Investigating habitat-specific plant species pools under climate change

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Abstract

We used 474 European plant species to analyse the impacts of climate and land-use change on the composition of habitat-specific species pools in Germany. We quantified changes in the probability of occurrence of species in a grid cell using an ensemble of three statistical modelling techniques, namely generalized linear models (GLMs), generalized additive models (GAMs) and random forests (RFs), under three scenarios (average change +2.2, +2.9, and +3.8 °C up to 2080). We evaluated the impact on single species occurrence and resulting species pools considering their affiliation to ten major terrestrial habitat types in both current (1961–90) and future projections (2051–80). Current habitat-specific species pools declined in size across all scenarios, e.g. by 24 ± 13% (mean ± s.d.) under the most severe scenario. We show that species responses may strongly vary among scenarios and different habitats with a minimum average projected range loss of 14% (±18%; species typical to urban habitats under moderate climate change assumptions, average temperature increase +2.2 °C) to a maximum average projected range loss of 56% (±29%; species assemblages from mountain communities below the alpine zone at +3.8 °C). A separate analysis of species composition in habitat-specific species pools revealed a significant interaction between the scenario and the major habitat classes. We found a higher risk for habitat types with high conservation value characterised by a significant association between number of nationally endangered species and projected range loss in major habitats. Thus, habitat-specific management and application of measures favouring dispersal are required for mitigation of climate change impacts.

Zusammenfassung

Wir nutzten 474 Europäische Pflanzenarten, um Änderungen in der Zusammensetzung von Biotop-spezifischem Artengemeinschaften unter Klima- und Landnutzungswandel in Deutschland zu erfassen. Mit Hilfe von statistischen Modellierungsverfahren, nämlich Generalisierte lineare Modelle (GLM), Generalisierte additive Modelle (GAM), Random Forests (RF), berechneten wir, wie sich unter drei Szenarien (mittlerere Temperaturerhöhung +2.2, +2.9, +3.8 °C bis 2080) potenzielle Areale der Pflanzarten verändern. Für die ausgewählten Einzelarten und Artengemeinschaften verglichen wir die durch Klimawandel resultierenden Möglichkeiten des gemeinsamen Vorkommens zwischen der Klimanormalperiode (1961–90) und den Szenarien (2051–80) in zehn Hauptbiotopen. Unter der Annahme einer starken Klimaänderung (mittlerere Änderung der Temperatur +3.8 °C bis 2080) reduzieren sich gemeinsame Vorkommen der Arten pro Biototyp im Mittel um 24 ± 13% (Mittelwert ± s.d.). Die Artreaktionen variieren sowohl zwischen den Szenarien als auch den Biotopen, so dass der Verlust an potentiell...
Verbreitungsgebiet in Deutschland von 14% (±18%; für Arten der ur­bunden Gebiete bei moderater Klimaänderung +2.2 °C) bis zu 56% (±29% für Arten montaner Gemeinschaften unterhalb der alpinen Zone bei +3.8 °C) reicht. Eine Analyse zu Veränderungen der für Biotop-spezifischen regionalen Vorkommen von Pflanzenarten ergab statistisch signifikante Interaktionen zwischen Szenario und Biotoptyp. Wir identifizierten ein höheres Risiko für Biotope mit hohem Naturschutzgewicht, charakterisiert durch einen signifikanten positiven Zusammenhang zwischen der Anzahl an in Deutschland geschützten Arten und dem Verlust an potentiellem Verbreitungsgebiet. Bei Berücksichtigung dieser Zusammenhänge gewinnen Biotop­spezifische Managementmaßnahmen unter Klimawandel damit an Bedeutung, die insbesondere eine Ausbreitung der Pflanzenarten fördern müssen.

