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HOW ARE PLANT SPECIES IN CENTRAL EUROPEAN BEECH (*FAGUS SYLVATICA* L.) FORESTS AFFECTED BY TEMPERATURE CHANGES? - SHIFT OF POTENTIAL SUITABLE HABITATS UNDER GLOBAL WARMING

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Abstract – This study reveals which temperature range is favoured or avoided by 156 forest plant species and how the distribution of potential suitable habitats of species in beech forests may change in the future. We performed 140 phytosociological relevés along a temperature gradient (4.1 to 9.8 °C) in Bavaria, southern Germany, on south exposed slopes. One half of the plots were located on acidic substrate, the other half on base-rich substrate. Generalized linear models (GLM) were used to analyse species occurrence along the temperature gradient and to model habitats for species in beech forests under a present (1971-2000) and a future climate (2071-2100) scenario assuming a temperature increase of 1.8 °C. Herb species of beech forests are more adapted to lower temperatures and tree species more to higher temperatures. Current habitats will clearly change under increasing temperatures. We found large habitat losses for *Luzula sylvatica* (Huds.) Gaudin, *Maianthemum bifolium* (L.) F. W. Schmidt, *Picea abies* (L.) H. Karst., *Prenanthes purpurea* L. and large habitat gains for *Carpinus betulus* L., *Impatiens parviflora* DC., *Prunus avium* (L.) L. and *Quercus petraea* (Matt.) Liebl. on both substrates. Forestry will be affected positively as well as negatively with a change in tree cultivation. Losses in biodiversity might be strong for mountainous forests and must also be considered in future conservation plans.

Keywords: climate change, climatic gradient, cold-adapted species, warm-adapted species, ecological boundaries, habitat modelling, forest management, nature conservation

Introduction

Due to climate change, temperatures have been increasing for decades: global mean temperature rose by 0.74 °C from 1906 to 2005 (Trenberth et al., 2007). In Germany the temperature increase is the most dominant ongoing trend in climate change, especially during winter time (Schönwiese et al., 2006). The mean annual temperature in Bavaria, a federal state in southern Germany, increased by between 0.6 and 1.2 °C depending on the region, and December average temperature by between 1.8 and 2.5 °C from 1931 to 2000, respectively (KLIWA, 2005). Temperatures are expected to increase even more in this century. At the end of the 21st century an increase of the global mean temperature of between 1.1 and 6.1 °C compared to the average of 1980 to 1999 is expected (Moomaw et al., 2011), and for Germany between 2.5 and 3.5 °C (UBA, 2006).

As a consequence, species may either persist, go extinct, or migrate, resulting in changed distribution areas. In the northern Mediterranean mountains of Spain, both the altitudinal upward shifting of *Fagus sylvatica* and the replacement of lower altitudinal beech forests by *Quercus ilex* L. are reported (Peñuelas & Boada, 2003). For southern Switzerland an increase in frequency of evergreen

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thermophilous species (Walther, 1997; Carraro et al., 1999) and a decrease in frequency of mountain species (Walther, 1997) are documented. The process whereby the more cold-adapted species decline, and the more warm-adapted species increase is described as “thermophilization” (Gottfried et al., 2012). An average northward shift of the range of terrestrial plants by 6.1 km per decade in the northern hemisphere has been reported for the last 50 years (Thuiller, 2007). For northern Europe the northwards movement of *Ilex aquifolium* L. is described in detail (Berger et al., 2007).

The ongoing change of climate therefore will have strong consequences for many plant species in Europe. Thuiller et al. (2005) studied the recent distribution of 1,350 plant species in Europe using different climate change models and revealed that more than half of the species could be threatened or be vulnerable by 2080. In recent years under the aspect of global change, forest ecologists have performed altitudinal gradient studies all over the world (Fischer et al., 2011). Temperature can be estimated from the altitude of the plots because of the tight correlation of both variables (Vetaas, 2000). Consequently, altitudinal gradients can be interpreted as temperature gradients.

Dullinger et al. (2012) predict an area reduction of the current mean size by 44 to 50% at the end of the 21st century for 150 high mountain plant species of the European Alps. An upward shifting of species is observed in the high mountains of the Alps (Grabher et al., 1994; Parolo & Rossi, 2008).

Species distribution modelling has become important under the aspect of global warming and studies dealing with modelling of future changes of suitable habitats or species distribution have been performed mostly in America (Box et al., 1999; Schrag et al., 2008; van Zooneveld et al,. 2009) and in Europe (Bakkenes et al., 2002; Benito Garzón et al., 2008; Ruiz-Labourdette et al., 2012) in recent years.

What are the consequences for forests in central Europe? A long-term study in Bavarian beech forests (Jantsch et al., 2013) showed that the most significant change in species composition relating to temperature was an increase of the thermophilous tree species *Juglans regia* L. But apart from global warming, other reasons such as a reduced utilization pressure on the nuts could also be the reason for this increase. However, a further increase of temperature could affect more herb and tree species and their distribution areas.

Based on this assumption, we investigated the statistical relationship of 156 forest plant species (129 vascular plants and 27 bryophytes) in beech forests in Bavaria to mean annual temperature along a temperature gradient. Our objectives were to reveal (i) which temperature range is favoured or avoided by individual forest plant species and (ii) how the distribution of potential suitable habitats of species in beech forests may change in the future.

MATERIALS AND METHODS

Study area and selection of forest stands

We selected 140 forest stands distributed in the Federal State of Bavaria in Germany (Figure 1a), with 70 of them on acidic soils, 70 on base-rich soils (Figure 1b, c).

For the selection of the stands, four criteria were used: (i) size of the forest area larger than 200 ha; (ii) a beech proportion of more than 50% on at least 10 ha; (iii) stand on either acidic or base-rich substrate; (iv) south exposed slope (between south-east and south-west) or slightly south exposed hilltop. In each suitable forest stand one plot was chosen with a maximum distance of at least 1 km to the next plot. This selection was performed in the geographical information system ArcGIS 9.3 by using digital aerial photographs as well as topographical, forest, geological and substrate maps. The mean annual temperature was obtained from a temperature map of Bavaria (Zimmermann et al., 2007). The assignment of the plots to the substrate type was based on the information of the geological map of Bavaria at the scale 1:500.000 (BLFU, 2009) and a map distinguishing five different types of base saturation in the soil (Kölling et al., 1996; Kölling, 2010). Base saturation types 1 and 2 were attributed to base-rich soils, base saturation types 4 and 5 to acidic soils, base saturation type 3, regarded as intermediate, was not considered in order to get two distinctive groups. An assignment to substrate type was necessary because many species in central Europe only occur on base-rich substrate (Ewald, 2003). Southern exposition was chosen in order to get the gradient as long as possible to the warm side. The selected plots cover the whole temperature range of beech forests in Bavaria: from 4.1 to 9.8 °C on acidic soils and from 4.2 to 9.1 °C on base-rich soils, respectively. This corresponds to an altitudinal gradient from 140 to 1,200 m a.s.l. on the acidic substrate and from 220 to 1,400 m a.s.l. on the base-rich substrate.

