}}{K_{it}} \right)^\omega \]  

(3)  

2.1.4. Dispersal  
Following Münkemüller and Johst (2006), the percentage of emigrants/dispersing individuals \( P_{e, it} \) at timestep \( t \) leaving a local patch \( i \) is determined by:

\[ P_{e, it} = \min \left( 0.9, \frac{\left( \frac{N_{it}}{K_{it}} \right)^\omega}{\nu} \right) \]  

(4)  

where \( \nu \) is set to 15% for this study and \( \omega \) is set to 0, eliminating density dependence as a factor influencing the percentage of emigrants. Emigrating or dispersing individuals are randomly distributed in the simulated landscape with an exponentially decreasing dispersal probability \( p(d) \) with increasing distance \( d \) from the origin:

\[ p(d) = \exp \left( -\frac{d}{D} \right) \]  

(5)  

The species specific mean dispersal distance used throughout this study was \( D = 10 \) grid cells. We compared two contrasting dispersal types, distinguishing between individuals that were not able to actively search for new habitat and individuals that had some degree of active search ability. In particular, we compared scenarios with one vs. 10 ‘dispersal attempts’ per individual, i.e. the dispersing individual had either one ‘search’ attempt to ‘find’ a suitable habitat patch or the dispersal procedure for an individual was repeated up to 10 times until a suitable habitat patch was found. If the individual did not find a suitable habitat patch, the individual was assumed to have died during the emigration/dispersal phase, otherwise it was added to the local population.

2.1.5. Simulated functional types  
We systematically investigated the response of four basic, contrasting functional types (Table 2). Functional types are used here in the sense of ‘functional response groups’, as described by Lavorel and Garnier (2002), which are species that form user-defined groups with similar biological traits leading to similar responses to environmental resources and disturbances. The four functional types represent different rates of population turnover (K-strategies vs. r-strategies) and different levels of overall abundance (common vs. rare species). Two functional types (\( H_1 \) and \( L_1 \)) resemble ‘K-strategists’, both with a low local population growth rate, low disturbance rate, and compensatory density regulation (\( b = 1 \) in Eq. (1)). The \( H_1 \) type has a high landscape level abundance (i.e. high carrying capacity, regulated by a high initial overall carrying capacity \( K_{total} \)) The \( L_1 \) type has a low landscape level abundance (low \( K_{total} \)). It also has a slightly higher growth rate than \( H_1 \) and experiences a lower disturbance rate and a reduced negative effect due to climate change. These characteristics compensate for a lower landscape capacity and can still produce a persistent population. The two other types, \( H_1^T \) and \( L_1^T \), resemble ‘r-strategists’ with high population growth rates, again with contrasting landscape capacities \( K_{total} \). Both types experience a high local population turnover but for different reasons: Whereas \( H_1^T \) suffers from high local disturbance rates, \( L_1^T \) has higher density overregulation (\( b > 1 \) in Eq. (1)). All parameter values (Table 2) were chosen to guarantee for all types (i) a dynamic regional equilibrium under conditions of no climate change and (ii) regional survival for several hundred years with climate change, but no landscape change.

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Summary matrix of contrasting species types investigated.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low local turnover</td>
</tr>
<tr>
<td>Type</td>
<td>( H_1 )</td>
</tr>
<tr>
<td>Growth rate ( R_0 )</td>
<td>1.3</td>
</tr>
<tr>
<td>Landscape ( K_{total} )</td>
<td>5 \times 10^5</td>
</tr>
<tr>
<td>Density regulation ( b )</td>
<td>1.0</td>
</tr>
<tr>
<td>Disturbance rate ( p_d )</td>
<td>0.05</td>
</tr>
<tr>
<td>Climate Change effect ( T^{-1} )</td>
<td>1000</td>
</tr>
</tbody>
</table>

The mean dispersal distance for all types is \( D = 10 \), and emigrating individuals have either one (‘default scenario’) or ten (‘search scenario’) attempts to find a suitable new habitat.