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**Keywords:** Climate change impacts; Range change; Plant species distribution modelling; Dissimilarity; Germany

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**Introduction**

Local plant species pools are temporary associations that are likely to be reassembled under global climate change (Woodward 1987). Considering the recently observed effects, like the migration of species initiated by the recent warming process (Parolo & Rossi 2008 and publications cited therein), species distribution models (SDMs) are used to gain insights in potential future distributions and use extrapolation in space and time to assess potential pressures on biodiversity (see reviews by Thuiller et al. 2008; Thuiller, Lafourcade, Engler, & Araújo 2009). These modelling results are often illustrated with grid maps showing the climatically suitable areas for a species before and after a ‘treatment’ (i.e., under baseline climate and climate scenario assumptions, cf. Guisan & Zimmermann 2000). These projected environmental changes imply large effects over the coming decades, with negative consequences for the flora whilst species range reduction coincides with local species loss (Pompe et al. 2008). Particular species will disappear locally, and new species will appear. Therefore, additional questions about the sensitivity of the current assemblages of species, i.e. habitat-specific pools, to climate change arise. A classification above the species level and/or study of local species richness may enable the assessment of potential impacts in habitats rather than at the individual species level only. Classifying species by traits, functional types or environmental constraints may yield species groups that face ecologically similar conditions (Westoby, Falster, Moles, Vesk, & Wright 2002; Broennimann et al. 2006; Bernhardt-Römermann et al. 2008). The distribution of habitats (and their common species pool) can potentially be predicted from environmental variables (cf. Römermann, Tackenberg, Scheuerer, May, & Poschlod 2007 and publications cited therein). However, the direct determination of how climate change impacts on habitats is a difficult task. Data availability is one problem (e.g. Römermann et al. 2007), and the idiosyncratic responses of individual species to climate change make it difficult to use pure community-based models (Elith, Graham, Anderson, Dudík, & Ferrier 2006). With the exception of studies conducted by Berry, Dawson, Harrison, Pearson, and Butt (2003) and Normand, Svenning, and Skov (2007), little attention has been paid to habitat-specific species pools. However, these two studies investigated how and to what extent different species occurring in different habitats will be affected by climate change. According to their results, losses as well as migration of species typical for a habitat often do occur neither synchronously nor with an identical spatial pattern. Differences in local turnover of species therefore will lead to new species assemblages (i.e. compositional change).

For these reasons, we address here the question of how the information about individual species responses that can be extracted from species distribution models can be used to study consequences for major terrestrial habitats. We ask which major habitats might be more affected by species-specific range changes under different climate change scenarios. Thus, we assessed to which degree the habitat-specific species pools from which species in individual habitats are recruited might change. A habitat-specific species pool describes the occurrence of species that can grow in a specific habitat within a regional species pool of a distinct area. We quantified whether these estimates are consistent across different types of major habitats and scenarios, or whether certain habitat classes are more vulnerable under specific scenarios than others.

**Methods**

**Data**

Our modelling framework is based on environmental niche models developed by Pompe et al. (2008): Plant species distribution data were derived from the European database *Atlas Florae Europaeae* (AFE, maintained by the Botanical Museum, University of Helsinki, at a gridded resolution of 50 km × 50 km). Environmental data for the baseline (1961–90) and the scenario period (2051–80) were generated and provided within the project ALARM (Assessing Large scale environmental Risks for biodiversity with tested Methods; Settele et al., 2005). We derived a set of 38 climatic variables, four land-use types (as percentage of forest, grassland, cropland, urban area in a grid cell) and soil variables (European Soil Database 2004) at the 50 km × 50 km resolution of the AFE data (n = 2141 grid cells) and for Germany on a 10° longitude × 6° latitude grid (i.e. ca. 12 km × 11 km,
2995 grid cells), which is the grid resolution of the German plant distribution database FLORKART (www.floraweb.de). We then applied different scenarios that represent potential changes in temperature and precipitation in possible futures (Spangenberg 2007) which covered the German grid cells up to 2080: the moderate scenario SEDG (Sustainable Europe Development Goal, climate derived from IPCC SRES scenario B1, resulting on average in +2.2 °C temperature increase for Germany), the intermediate scenario BAMBU (Business As Might Be Usual, A2, +2.9 °C), and the severe scenario GRAS (GRrowth Applied Strategy, A1FI, +3.8 °C; see Table S1, Pompe et al. 2008). These scenarios varied in different features of climate changes (e.g. decreasing summer and increasing winter precipitations) and land-use pressures (see Table S1, Fig. S4). Overall, the land-use types crop-land and grassland are projected to decline across Europe (Rounsevell, Ewert, Reginster, Leemans, & Carter 2005).