The final selection of the plots was carried out in the field, using additional plot criteria (i) >50% cover of beech in the tree layer; (ii) total coverage of the tree layer not less than 80%; (iii) age of tree stand at least 80 years; (iv) rock coverage of the plot less than 20%; (v) not more than 30° slope inclination.

Sampling of vegetation relevés

Each plot comprised a central area of 196 m² (14 m x 14 m) for bryophyte records on soil, dead wood, roots and rocks, and an enlarged area of 900 m² (30 m x 30 m) with the same center point as the small area for tree, shrub and herb layer records. Plot sizes were exactly defined in the field by

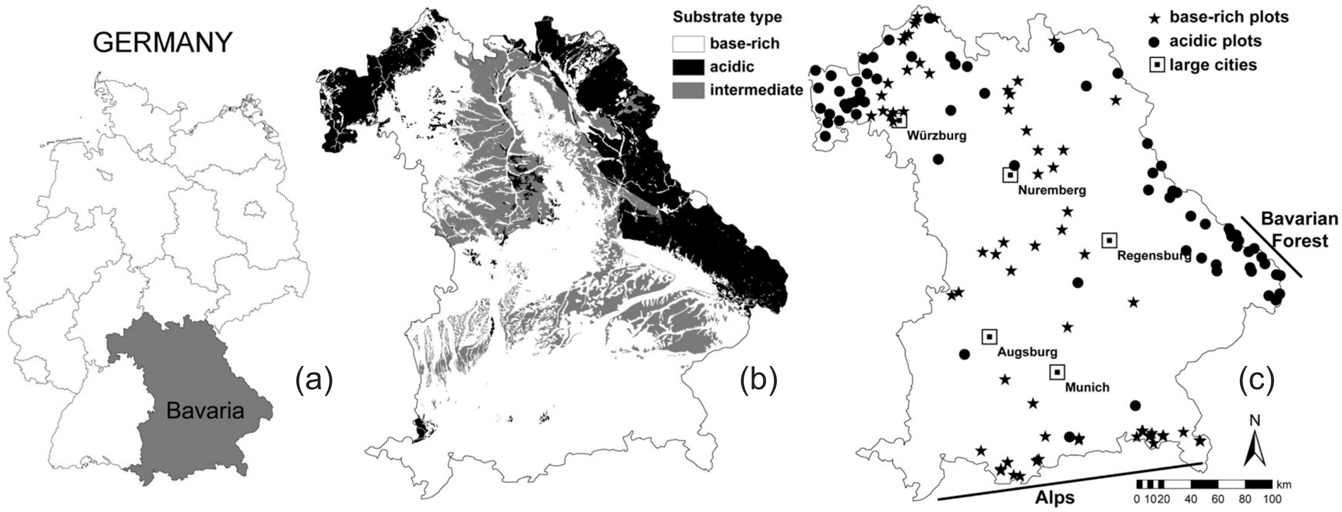

Figure 1. (a) Location of the Federal State of Bavaria in Germany; (b) distribution of the three substrate types: base-rich, acidic, intermediate, respectively; (c) the location of the 70 plots on acidic substrate (black dots) and of the 70 plots on base-rich substrate (black stars). White squares with black center mark the position of the five largest cities in Bavaria. Border lines of Germany and the federal states of Germany © Bundesamt für Kartographie und Geodäsie, Frankfurt am Main, 2011.

ranging poles and tape measures.

Nomenclature for the scientific names of the vascular plant species follows Erhardt et al. (2000), for bryophyte species Koperski et al. (2000).

Dataset

For all analyses we used presence/absence data of the species. We excluded all rare plant species which occurred less than seven times as rare species, that might represent random occurrences.

Climate data

We obtained climatic parameters for our plots from a spatial interpolated climate model for the period 1971 to 2000 (Hera et al., 2012) as reference for the present climate. The bases for this climate model are daily measurements from around 80 climate stations for temperature and from around 570 stations for precipitation in Bavaria, from the German Meteorological Service for this 30 year period. To calculate the climatic parameters for the time period 2071 to 2100, the WETTREG B1 scenario (Spekat et al., 2007) was used. WETTREG B1 is a moderate warming scenario which assumes an increase of 1.8 °C of the mean annual temperature until 2100. The spatial resolution in both cases was 50 m x 50 m. The change in the distribution of temperature values of the raster cells between the recent and the future climate scenario in Bavaria was analysed.

Creating maps

Based on the available climate data we calculated the mean annual temperature in a grid of 250 m x 250 m for Bavaria from the monthly averages of the climate model for the periods 1971 to 2000 and 2071-2100. As we used the two substrate types “acidic” and “base-rich” as one criterion for plot selection and model building, we had to consider this classification also in the distribution modelling. Based on the geological map of Bavaria 1:500.000 (BLFU, 2009) as well as the soil map separating five different types of base saturation (Kölling et al., 1996; Kölling, 2010) we generated a grid map with 250 m resolution with the classes acidic, base-rich, and intermediate. The maptools-package (Lewin-Koh et al., 2012) was used for creating the raster files in R statistics (R Development Core Team, 2012).

Statistical Analysis

Canonical correspondence analyses (CCA) were applied to analyse the dependence of the species composition on environmental variables and to evaluate the importance of the temperature factor in the dataset by using the vegan-package (Oksanen et al., 2012) in R statistics.

For the climatic parameters we tested mean annual temperature (TEMP) and annual precipitation sum (PREC). Slope (SLOPE) and aspect (ASPECT) were obtained from a digital elevation model (BVW, 2011). Substrate (SUBSTRATE) was a factor variable with two categories: acidic and base rich. With regard to soil factors, the exchangeable calcium (CA) and magnesium (MG) stock in the soil and the base-saturation type (BST on a scale 1 to 5) were extracted from modelled maps (unpublished, version of 2007).

The significance of all selected environmental factors in the CCA was tested with an analysis of variance (ANOVA) with the Monte-Carlo-significance test and the insignificant factors were removed from further analysis. The explained dispersion of the species in the CCA was calculated.

A correlation between number of species per plot and mean annual temperature of the plot was analysed using a linear regression.