For model initialisation all suitable habitat patches contained a random population size ranging from two individuals to the local carrying capacity \( K_{it} \). For an initial phase of 100 years no changes in climate or landscape pattern occurred, allowing for the establishment of a dynamic population equilibrium. As an output variable in all environmental change simulations, we used the mean time to (regional) population extinction \( T_r \). \( T_r \) is a suitable measure for comparing scenarios of deteriorating environmental conditions that lead to population extinction (e.g. Grimm and Wissel, 2004; Wichmann et al., 2005; Münzbergová et al., 2005; Körner and Jeltsch, 2008). \( T_r \) values were calculated by averaging the extinction times in 5000 simulation runs, based on 50 different landscape realisations for a given fragmentation level and 100 replicates per landscape realisation.

In a first set of simulation experiments we tested the general performance of the four contrasting functional types under fragmentation level \( H = 0.7 \) (i) without climatic change and without correlated climatic fluctuations (\( \epsilon_t = 0 \)), (ii) with climatic change but without landscape changes. Simulations under (i) give a general idea of the performance of the four contrasting functional types in a fragmented landscape. In (ii), we compare how the functional types respond to climate change alone, and we test how this response depends on the percentage of dispersed individuals per timestep and the capability of emigrating individuals to find a new suitable habitat.

In a second set of simulations, we analyse the effects of different combinations of climatic changes and positively or negatively correlated landscape changes (Table 1) on the four functional types in the two dispersal scenarios. In these simulations, we systematically vary the rates of habitat degradation and habitat loss, \( \delta \) and
Table 3
Summary of simulated functional type dynamics without climate change or correlated climatic fluctuations ($\varepsilon = 0$) after an initial phase of 100 years.

<table>
<thead>
<tr>
<th>Type</th>
<th>$N_{\text{total}}$ (Mean)</th>
<th>Relative patch extinction rate (% of occupied patches per timestep)</th>
<th>Relative patch colonization rate (% of occupied patches per timestep)</th>
<th>Occupied patches (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_T$</td>
<td>110,326</td>
<td>5.7</td>
<td>5.6</td>
<td>71.4</td>
</tr>
<tr>
<td></td>
<td>21,488</td>
<td>0.6</td>
<td>0.5</td>
<td>5.6</td>
</tr>
<tr>
<td>$H_T^L$</td>
<td>59,510</td>
<td>40.1</td>
<td>40.0</td>
<td>41.1</td>
</tr>
<tr>
<td></td>
<td>10,265</td>
<td>2.4</td>
<td>1.5</td>
<td>3.8</td>
</tr>
<tr>
<td>$L_T$</td>
<td>4,127</td>
<td>4.2</td>
<td>4.0</td>
<td>19.8</td>
</tr>
<tr>
<td></td>
<td>634</td>
<td>1.0</td>
<td>0.9</td>
<td>3.3</td>
</tr>
<tr>
<td>$L_T^L$</td>
<td>1,143</td>
<td>23.2</td>
<td>23.0</td>
<td>6.5</td>
</tr>
<tr>
<td></td>
<td>521</td>
<td>5.1</td>
<td>4.2</td>
<td>3.0</td>
</tr>
</tbody>
</table>

Mean values and standard deviations of 100 replicates (10 landscape realisations of same fragmentation intensity, 10 replicates per landscape). Low landscape fragmentation ($H = 0.7$); for further parameters see Table 2.

These simulations show the general effects of different rates of landscape change correlated with climate change on regional population survival in a systematic way. However, the effects of habitat degradation vs. loss and of improvement vs. gain are not directly comparable, as the same rates of landscape change lead to different changes in the overall landscape capacity, depending on whether the habitat is degraded or lost (improved or gained). Therefore we perform a final set of simulations, where we set a fixed value for the change in regional carrying capacity $K_{\text{total}}$ at a certain point in time ($\Delta K_{\text{total}} = \pm 10\%$ after 100 years) and adjust the rates of landscape change accordingly, so that the fixed $K_{\text{total}}$ is met in all scenarios.