To assess habitat-specific effects, we extracted the association of each species with specific habitats from BiolFlor (Klotz, Kühn, & Durka 2002), a database of biological and ecological traits of Central European plant species. Hence, we considered 474 species as classified by Haeupler (2002) as typical for ten major terrestrial habitats (Table 1). We accounted for the fact that species can be present in more than one major habitat type.

### Species distribution models

We used the BIOMOD framework (Thuiller 2003; Thuiller et al. 2009) within the statistical and programming environment ‘R’ (R Development Core Team 2009) to model species distributions. We applied generalized linear models (GLMs), generalized additive models (GAMs) and random forests (RFs), integrating the environmental variables described above (see Pompe et al. 2008 for details). The performance of the models was analysed using Cohen’s Kappa statistic generally showing a good to high agreement (Kappa > 0.6; across all methods and species; see Pompe et al. 2008). Within BIOMOD we used a Kappa maximizing approach to transform the suitability surfaces into presence/absence data. We considered modelled gridded species distribution under baseline and scenario conditions in SEDG, BAMBU, and GRAS that might be expected in Germany under the assumption of constant land-use (nl, i.e., the same land-use fractions per grid cell were used for current and future simulations) and land-use change (l) up to 2080 (see Table S1). Under a given set of changing climatic conditions and land-use, the capacity of a species to reach new potential habitats through dispersal is an important factor that determines future species ranges. We, therefore, considered two alternative dispersal options: no dispersal and unlimited dispersal (resulting in 3 × 2 × 2 = 12 scenarios altogether). We computed the proportion of cells that would be lost (as the quotient of the number of grid cells that were lost (n_l) and the number of grid cells occupied in the baseline projection (n_0); ranges from 0 up to 100%) or gained (as the quotient of the number of grid cells that were gained under unlimited dispersal (n_g) and n_l; ranges from 0 up to [n_g/n_0 × 100%]). Note that range gain can exceed 100%. We calculated range change as difference between percent range gain and percent range loss. We previously showed (Pompe et al. 2008) that species distribution models fitted with the three modelling techniques GLMs, GAMs, and RFs differed from each other. Marmion, Parviainen, Luoto, Heikkinen, and Thuiller (2009) recommended computing the mean over several applied modelling algorithms to derive a more robust projection than just using any single individual model result or other diverse consensus methods. Hence, we calculated the arithmetic mean of modelled range loss, range gain, range change from GLMs, GAMs, and RFs. We checked the data for normality and homogeneity of variances. We applied a two-way ANOVA on ranks in order to test significant differences between the future projections. First, we tested the main effects and interactions between climate scenarios and the two land-use assumptions. Second, under the assumption of climate and land-use change (l) we analysed the main effects ‘scenario’ and ‘habitat’ and the interaction between ‘scenario’ and ‘habitat’ for species range loss, range gain and range change. If the ANOVAs showed significant differences among groups (p<0.05), post hoc Tukey tests were performed (using the Holm’s correction procedure). The degree to which the species in a major habitat are affected either adversely or beneficially (under unlimited dispersal) was further assessed by analysing the species listed in the Red List in Germany (n=98, see Ludwig & Schnittler 1996). We analysed the association (using Kendall’s τ) between proportion of Red List species and their median projected range loss or range gain per major habitat type.