The response of individual plant species to mean annual temperature was analysed using two different generalized linear models (GLM) in R statistics (R Development Core Team, 2012): a sigmoid model and a unimodal model. We first checked for all plant species whether there was a significant interaction between temperature and substrate (acidic or base-rich) in any of both GLM models. The occurrences of plant species with a significant interaction between temperature and substrate were assigned to the acidic or base-rich substrate group and analysed separately. Plant species that occurred on only one type of substrate were also analysed separately.

For all species we calculated both a sigmoid model and a unimodal model. We chose the model that had a significant regression parameter of the second order polygon and, as a second option, the model with the better explained deviance. We assumed an influence of temperature on the occurrence of all species with a significant regression parameter in one of both models.

The curve of a sigmoid model can increase to the left or right side. If the slope of the curve of the sigmoid model increased to the left side (lower temperature range, colder climate), we attributed the species as adapted to lower temperatures, and to higher temperatures, if the slope of the curve increased to the right side (higher temperature range, warmer climate). The upper and lower ecological temperature boundaries are the intersection of the modelled probability of occurrence with the a priori probability of occurrence of the selected species. In the case of a sigmoid model there is only one (upper or lower) boundary. In the case of unimodal models the lower and upper boundaries of the ecological amplitude are given. With a unimodal model the whole ecological amplitude can be described, whereas for sigmoid models only the warmer or colder end of the distribution of the species is captured in the Bavarian range of temperatures. Species with a unimodal model were attributed as adapted to intermediate temperatures. A significance level of 95% was used for all decisions.

Modelling of the potential habitat suitability

For modelling the potential habitat suitability for the different plant species living in beech forests under the recent climate 1971-2000 and under the assumed climate of the years 2071-2100, respectively, the climate models and the GLMs were used in the dismo-package (Hijmans et al., 2012) in R statistics (R Development Core Team, 2012).

The threshold for the potential occurrence of the species was calculated as the logit-transformed prior probability:

$$threshold = log \frac{p_i / p_n}{1 - (p_i / p_n)}$$

p_i = count of presences, p_n = count of plots

Areas where the conditional probability for species occurrence was higher than the a priori probability were marked with dark grey colour in our models. Light grey shows areas where the conditional probability for species occurrence was lower than the a priori probability, or unsuitable geology was provided for the species in the modelled map (acidic areas for a base-rich soil preferring species). The values for the ecological boundaries or amplitude were calculated by the intercept and slope of the GLM and the threshold (Fischer, 1994).

To evaluate the accuracy of the models the AUC (area under the receiver operating curve) value was calculated with the PresenceAbsence-package (Freeman & Moisen, 2008) in R statistics (R Development Core Team, 2012). The closer AUC is to 1, the better the model is. An AUC around 0.5 reveals that the calculated model is not better than a random model. For modelling the habitat suitability we have chosen species with models with an AUC ≥ 0.80, which are seen as models with good performance (Hosmer & Lemeshow, 2000).

RESULTS

The importance of temperature

The best explanatory variables in the CCA from all relevés were substrate with 8.6%, base saturation with 7.7% and mean annual temperature with 7.6%. Annual precipitation sum explained 7.2% (Table 1). The variable substrate clearly separated the dataset in the ordination diagram of the CCA in

Table 1. Explained percentage dispersion of significant environmental factors in the CCA with their significance value underneath (ns=not significant), for the whole dataset and separated into the acidic and base-rich relevés. The values of the three best explanatory environmental factors in each ordination are marked bold. ASPECT = exposition [°], CA = exchangeable Calcium stock in the mineral soil, BST = base saturation type according to Kölling et al. (1996), MG = exchangeable Magnesium stock in the mineral soil, PREC = annual precipitation sum [mm], SLOPE = slope [°], SUBSTRATE = substrate type of the plot (acidic or base-rich), TEMP = annual average temperature [°C].

	all relevés CCA [%]	**base-rich relevés CCA [%]**	**acidic relevés CCA [%]**
TEMP	**7.6**	**14.6**	**9.9**
	0.0001	0.0001	0.0001
PREC	7.2	**12.5**	ns
	0.0001	0.0172	ns
SLOPE	2.6	**4.5**	**2.4**
	0.0001	0.0002	0.0067
ASPECT	0.9	ns	ns
	0.0263	ns	ns
CA	4.4	2.2	ns
	0.0001	0.0450	ns
MG	3.5	ns	ns
	0.0020	ns	ns
BST	**7.7**	3.0	3.0
	0.0001	0.0004	ns
SUBSTRATE	**8.6**	ns	ns
	0.0001	ns	ns
total	22.8	23.6	12.0
	0.005	0.005	0.005

the acidic and base-rich relevés along the most important 1st axis (Figure 2).

For the relevés on acidic soils mean annual temperature explained 9.9% of the dispersion in the CCA (Table 1). With an explained dispersion of 14.6% in the CCA, the highest value for mean annual temperature was obtained for the base-rich relevés (Table 1). We found that mean annual temperature had the strongest influence on species composition of all studied variables in the two separated substrate types.

On the base-rich substrate species number decreased with increasing temperature (Figure 3a), whereas it was independent of temperature on acidic soils (Figure 3b). We found a coefficient of determination of 0.45 on the base-rich substrate, indicating a correlation between species number and temperature. On the acidic substrate, species number was generally lower (Figure 3b), and species number and temperature were not correlated (coefficient of determination 0.05).

For our present climate 53% of the area of Bavaria had a mean annual temperature between 8 and 9 °C, and 29% a mean annual temperature between 7 and 8 °C, so that 82% of the area shared a mean annual temperature between 7 and 9 °C. A further 3% of the area had a temperature over 9 °C (Figure 4a). In the future climate scenario 11% of the area shared a temperature between 8 and 9 °C and 82% of the area had a temperature between 9 and 11 °C (40% between 9 and 10 °C, 42% between 10 and 11 °C). A small area proportion of 1% will even obtain a temperature between 11 and 12 °C, which is not present in our study area at all nowadays (Figure 4b).