3. Results

Comparing the dynamics of the four different functional types in a simplified environment (fragmentation level $H = 0.7$) without climatic changes and without correlated climatic fluctuations (i.e., $\varepsilon = 0$) shows that, as expected, types $H_T$ and $H_T^L$ have a much higher regional abundance than types $L_T$ and $L_T^L$ (Table 3), since more patches are occupied resulting in more individuals being present. Types $H_T^L$ and $L_T^L$ have much higher extinction and colonization rates (i.e. a higher turnover) at the single patch level. Type specific colonization and extinction rates have almost identical values indicating that all functional types are in (dynamic) equilibrium. These results also hold for higher fragmentation levels (not shown here).

Including climatic fluctuations and changes in the model leads to species extinction in a time frame that depends on the specific functional type and dispersal scenario. Fig. 2 shows an example of the effect of differing dispersal rates on regional $T_m$ under climate change without a corresponding landscape change. The two functional types with low local turnover ($H_T$ and $L_T$) have a similar time to extinction under climate change and show a similar pattern where a small amount of dispersal is positive but too many dispersers are negative due to the local loss of individuals. Clearly, the latter effect is reduced if individuals have several attempts to

Fig. 2. Effect of % of dispersed individuals per timestep on regional survival ($T_m$) of the simulated populations in a less fragmented landscape ($H = 0.7$). Mean dispersal distance $D = 10$, no density dependence of dispersal; ‘default scenario’: one search attempt for emigrating individuals; ‘search scenario’: up to 10 attempts to find a suitable habitat for each dispersing individual. Further details on functional types are given in Table 2. $T_m$ values were calculated on the basis of 50 different landscape realisations for a given fragmentation level with 100 replicates per landscape realisation leading to 5000 simulation runs per $T_m$ value.
find a suitable habitat (search scenario). In contrast to the previous pattern, for the functional types $H_T$ and $L_T$, increasing the dispersal rate leads to an increase of the regional survival for all tested scenarios. Both functional types experience a high local turnover, i.e. they depend on colonisation events due to high local extinction rates. As before, both types have a similar time to extinction under climate change, despite their contrasting abundance levels.

Combining climatic changes with gradual local habitat degradation or improvement has the strongest effect on type $L_T$, a moderate effect on type $L_T$ and type $H_T$ (Fig. 3). In the tested range of habitat degradation, the mean time to extinction can change up to 50% for the most sensitive type $L_T$, up to 10% for types $L_T$ and $H_T$ and less than 2% for type $H_T$. For all types and in both tested dispersal scenarios we generally find a higher $T_m$ value for low, as compared to high, fragmentation levels (Fig. 2). However, the difference in $T_m$ values between the two contrasting fragmentation levels is reduced in the ‘search scenario’, i.e. when individuals have several chances to find a suitable habitat patch.

Correlating climatic changes with habitat loss or gain leads to similar responses of the tested functional types to the situation of habitat degradation or improvement (Fig. 4). While type $H_T$ shows almost no effect, type $L_T$ shows the strongest response with a reduction of $T_m$ values to ~50% already for low rates of habitat loss (i.e. $\phi = 0.2$). Types $H_T$ and $L_T$ show an intermediate response. Again, the search scenario, i.e. the increased chance of individuals to find a suitable habitat, leads to higher regional survival and diminishes the difference between highly and less fragmented landscapes. Interestingly the absolute effect of habitat loss (i.e., the change in $T_m$ values) is stronger than the (positive) effect of habitat gain whereas the absolute effects of habitat degradation and habitat improvement are of the same order of magnitude.