### Habitat-specific species pool

A habitat-specific species pool described the modelled occurrence of species that can grow in a specific habitat (n=10, see Table 1) within our regional species pool of a 6’×10‘ area. We calculated the losses (L) and gains (G) of species, and species numbers (SR) per grid cell assigned to the major habitat types. The Wilcoxon signed rank test was applied to test differences of species richness of habitat-specific species pools per grid cell (n=2995) between current and scenario projections. The Sørensen similarity ($\beta_{\text{sim}}$) index was computed as a simple measure of beta diversity per grid cell and major habitat, to analyse species overlap between the projected species pools. $\beta_{\text{sim}}$ was calculated as $S_{0,1}/(0.5(S_0+S_1))$, where $S_{0,1}$ is the number of species common to current and scenario projection and $S_0$ is the total found in a grid cell currently and $S_1$ under scenario projection. Dissimilarity in species composition was measured as the complement of the Sørensen similarity index ($d=1-\beta_{\text{sim}}$). It ranges from 0, indicating that all species which are present in the current projection are also present in the scenario projection, to 1, indicating no species in common. Further we
calculated an index ($I_h$) of how many species assigned to a specific major habitat co-occur in a grid cell (using unlimited dispersal assumption). We computed $I_h$ as the quotient of the number of typical species from a specific major habitat type per grid cell and the total number of typical species per habitat type. We calculated the arithmetic mean and the coefficient of variation of $I_h$ that were obtained using the GLMs, GAMs, and RFs. $I_h$ ranges from 0 (no habitat-specific species co-occur) to 1 (all habitat-specific species co-occur) per grid cell (see Fig. S1). We applied Kendall’s rank correlation comparing $I_h$ based on observed species distribution (using FLORKART) with $I_h$ from the modelled species ranges for the baseline. We used the Wilcoxon signed rank test to compare $I_h$ for the baseline with scenario projections. If a one-way ANOVA on ranks showed a significant effect, we applied the Wilcoxon rank test with Holm’s correction for pair-wise comparisons of $I_h$ from SEDG, BAMBU, and GRAS. The above-mentioned tests were also applied using only $I_h > 0$ to avoid potential bias due to zero values (i.e. grid cells without species typical for a habitat). We calculated the proportion of change in $I_h$ in a grid cell between the baseline (1961–90) and the projected future (2051–80) distributions. We additionally performed a two-way ANOVA and a post hoc Tukey test to compare differences in change of $I_h$. Neither phylogenetic nor spatial dependences were relevant in the analyses.

**Results**

**Species range change**

We found changes in species range sizes that correlated with the severity of the scenarios (23–39% for mean range loss across scenarios). Range loss ($F_{2,474} = 86.7$, df = 2), range gain ($F_{2,474} = 6.7$, df = 2) and range change ($F_{2,474} = 25.1$, df = 2) significantly differed (two-way ANOVA on ranks, $n = 474$, $p < 0.05$) between the three climate change scenarios up to 2080. There were significant differences between SEDG, BAMBU, and GRAS for range loss, between SEDG and GRAS for range gain, and significant differences between SEDG and GRAS, as well as BAMBU and GRAS for species range change (Tukey post hoc tests, $p < 0.05$). No significant difference was found between the two land-use scenarios (1 and nl) and no significant land-use climate interaction (see Table S2 for data). Hence, we subsequently present habitat-specific projections for the combined land-use and climate scenario (1) only (see Table S3).

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Habitat type</th>
<th>$N$</th>
</tr>
</thead>
<tbody>
<tr>
<td>T1</td>
<td>Woodlands</td>
<td>139</td>
</tr>
<tr>
<td>T2</td>
<td>Bush- and shrublands, clearings</td>
<td>59</td>
</tr>
<tr>
<td>T3</td>
<td>Tall herb communities, bushes, and turfs near or above treeline</td>
<td>67</td>
</tr>
<tr>
<td>T4</td>
<td>Dwarf scrub communities below alpine areas</td>
<td>9</td>
</tr>
<tr>
<td>T5</td>
<td>Boulder and scree habitats without woody species</td>
<td>63</td>
</tr>
<tr>
<td>T6</td>
<td>Nutrient poor grasslands</td>
<td>100</td>
</tr>
<tr>
<td>T7</td>
<td>Meadows and pastures</td>
<td>68</td>
</tr>
<tr>
<td>T8</td>
<td>Forbs communities, forest grassland ecotones, and tall herb slopes outside floodplains</td>
<td>105</td>
</tr>
<tr>
<td>T9</td>
<td>Plant cultures (except meadows, pastures, forests)</td>
<td>78</td>
</tr>
<tr>
<td>T10</td>
<td>Urban-industrial and other commercially influenced formations</td>
<td>82</td>
</tr>
</tbody>
</table>