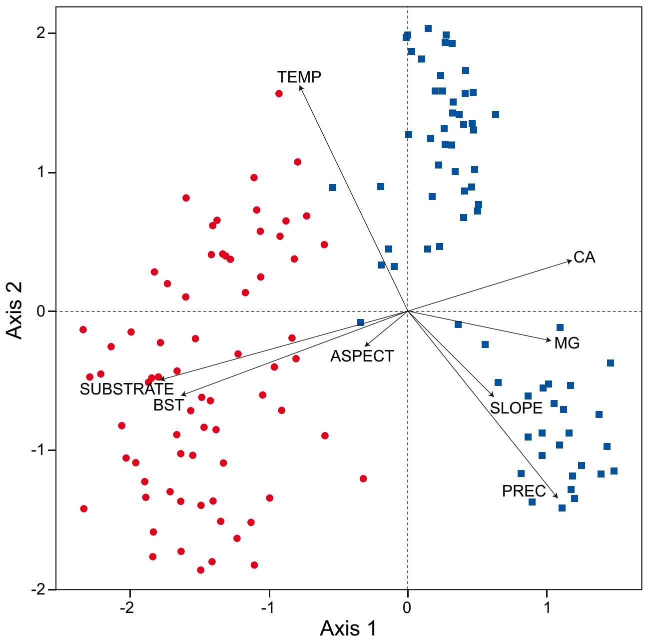

Figure 2. Biplot of all relevés and their environmental factors from the canonical correspondence analysis (CCA). Relevés from acidic plots are represented by red dots and relevés from base-rich soils by blue squares. ASPECT = exposition [°], CA = exchangeable Calcium stock in the mineral soil, BST = base saturation type according to Kölling et al. (1996), MG = exchangeable Magnesium stock in the mineral soil, PREC = annual precipitation sum [mm], SLOPE = slope [°], SUBSTRATE = substrate type of the plot (acidic or base-rich), TEMP = annual average temperature [°C].

Preferred temperature ranges of plant species

The substrate also played an important role in the species interaction with temperature: for most species occurring on both substrates a significant interaction between substrate and temperature was found, hence we calculated two separate GLMs.

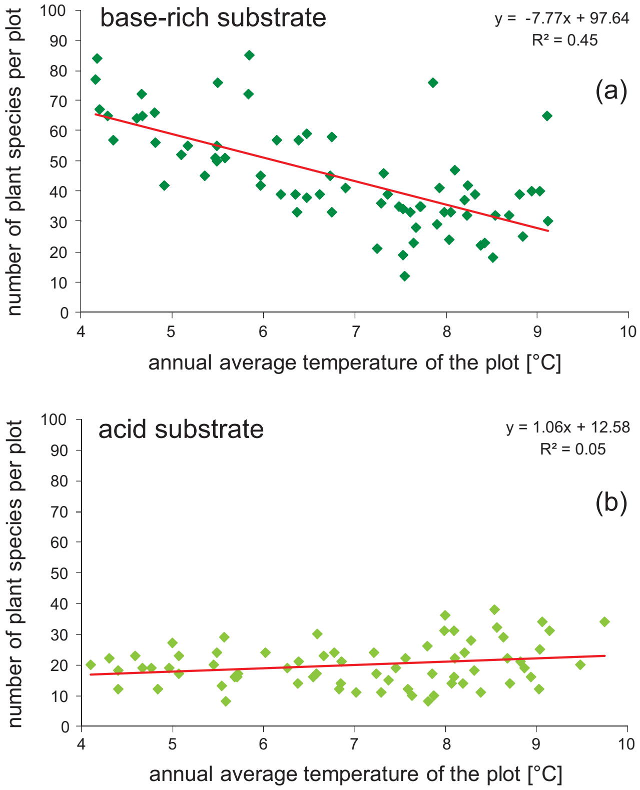

Figure 3. Number of plants species (vascular plant species and bryophyte species) per plot with the corresponding annual average temperature of the location for plots on base-rich substrate (a) and for plots on acidic substrate (b), respectively. Linear equation (y) and coefficient of determination (R²) are displayed in the right corner of each figure.

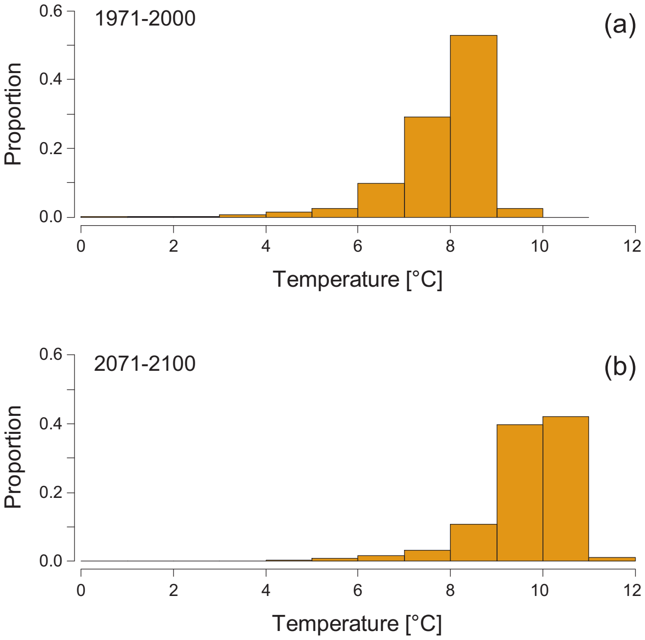

Figure 4. Distribution of the temperature values of the raster cells in Bavaria: (a) the model for the present (1971-2000), (b) the WETTREG B1 model for the future (2071-2100).

A total of 103 plant species (66%) preferred the base-rich substrate. For 92 vascular plant species and 11 bryophyte species we calculated GLMs on this substrate type. Of these 68 vascular plant species and 8 bryophyte species (74% of all analysed species on base-rich substrate) indicated significant responses to the temperature gradient (Table 2). We found 29 cold-adapted vascular plant species (e.g. *Polygonatum verticillatum* (L.) All., Figure 5a) and 4 cold-adapted bryophyte species in our beech forest data set, which proved to have models with good performance according to their AUC (area under the receiver operating curve, bold marked species in Table 2). Two vascular plant species showed a preference for intermediate temperatures (e.g. *Senecio ovatus* (P. Gaertn., B. Mey. & Scherb.) Willd., Figure 5b) and 8 vascular plant species indicated a preference for higher temperatures (e.g. *Acer campestre* L., Figure 5c) with an AUC ≥ 0.80. Of all analysed species on base-rich substrate, 46% indicated a preference for lower temperatures, 10% for intermediate temperatures, 18% for higher temperatures and 26% showed no preference.

For 21 vascular plant species and for 10 bryophyte species on acidic substrate we calculated GLMs. Here 11 vascular plants species and 3 bryophyte taxa (45% of all analysed species on acidic substrate) indicated significant responses to the temperature gradient (Table 3). On the acidic substrate the vascular plant species *Carex ovalis* Good., *Maianthemum bifolium* and the 2 bryophytes *Lophocolea heterophylla* (Schrad.) Dumort. and *Paraleucobryum longifolium* (Hedw.) Loeske indicated an adaption to lower temperatures with a well performing model (bold-marked in Table 3). The 2 tree species *Carpinus betulus* and *Prunus avium* indicated a suitable model for the preference of higher temperatures. Of all analysed species on acidic substrate, 19% indicated a preference for lower temperatures, 6% for intermediate temperatures, 19% for higher temperatures and 55% no preference.