Fig. 5 compares the responses of functional types to climate correlated habitat degradation/improvement vs. loss/gain if landscape change is fixed to a 10% decrease or increase of total landscape capacity after 100 years in all scenarios (shown only for the three functional types that exhibited a noticeable response in the previous scenarios, i.e. $H_T$, $L_T$ and $L_T$). The comparison confirms the extreme sensitivity of type $L_T$ which is characterized by a low capacity and a high local turnover caused by a high population growth rate combined with density overregulation. Comparing the two other types $H_T$ is slightly less sensitive than type $L_T$ for most scenarios. A striking finding is that negative effects (i.e. habitat degradation or loss) are always stronger than positive effects (habitat improvement or gain). As expected, we generally find stronger effects for more fragmented landscapes but this difference is less pronounced for the search scenario. Comparing simulations clearly shows that habitat improvement or restoration is always better than habitat gain, since the negative effects of climatic changes are counteracted more by improving local habitat conditions rather than by restoring new habitat. Interestingly there is no such clear pattern for negative effects: here, both habitat degradation and habitat loss can dominate depending on the functional type and the specific scenario. For example, type $L_T$ responds more strongly...
Fig. 4. Effect of habitat loss or gain (i.e. loss of existing or gain of new habitat patches) on regional survival of the simulated functional types (with rate of habitat loss $\varphi$, see Table 1). ‘Default scenario’ and ‘search scenario’ (see Fig. 2) are compared for highly ($H=0.1$, compare Fig. 1) and less fragmented landscapes ($H=0.7$, compare Fig. 1). For $T_m$ value calculation see Fig. 2.

Fig. 5. Comparison of the effects of habitat gain, improvement, loss, and degradation for three functional types ($H_T$, $L_T$, $L^T$) under the same level of changes in the landscape capacity ($\Delta K_{total} = \pm 10\%$ after 100 years). The resulting difference in mean time to extinction $\Delta T_m$ is given for two levels of landscape fragmentation (top: less fragmented landscape, $H=0.7$; bottom: highly fragmented landscape, $H=0.1$) and two contrasting dispersal scenarios (left columns: default scenario; right columns: search scenario). For $T_m$ value calculation see Fig. 2.
to habitat loss whereas type $L^1$ shows a stronger response to habitat degradation. Also in a single functional type the relative role of habitat degradation vs. habitat loss can change: e.g., in the more fragmented landscape, habitat degradation under the search scenario leads to a more pronounced decrease of regional survival for type $H^2$ than habitat loss. This finding is reversed, if emigrating individuals only have a single chance to find a suitable habitat (no search scenario). This contrasting effect is less pronounced for the less fragmented landscape.

4. Discussion

It is widely accepted that local population processes can significantly influence the response of species to climatic changes (Akgalaya et al., 2004; Jeltsch et al., 2008; Anderson et al., 2009). While several recent studies explore the role of population processes in non-homogenous environments for species range shifts under climate change (e.g. Travis, 2003; Opdam and Wascher, 2004; Pearson et al., 2004; Adahl et al., 2006; Best et al., 2007) only a few studies analyse the impacts of the combined effects of climate and habitat changes on population extinction on a regional scale (Zurell et al., 2009). In either case the problem remains that the necessary detailed information on population processes is only available for a limited number of species (Jeltsch et al., 2008; Laidre et al., 2008). Therefore, more generic approaches are needed that allow for a more general understanding of species responses to combined climate and landscape changes and that can be applied to a broader range of species (Keith et al., 2008). Here, we tested four functional types that represent a broad spectrum of species characterised by their landscape level carrying capacity, the local population turnover rates at the patch level and dispersal characteristics. As expected, simulation results show that correlated changes between habitat and climatic conditions can accelerate (in case of habitat loss or degradation) or slow down (in case of habitat gain or improvement) regional species extinction. However, the strength of the combined changes depends on local turnover at the patch level, the overall landscape capacity of the species, and its specific dispersal characteristics.