Range loss ($F_{2,474} = 24.0$, df = 9), range gain ($F_{2,474} = 18.1$, df = 9) and species range change ($F_{2,474} = 12.1$, df = 9) were significantly different between major habitats (two-way ANOVA on ranks, $p < 0.001$, Fig. 1). We found a significant scenario effect ($p < 0.001$) on range loss ($F_{2,474} = 72.8$, df = 2) and range change ($F_{2,474} = 29.3$, df = 2) with all individual scenarios differing from each other (post hoc Tukey tests, $p < 0.05$, Fig. 1). The interaction between major habitats and scenario was not significant ($p > 0.05$). The highest number of significant differences between the different habitat groups was detected for range gain ($n = 26$), followed by range loss ($n = 25$), and range change ($n = 22$) (Fig. 1). Pair-wise comparisons showed that the species pools of tall herb communities, bushes, and turfs near or above the treeline (T3) were most sensitive, followed by dwarf shrub communities below alpine areas (T4). The species assigned to forb communities, forest grassland ecotones and tall herb slopes outside floodplains (T8), plant cultures (T9), and urban, commercial, and industrial areas (T10) were least negatively impacted. We found the highest range gains in areas that were climatically suitable areas for the species of tall herb communities, bushes, and turfs near or above the treeline (T3), boulder and scree habitats without woody species (T5) and for nutrient poor grasslands (T6). For all major habitats median range losses were higher than median range gain (Fig. 1).

The median range loss tended to vary with number of Red List species in the major habitat types. Major habitat types containing a higher proportion of modelled Red List species lost a significantly higher fraction of their species under climate change ($\tau = 0.49$, $p < 0.048$). We did not identify a significant relationship between median range gain and the proportion of Red List species ($\tau = 0.27$, $p = 0.28$).

**Habitat-specific species pool**

Species richness per grid cell was significantly smaller in future climates (assuming unlimited dispersal, $p < 0.05$, Wilcoxon signed rank test) than under current climate (except in T6 under SEDG, T8 under SEDG, BAMBU). Mean Sørensen dissimilarity ($d$) increased significantly from SEDG ($d = 0.15$, averaged across the major habitats and grid cells), through BAMBU ($d = 0.17$), to GRAS ($d = 0.30$; Wilcoxon
Fig. 1. Influence of habitat type (A) and scenario (B) on range loss, range gain (logarithmic scale), and species range change (logarithmic scale) [%] in ten major habitat types. Habitat type (A) averaged across all scenarios (assuming climate and land use change I) and species typical for a habitat type (see Table 1 for explanation). Estimates were calculated from differences in projected range sizes assuming no dispersal (range loss) and unlimited dispersal (range gain, species range change) per species [%] between baseline (1961–90) and future distribution (2051–80). Scenario (B): range loss, range gain, and species range change [%] under three alternative climate and land-use change (I) scenarios SEDG (+2.2°C), BAMBU (+2.9°C), and GRAS (+3.8°C) across all major habitat types up to 2080. Note that we did not find interaction effects for the estimates range loss, range gain, and species range change, respectively. Different letters below indicate significant differences at \( p < 0.05 \) after pair-wise comparisons (Tukey post hoc test after ANOVA on ranks, \( p < 0.05 \)).

The results did not change when grid cells that have no habitat-specific species for a habitat type were excluded from the calculation of \( I_h \) (data not shown).

Averaged across all habitat types, we found a decrease in \( I_h \) ranging from \(-3.4 \pm 5.7\%\) (mean ± s.d., SEDG), through \(-8.4 \pm 9.0\%\) (BAMBU), to \(-24.2 \pm 12.9\%\) (GRAS; see Fig. S2). For the species characterizing the major habitat types, we found a general decrease of \( I_h \) in the north-eastern and south-western parts of Germany. We found an increase of \( I_h \) only in the southern parts of the mountain regions (i.e., T8, T9, T10, see Fig. S2). The two-way ANOVA revealed significant main effects on \( I_h \) values for climate scenario