For 32 vascular plant species and 10 bryophytes there was no interrelation detectable between temperature and substrate. Accordingly, their response to temperature was analysed for both substrates together (Table 4). Out of these 42 recorded plant species, 19 vascular species and 2 bryophyte species showed significant responses to the temperature gradient. We found 4 cold-adapted vascular plant species with a good model: the 2 herbaceous *Luzula sylvatica* and *Prenanthes purpurea,* the dwarf shrub *Vaccinium myrtillus* L. and the tree *Picea abies.* The 2 tree species *Pinus sylvestris* L. and *Quercus petraea* and the herbaceous non-native *Impatiens parviflora* were the species preferring higher temperatures with a good model.

Of all analysed species on both substrates 21% indicated a preference to lower temperatures, 5% to intermediate temperatures, 24% to higher temperatures and 50% no preference.

Mostly herbaceous species were adapted to lower temperatures in beech forests, whereas mostly tree species preferred higher temperatures.

Table 2. Species analysed on base-rich substrate (species are sorted according to their ecological amplitude and their upper/lower boundary, respectively). Species with an AUC ≥ 0.80 are bold marked.

Species	**Area under curve (AUC)**	**Upper or/and lower boundary of the ecological amplitude [°C]**	**Significance of regression parameter in GLM**	**Explained deviance in GLM**	**Frequency of species on base-rich substrate**
Vascular plants					
Veronica urticifolia Jacq.	**0.98**	**<5.3**	**0.0062**	**0.72**	**10**
Homogyne alpina (L.) Cass.	**0.97**	**<5.4**	**0.0057**	**0.58**	**8**
Cardamine enneaphyllos (L.) Crantz	**0.93**	**<5.7**	**0.0060**	**0.40**	**7**
Valeriana montana L.	**0.94**	**<5.7**	**0.0016**	**0.51**	**10**
Polygala chamaebuxus L.	**0.93**	**<5.8**	**0.0020**	**0.42**	**9**
Knautia dipsacifolia Kreutzer	**0.93**	**<5.9**	**0.0002**	**0.49**	**14**
Sesleria albicans Kit. ex Schult.	**0.89**	**<5.9**	**0.0035**	**0.32**	**8**
Clinopodium vulgare L.	**0.85**	**<6.0**	**0.0079**	**0.25**	**7**
***Galium mollugo* agg.**	**0.91**	**<6.0**	**0.0004**	**0.39**	**12**
Lysimachia nemorum L.	**0.93**	**<6.0**	**0.0002**	**0.49**	**15**
Adenostyles glabra (Mill.) DC.	**0.96**	**<6.1**	**0.0001**	**0.61**	**19**
Calamagrostis varia (Schrad.) Host	**0.93**	**<6.1**	**<0.0001**	**0.51**	**18**
Deschampsia cespitosa (L.) P. Beauv**.**	**0.82**	**<6.1**	**0.0024**	**0.24**	**10**
Lamium flavidum F. Herm.	**0.89**	**<6.1**	**0.0003**	**0.34**	**13**
Polystichum aculeatum (L.) Roth	**0.82**	**<6.1**	**0.0083**	**0.19**	**8**
Galium rotundifolium L.	**0.82**	**<6.2**	**0.0009**	**0.23**	**13**
Ranunculus nemorosus DC.	**0.91**	**<6.2**	**<0.0001**	**0.43**	**17**
Salvia glutinosa L.	**0.87**	**<6.2**	**0.0005**	**0.29**	**13**
Solidago virgaurea L.	**0.86**	**<6.2**	**0.0001**	**0.31**	**16**
Primula elatior (L.) Hill	0.74	<6.3	0.0163	0.12	10
Aposeris foetida (L.) Less.	**0.81**	**<6.4**	**0.0004**	**0.21**	**17**
Polygonatum verticillatum (L.) All.	**0.98**	**<6.4**	**0.0005**	**0.73**	**26**
Carex alba Scop.	**0.88**	**<6.5**	**<0.0001**	**0.39**	**23**
Epipactis helleborine agg.	0.70	<6.5	0.0390	0.07	13
Maianthemum bifolium (L.) F. W. Schmidt	**0.83**	**<6.5**	**<0.0001**	**0.28**	**21**
Paris quadrifolia L.	0.79	<6.5	0.0005	0.19	19
Sanicula europaea L.	**0.84**	**<6.5**	**<0.0001**	**0.30**	**23**
Dryopteris dilatata (Hoffm.) A. Gray	0.69	<6.6	0.0203	0.08	17
Fragaria vesca L.	0.79	<6.6	0.0001	0.21	26
Hieracium murorum L.	**0.81**	**<6.6**	**0.0001**	**0.21**	**26**
Mycelis muralis (L.) Dumort.	0.79	<6.6	0.0002	0.20	26
Phyteuma spicatum L.	**0.90**	**<6.6**	**<0.0001**	**0.42**	**26**
Sorbus aria agg.	0.73	<6.6	0.0035	0.12	20
Sorbus aucuparia L.	**0.83**	**<6.6**	**<0.0001**	**0.25**	**26**
Daphne mezereum L.	0.66	<6.8	0.0179	0.06	35
Hepatica nobilis Garsault	0.73	<6.8	0.0013	0.13	32
Melica nutans L.	0.73	<6.9	0.0024	0.11	39
Viola reichenbachiana Jord. ex Boreau /*riviniana* Rchb. /*x bavarica* Schrank	0.76	<7.0	0.0036	0.11	45
Mercurialis perennis L.	**0.88**	**<7.3**	**0.0002**	**0.33**	**49**
Acer pseudoplatanus L.	**0.87**	**<7.7**	**0.0046**	**0.30**	**60**
Bryophytes					
Dicranodontium denudatum (Brid.) E. Britton	**0.90**	**<6.0**	**0.0004**	**0.38**	**12**
Fissidens dubius P. Beauv**.**	**0.89**	**<6.0**	**0.0013**	**0.32**	**10**
Ctenidium molluscum (Hedw.) Mitt.	**0.91**	**<6.2**	**<0.0001**	**0.41**	**18**
Fissidens taxifolius Hedw.	0.78	<6.2	0.0234	0.14	7
Tortella tortuosa (Hedw.) Limpr**.**	**0.98**	**<6.4**	**0.0003**	**0.71**	**25**
Dicranum scoparium Hedw.	0.78	<6.6	0.0003	0.19	24
Isothecium alopecuroides (Dubois) Isov.	0.71	<6.8	0.0026	0.11	35