4.1. Which type of species are most prone to regional extinction?

Under all scenarios of correlated climate deterioration and habitat changes we found the highest sensitivity for functional types representing species with a low landscape capacity but a high population growth rate and a strong density regulation causing a high turnover at the local patch level. These species depend strongly on the colonization of new suitable habitat. Lowest sensitivity was found for more inert functional types with a low growth rate but a high landscape capacity. Simulations show that functional types resembling both, ‘r’- and ‘K’-strategists can be affected by correlated climate and landscape changes. Extinction risks for all types were higher in more fragmented landscapes, whereas dispersal revealed a more ambiguous pattern depending on the trade off between losing the dispersing individuals at the source patch and the gain of finding and colonizing new suitable habitat patches. Interestingly, at a first glance, these results seem to contradict recent range shift models that have focused on the ability of species to keep track of a rapidly shifting climate window. Based on an earlier study of Travis (2003), Best et al. (2007) found that dynamic species with high population growth rates and high density regulation (so-called ‘scrambler species’) are predicted to cope better with climate change impacts than species with lower growth rates and lower density regulation (‘contester species’). The main reason for this finding is that the more dynamic ‘scrambler species’ spread through the landscape at a much faster rate than ‘contester species’ and are thus better suited to keep track of shifting climatic windows (Best et al., 2007). In contrast to these studies, we focused on regional persistence under correlated climatic and habitat changes. Given this restricted range and the changing regional environmental conditions, a highly dynamic strategy of colonizing new habitat patches is by far more risky than persistence within established patches. Thus, under this regional perspective, ‘contester species’ may perform better than ‘scrambler species’. However, this also depends on the overall abundance or landscape capacity and on dispersal abilities.

Clearly, species conservation and management under climate change requires a combination of a regional and a biogeographical perspective. Thus a fusion of the regional approach presented here with range shift models simulating directional climate change is a promising future direction to improve our understanding of climate change impacts on biodiversity. The question under which conditions regional processes dominate over biogeographical processes and vice versa remains a key challenge for a climate-adaptive nature conservation.

The principle finding that species with a low landscape capacity are specifically endangered in more fragmented landscapes agrees well with a recent analysis on threatened species management in the face of climate change, where species with small populations and specialized habitat requirements are predicted to be particularly vulnerable (Adam, 2009). Similarly, in a study on the impacts of climate warming induced habitat alterations on Arctic marine mammals, Laidre et al. (2008) conclude that the least sensitive mammals were those with large population sizes and flexible habitat requirements, the latter also indicating a high local patch level persistence.

The relative role of habitat fragmentation clearly depends on the ability of species to find and successfully colonize new habitat. Correspondingly our ‘search’ scenario, mimicking the ability of individuals to search effectively for suitable new habitats, leads to higher survival times and reduces the negative effects of increased levels of habitat fragmentation. The importance of dispersal and colonization characteristics for species survival in fragmented landscapes under climate change has also been highlighted by Travis (2003), who explored species’ range shifts.