test, \( p < 0.01 \), see Table S4). Modelled \( I_h \) were positively correlated with \( I_h \) of the observed species distributions in Germany \((0.39 \pm 0.11; \text{mean} \pm \text{s.d.,} \ p < 0.01, \text{see Fig. S1}), \) but were significantly higher \((p < 0.01, \text{Wilcoxon test})\). \( I_h \) in the scenarios were significantly smaller than the \( I_h \) for the baseline projections (Wilcoxon signed rank test, \( p < 0.05 \)), except the \( I_h \) for the species representing urban formations (T10), nutrient poor grasslands (T6) and forb communities (T8) which showed significantly higher \( I_h \) under the moderate (SEDG) or intermediate (BAMBU) scenario \((p < 0.05, \text{Fig. 2})\). \( I_h \) significantly declined in all major habitat classes from SEDG to BAMBU to GRAS (Wilcoxon test, \( p < 0.05 \)).
Fig. 2. Index of habitat-specific species assemblages \((I_h)\) for the major habitat types (see Table 1 for habitat types) under current (1961–90) and scenario projections assuming climate and land-use change under unlimited dispersal (2051–80; SEDG, BAMBU, GRAS) using modelled species presence/absence \((n = 474)\) (see text for explanation). The Wilcoxon signed rank test \((p < 0.01)\) indicated significant differences of \(I_h\) under the baseline and the alternative scenario projections; *under SEDG \(I_h\) is greater than under the baseline projection; **under SEDG and BAMBU \(I_h\) is greater than under the baseline projection. The change of \(I_h\) was significantly different between the alternative scenarios. \(I_h\) decreased from SEDG, via BAMBU to GRAS (Wilcoxon rank sum tests adjusted by Holm correction, \(p < 0.05)\).

\[F = 15195.0, \text{df} = 2\] and major habitat type \(F = 3137.6, \text{df} = 9\), as well as a significant interaction between scenario and habitat type \(F = 236.4, \text{df} = 18, p < 0.001\). This means that the habitat-specific species pools differed at the levels of the scenarios (see Fig. S3). Pair-wise multiple comparisons (Tukey test with Holm correction, \(p < 0.05)\) showed significant differences for the proportional change in \(I_h\) between most major habitats (except T1 vs. T5 in SEDG, T9 vs. T10 in GRAS), as well as between the different scenarios (except T9 in SEDG and BAMBU).

Discussion

Currently more than two thirds of habitat types in Germany are classified as endangered (Riecken, Finck, Raths, Schröder, & Ssymank 2006) because of destruction, fragmentation or degradation. Nature conservation policy, management planning, or farming policy (i.e. human behaviour and management) can either have positive or negative impacts on current as well as future habitats and habitat-specific species pools. The potential impact of climate change on habitats and their species pools is still poorly understood. By extending common species distribution modelling approaches, we propose a new, but simple method for analysing habitat-specific plant species pools under projections of future climate and land-use changes. We analysed species range change with regard to the modelled occurrence of habitat-specific species of \(6'\times10'\) grid-elements to determine which habitat-specific species pools may be most vulnerable.