follows →

Species	Area under curve (AUC)	Upper or/and lower boundary of the ecological amplitude [°C]	Significance of regression parameter in GLM	Explained deviance in GLM	Frequency of species on base-rich substrate
Vascular plants					
Senecio ovatus (P. Gaertn., B. Mey. & Scherb.) Willd.	**0.83**	**4.2-7.1**	**0.0015**	**0.41**	**25**
Hordelymus europaeus (L.) Jess. ex Harz	0.76	4.3-7.4	0.0037	0.24	30
Ulmus glabra Huds.	0.56	5.1-7.8	0.0366	0.08	17
Actaea spicata L.	0.58	5.6-7.5	0.0408	0.24	7
Sambucus racemosa L.	0.54	5.8-7.6	0.0274	0.33	8
Urtica dioica L.	0.64	6.1-8.6	0.0309	0.13	19
Milium effusum L.	0.70	6.3-8.9	0.0352	0.17	23
Crataegus monogyna Jacq.	**0.82**	**6.8-9.1**	**0.0131**	**0.38**	**24**
Acer platanoides L.	0.77	6.5-9.3	0.0339	0.27	27
Bryophyte					
Schistidium apocarpum (Hedw.) Bruch & Schimp.	0.75	4.2-7.1	0.0469	0.18	14
Vascular plants					
Fraxinus excelsior L.	0.65	>6.6	0.0405	0.05	51
Anemone nemorosa L.	0.67	>6.8	0.0154	0.07	41
Vicia sepium L.	**0.81**	**>7.0**	**0.0002**	**0.21**	**28**
Convallaria majalis L.	0.72	>7.1	0.0105	0.10	18
Lonicera xylosteum L.	0.75	>7.1	0.0040	0.13	19
Luzula luzuloides (Lam.) Dandy et Wilmott	0.70	>7.2	0.0490	0.08	10
Melica uniflora Retz.	0.76	>7.2	0.0023	0.16	18
Polygonatum multiflorum (L.) All.	0.74	>7.2	0.0077	0.12	16
Prunus avium (L.) L.	**0.82**	**>7.2**	**0.0002**	**0.24**	**23**
Sambucus nigra L.	0.75	>7.2	0.0072	0.13	15
Acer campestre L.	**0.92**	**>7.3**	**<0.0001**	**0.53**	**27**
Alliaria petiolata (M. Bieb.) Cavara et Grande	0.71	>7.3	0.0382	0.10	10
Cephalanthera damasonium (Mill.) Druce	0.77	>7.3	0.0013	0.20	18
Hedera helix L.	**0.82**	**>7.3**	**0.0006**	**0.25**	**18**
Lathyrus vernus (L.) Bernh.	**0.89**	**>7.3**	**<0.0001**	**0.41**	**23**
Carpinus betulus L.	**0.91**	**>7.5**	**0.0002**	**0.45**	**20**
Galium sylvaticum L.	0.79	>7.5	0.0142	0.18	9
Juglans regia L.	**0.84**	**>7.5**	**0.0010**	**0.30**	**15**
Sorbus torminalis (L.) Crantz	**0.88**	**>7.7**	**0.0095**	**0.29**	**8**

- unsuitable model (parabolic form): vascular plants: *Carex flacca* Schreb., *Carex montana* L.
- no significant regression parameters in any GLM: vascular plants: *Ajuga reptans* L., *Asarum europaeum* L., *Atropa bella-donna* L., *Brachypodium sylvaticum* (Huds.) P. Beauv., *Bromus benekenii* (Lange) Trimen, *Campanula trachelium* L., *Carex digitata* L., *Carex sylvatica* Huds., *Cephalanthera rubra* (L.) Rich., *Clematis vitalba* L., *Dactylis polygamya* Horv., *Dryopteris carthusiana* (Vill.) H. P. Fuchs, *Epipactis atrorubens* (Bernh.) Besser, *Galium odoratum* (L.) Scop., *Geranium robertianum* L., *Geum urbanum* L., *Lamium montanum* (Pers.) Hoffm. ex Kabath, *Lilium martagon* L., *Neottia nidus-avis* (L.) Rich., *Stachys sylvatica* L., *Tilia platyphyllos* Scop. and *Veronica chamaedrys* L., bryophytes: *Brachythecium velutinum* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw. and *Polytrichum formosum* Hedw.

Changing potential habitat suitability in the future

All species which adapted to lower temperatures (listed in Tables 2 to 4) showed a reduced potential habitat suitability in the future maps, whereas species which are adapted to higher temperatures had an increasing potential habitat suitability in the future maps.

The expected changes were visible especially for the herbaceous species which showed significant responses to the temperature gradient on acidic as well as on base-rich substrate, i.e. *Luzula sylvatica* (Figure 6a), *Prenanthes purpurea* (Figure 6b; same model is valid for *Vaccinium myrtillus*) and *Maianthemum bifolium* (Figure 6c). With increasing temperatures all these species might lose their suitable beech forest habitats outside the Alps almost completely (Figure 6a, b, c). Only small areas might persist in the colder mountain range called Bavarian Forest (southeastern part of Bavaria). Also their current suitable habitats in the mixed beech forests of the Alps might be reduced at least by half. The tree species which might be