4.2. Habitat loss vs. habitat degradation

There are an increasing number of studies that explicitly distinguish between effects caused by habitat fragmentation on species dynamics and survival and effects caused by habitat loss (e.g. Schmiegelow and Monkkonen, 2002; Fahrig, 2003; Cushman, 2006; Betts et al., 2006; Korner and Jeltsch, 2008). In most cases the loss of suitable habitat has a stronger effect on species survival than the change of habitat patch distributions, i.e. increasing fragmentation. Especially for increasing levels of fragmentation species responses depend strongly on specific characteristics such as dispersal abilities, intrinsic growth rates or local density regulation (Fahrig, 2003; Henle et al., 2004a,b; Korner and Jeltsch, 2008). While habitat loss and fragmentation are often accompanied by habitat degradation only a few studies explicitly distinguish between the absolute loss of habitat patches and the relative degradation of existing habitats (Caley et al., 2001). In particular under scenarios of combined effects of climate and land use changes it is important to distinguish between both threats since they may occur separately or in combination. For similar levels of reduction of the landscape’s population capacity our study shows that species survival under climate change differs depending on whether capacity reduction is caused by habitat degradation or by habitat loss. The comparison of the two functional types ($L^1$ and $L^2$) with lower landscape level abundance revealed that species with low turnover rates at the patch level, including low colonisation rates, suffer more from...
habitats to remain robust in the face of climate change include maintaining and increasing the area of high quality habitats. Especially under the typical financial constraints, it should be carefully analysed whether the benefits expected to arise from increasing connectivity are higher than with alternative investments into habitat conservation and enhancement. Optimally, a threefold approach should be taken, as suggested by Harly et al. (2009), including: (i) facilitating the dispersal to and colonisation of new areas with suitable climates by creating functional habitat networks and enhancing interconnecting habitat, (ii) avoiding or reducing impacts related to climate change, and (iii) increasing the resilience of species and habitats to climate change within their existing ranges through habitat enhancement measures to improve survival and productivity rates. Though our ability to model species dynamics under climate change is continuously improving (e.g. Anderson et al. 2009) our ability to quantitatively predict regional survival remains relatively poor, given the complexity of community interactions and possible adaptation mechanisms at different levels (including genetics, behaviour). Therefore allowing for longer regional survival through active habitat enhancement might mean the difference between extinction and successful species adaptation to changing environmental conditions.

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Hargrove, W.W., Hoffman, F.M., Schwartz, P.M., 2006. Independent effects of climate change on Arctic marine mammals. Similarly, in a review on fragmentation effects, Henle et al. (2004a) conclude that species characterized by low population fluctuations (i.e., low turnover at the patch level) and low to moderate colonisation abilities should be less sensitive to the spatial effects of increasing habitat fragmentation. But they are expected to react more sensitively to habitat loss caused by abiotic, structural, and successional changes associated with the fragmentation process than species with high turn over rates and high colonisation abilities.

5. Conclusion—lessons for habitat management under climate change

While the relative importance of habitat loss or habitat degradation, in combination with climate change, differed among the functional types, an increase in regional capacity revealed a similar response pattern. For all types, habitat improvement led to higher survival times than habitat gain, i.e. the establishment of new habitat patches. This means that improving local habitat quality at a regional scale is a more promising conservation strategy under climate change than implementing new habitat patches. This robust result is interesting since it seems to contradict previous studies that suggest the establishment of additional habitat as corridors as an appropriate conservation strategy under climate change (e.g. Adam, 2009). However, the difference lies in whether conservation should focus on facilitating species range shifts following suitable climatic windows or whether more emphasis should be put on regional survival. This discussion has recently been addressed by Hodgson et al. (2009) who argue that the importance of connectivity is often being overemphasized and that strategies expected to remain robust in the face of climate change include maintaining and increasing the area of high quality habitats. Especially under the typical financial constraints, it should be carefully analysed whether the benefits expected to arise from increasing connectivity are higher than with alternative investments into habitat conservation and enhancement. Optimally, a threefold approach should be taken, as suggested by Harly et al. (2009), including: (i) facilitating the dispersal to and colonisation of new areas with suitable climates by creating functional habitat networks and enhancing interconnecting habitat, (ii) avoiding or reducing impacts related to climate change, and (iii) increasing the resilience of species and habitats to climate change within their existing ranges through habitat enhancement measures to improve survival and productivity rates. Though our ability to model species dynamics under climate change is continuously improving (e.g. Anderson et al. 2009) our ability to quantitatively predict regional survival remains relatively poor, given the complexity of community interactions and possible adaptation mechanisms at different levels (including genetics, behaviour). Therefore allowing for longer regional survival through active habitat enhancement might mean the difference between extinction and successful species adaptation to changing environmental conditions.

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