Our approach yields clear evidence of profound negative consequences of climate change for Central Europe’s habitat-specific plant species pools. The focus on nationally endangered species evidences a higher negative impact on habitats with high conservation value. A range expansion of certain species can be expected, but it remains an open question if dispersal speed will be high enough to allow for expansion into new climatically suitable regions. In addition, range shifts are not only climatically controlled. At the scale of our study, on average more than half of the variation in species ranges is explained by climate as the most important factor (Pompe et al. 2008). Population decline, range loss and range gains are species specific. Thus, climate change will not only have the commonly projected effect of a habitat shift as species ranges expand or retract, but will lead to changes in the composition of regional species pools, from which species within habitats are recruited. Our results indicate a decrease in the number of habitat-specific species co-occurring within regional species pools. This is particularly apparent for certain habitat types as species assemblages near or above treeline and dwarf scrub communities below alpine areas and less evident for urban formations and plant cultures. The dissimilarities of the investigated major habitats between current and scenario conditions increase. This underlines the point that there is a high potential for the reassembling of species pools in the future (e.g. Woodward 1987; Brueelheide 2003). Specifically, this will lead to (i) a disintegration of current habitat-specific species assemblages, and (ii) a compositional change of the regional species pools (through local loss and gain of new species). Changes in habitat-specific species pools may even be further increased because new species (European or non-European plants) that were not included in our study will potentially move to Germany (Walther et al., 2009; Bergmann et al. 2010). Climate change could trigger the expansion of invasive species. We hypothesize that more empty niches will be available for invasion after species have been lost from a regional habitat-specific species pool or species richness has declined through climate change.
The effect of climate change on species range loss, gain and change depends on the degree of climate change. This effect did not differ between the major habitat types, which was in contrast to our expectations. This might be explained by our coarse classification scheme used for the habitat groups, as well as by the individual response of species. However, analysing the index of co-occurrence which defines joint habitat-specific species pools, we found evidence for an interaction of the main effects major habitat and scenario. Thus, the climate change effect on the species composition of habitat-specific species pools differs between the major habitat types. Considering these interactions is important when evaluating the effects of global warming on habitats and their species assemblages. Several of the consequences could be specific to individual species or species groups. Studying traits or qualities of species groups associated with range contraction or range expansion can further support the analysis of species sensitivity under climate change (Pompe et al. 2009). A shift of certain species to higher elevations in mountain regions is the simplest case and can be associated with climate change (e.g., Skov & Svenning 2004; Thuiller, Lavorel, Araújo, Sykes, & Prentice 2005). Mountain species might be able to shift their realised ranges to higher altitudes if dispersal into these newly available fractions of suitable ranges is not restricted (Dirnböck, Dullinger, & Grabherr 2003; Lenoir, Gégout, Marquet, de Ruffray, & Brisse 2008; Trivedi, Berry, Morecroft, & Dawson 2008; Trivedi, Morecroft, Berry, & Dawson 2008; Bässler et al. 2009). However, this process may be limited by the harshness of the ground, especially by the presence of scree slopes and boulder fields (Moen, Aune, Edenius, & Angerbjörn 2004). Generally, in more heterogeneous landscapes (e.g., with respect to topography) a high number of habitat-specific species may face a lower risk of becoming regionally extinct because the heterogeneity in habitats will increase the chance that climatically and ecologically similar habitats will be available in the neighbourhood (Luoto & Heikkinen 2008). Still, many regions, especially in the north of Germany, are relatively flat so that certain species will have fewer chances to find suitable habitats by dispersing upslope or to northern aspects. In central German mountain ranges were elevations are not as high as in the Alps, species might experience difficulties in moving upslope. The uncertainty about the precise effects of future climate change at regional scales is high (Trivedi, Berry, et al. 2008; Trivedi, Morecroft, et al. 2008). Our results describe potential changes in bioclimatically suitable areas in Germany, not actual distributions of plant species, and are to be interpreted with care (see Guisan & Zimmerman 2000; Pearson & Dawson 2003; Liu, Berry, Dawson, & Pearson, 2005; Welk & Brueelheide 2006; Dormann 2007 about general uncertainties in species distribution models). Our coarse resolution of the grid cells does not represent the regionally distinct patterns of different landscapes. Therefore, on the one hand, models may overestimate climatic tolerances of species (Trivedi, Berry, et al. 2008). On the other hand, they may miss small-scale spatial heterogeneity and altitudinal variation and therefore overestimate species losses (Randin et al. 2009). Human activities may increase or decrease habitat suitability for species (Parton, Ojima, & Schimel 1994; Holzkmper, Lausch, & Seppelt 2006). Nitrogen deposition and human management (e.g. surplus land additionally used for biofuels) that are highly affected by decisions taken at regional scales by land-owners such as farmers under the EU’s Common Agricultural Policy (CAP) will have direct impacts on such assemblages (Parton et al. 1994; Nagy et al. 2009).

A combination of different modelling tools in regional climate and land-use change assessment are needed to understand relative and synergistic effects of range shifts, habitat shifts, landscape structure and population dynamics. It is necessary to consider these elements in addition to climate change when developing realistic future scenarios in risk assessment. Further studies applying hybrid modelling approaches (as proposed by Hickler et al. 2009) might improve results by combining the modelling of habitats with the modelling of the species’ environmental envelopes and biotic interactions. Beyond these lines of further model development, there is no doubt, however, that modelling exercises need to be complemented by experimental, as well as field research across spatial and ecologically heterogeneous scales. An approach with mutual feedback among the different scientific approaches is necessary to provide deeper insight into the details of long-term ecological responses.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2010.08.007.
References