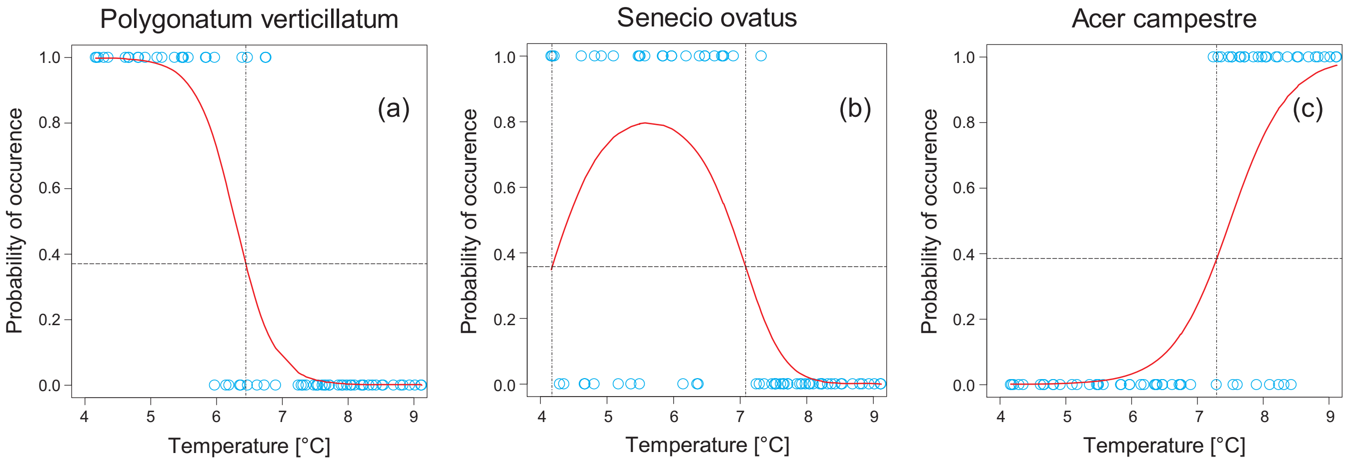

Figure 5. Examples for three species with a significant regression parameter of the second order polygon. Above the dashed y-line in the graphs the conditional probability of occurrence of the species is higher than the a priori probability. (a) The sigmoid model of the cold-adapted species *Polygonatum verticillatum*; (b) the unimodal model for the intermediate temperature adapted species *Senecio ovatus*; (c) the sigmoid model for the warm-adapted species *Acer campestre*. The point of intersection of the y-line with the dashed dotted x-line shows in (a) the upper ecological boundary and in (c) the lower ecological boundary for a high probability of species occurrence. The two intersection points in (b) mark the lower (left) and upper (right) ecological boundary and thus show the whole ecological amplitude for a high probability of the species occurrence.

Table 3. Species analysed on acidic substrate (species are sorted according to their ecological amplitude or their upper/lower boundary, respectively). Species with an AUC ≥ 0.80 are bold marked.

Species	**Area under curve (AUC)**	**Upper or/and lower boundary of the ecological amplitude [°C]**	**Significance of regression parameter in GLM**	**Explained deviance in GLM**	**Frequency of species on acid substrate**
Vascular plants					
Maianthemum bifolium (L.) F. W. Schmidt	**0.86**	**<6.1**	**0.0040**	**0.28**	**8**
Carex ovalis Good.	**0.80**	**<6.5**	**0.0018**	**0.19**	**13**
Dryopteris dilatata (Hoffm.) A. Gray	0.74	<7.1	0.0008	0.15	38
Sorbus aucuparia L.	0.75	<7.1	0.0008	0.14	35
Bryophytes					
Lophocolea heterophylla (Schrad.) Dumort.	**0.83**	**<6.2**	**0.0085**	**0.23**	**7**
Paraleucobryum longifolium (Hedw.) Loeske	**0.94**	**<7.0**	**<0.0001**	**0.50**	**32**
Vascular plant					
Carex sylvatica Huds.	0.73	7.2-8.9	0.0383	0.30	11
Bryophyte					
Pohlia nutans (Hedw.) Lindb.	0.69	4.8-7.5	0.0373	0.17	10
Vascular plants					
Luzula luzuloides (Lam.) Dandy et Wilmott	0.69	>7.0	0.0067	0.09	35
Fraxinus excelsior L.	0.69	>7.4	0.0342	0.08	14
Milium effusum L.	0.73	>7.6	0.0426	0.11	8
Urtica dioica L.	0.79	>7.7	0.0213	0.17	8
Prunus avium (L.) L.	**0.89**	**>7.8**	**0.0011**	**0.35**	**14**
Carpinus betulus L.	**0.89**	**>7.9**	**0.0027**	**0.34**	**11**

- unsuitable model (parabolic form): bryophyte: *Dicranum montanum* Hedw.
- no significant regression parameters in any GLM: vascular plants: *Acer platanoides* L., *Acer pseudoplatanus* L., *Agrostis capillaris* L., *Anemone nemorosa* L., *Carex pilulifera* L., *Deschampsia flexuosa* (L.) Trin., *Dryopteris carthusiana* (Vill.) H. P. Fuchs, *Juncus effusus* L., *Mycelis muralis* (L.) Dumort., *Viola reichenbachiana* Jord. ex Boreau/*riviniana* Rchb./*x bavarica* Schrank, bryophytes: *Dicranella heteromalla* (Hedw.) Schimp., *Dicranum scoparium* Hedw., *Hypnum cupressiforme* Hedw., *Isothecium alopecuroides* (Dubois) Isov., *Polytrichum formosum* Hedw. and *Tetraphis pellucida* Hedw.

Table 4. Species analysed together from both substrates (species are sorted according to their ecological amplitude or their upper/lower boundary, respectively). Species with an AUC ≥ 0.80 are bold marked.

Species	Area under curve (AUC)	Upper or/and lower boundary of the ecological amplitude [°C]	Significance of regression parameter in GLM	Explained deviance in GLM	Frequency of species in the whole dataset
Vascular Plants					
Luzula sylvatica (Huds.) Gaudin	**0.91**	**<5.8**	**0.0002**	**0.35**	**13**
Gymnocarpium dryopteris (L.) Newman	0.76	<6.3	0.0172	0.11	8
Prenanthes purpurea L.	**0.94**	**<6.4**	**<0.0001**	**0.53**	**42**
Vaccinium myrtillus L.	**0.84**	**<6.4**	**<0.0001**	**0.29**	**36**
Abies alba Mill.	0.78	<6.7	<0.0001	0.17	44
Athyrium filix-femina (L.) Roth	0.69	<6.7	0.0004	0.08	41
Oxalis acetosella L.	0.76	<6.9	<0.0001	0.15	63
Picea abies (L.) H. Karst.	**0.80**	**<7.3**	**<0.0001**	**0.22**	**95**
Bryophyte					
Pterigynandrum filiforme Hedw.	0.78	<6.3	0.0131	0.11	9
Vascular Plants					
Festuca altissima All.	0.62	5.5-7.4	0.0249	0.26	8
Quercus robur L.	0.58	6.2-8.3	0.0113	0.14	17
Vascular Plants					
Corylus avellana L.	0.66	>7.2	0.0424	0.04	20
Poa nemoralis L.	0.64	>7.2	0.0279	0.04	27
Galeopsis tetrahit L.	0.67	>7.3	0.0205	0.06	19
Quercus petraea (Matt.) Liebl.	**0.92**	**>7.3**	**<0.0001**	**0.50**	**56**
Circaea lutetiana L.	0.74	>7.5	0.0126	0.10	12
Carex remota L.	0.78	>7.6	0.0005	0.17	19
Larix decidua Mill.	0.79	>7.6	0.0012	0.16	16
Pinus sylvestris L.	**0.82**	**>7.6**	**<0.0001**	**0.22**	**25**
Impatiens parviflora DC.	**0.83**	**>7.7**	**0.0002**	**0.24**	**18**
Bryophyte					
Brachythecium rutabulum (Hedw.) Schimp.	0.69	>7.2	0.0023	0.08	29

- unsuitable model (parabolic form): bryophyte: *Herzogiella seligeri* (Brid.) Z. Iwats.
- no significant regression parameters in any GLM: vascular plants: *Carex muricata* agg., *Dryopteris filix-mas* (L.) Schott, *Epilobium montanum* L., *Impatiens noli-tangere* L., *Lamium galeobdolon* (L.) L., *Luzula pilosa* (L.) Willd., *Moehringia trinervia* (L.) Clairv., *Rubus fruticosus* agg., *Rubus idaeus* L., *Rumex sanguineus* L., *Scrophularia nodosa* L., *Taraxacum officinale* agg. F. H. Wigg., *Veronica officinalis* L., bryophytes: *Atrichum undulatum* (Hedw.) P. Beauv., *Metzgeria furcata* (L.) Dumort., *Plagiomnium affine* (Blandow) T. J. Kop., *Plagiothecium laetum var. curvifolium* (Limpr.) Mastracci & M. Sauer, comb. nov., *Plagiothecium laetum* Schimp., *Pseudoleskeella catenulata* (Schrad.) Kindb. and *Thuidium tamariscinum* (Hedw.) Schimp.

affected most strongly by global warming on both substrates in beech forests are *Picea abies* (Figure 6d) and on base-rich substrate *Acer pseudoplatanus* L. (Figure 6e). *Picea abies* might lose, apart from small areas, nearly all its suitable habitats in beech forests in northern Bavaria and might only remain as part of beech forests in the higher parts of the Alps and the Bavarian Forest. The suitable habitats of *Acer pseudoplatanus* on the base-rich substrate might be limited

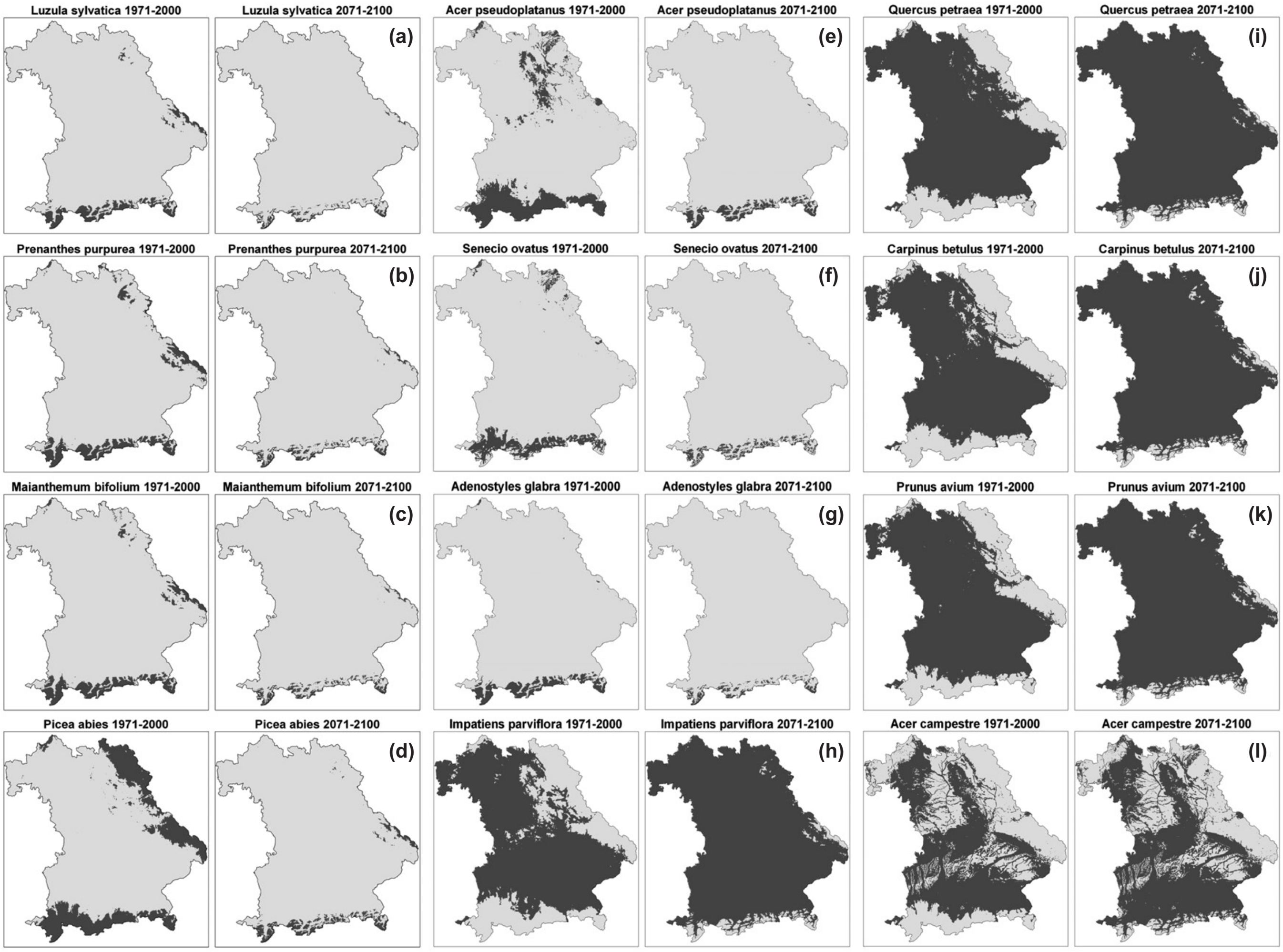

Figure 6. Maps of the modelled potential habitat suitability for selected species in south-exposed beech forests for the periods 1971-2000 and 2071-2100 from the GLMs. Areas in dark grey show where the conditional probability for species occurrence is higher than the a priori probability in our data set. Light grey shows areas where the conditional probability for species occurrence is lower than the a priori probability or the geology is unsuitable for the species occurrence.

almost to the Alps in a similar way.

Most of the herbaceous species and some bryophyte species growing on base-rich sites might lose most of their suitable habitats. For example, *Senecio ovatus* might lose all its suitable beech forest habitats in northern Bavaria (Figure 6f) and its suitable habitats might be restricted to small areas of the Alps. The suitable habitats of *Adenostyles glabra* (Mill.) DC. in the Alps might shrink by around 70% (Figure 6g). The same is obtained for *Calamagrostis varia* (Schrad.) Host, *Deschampsia cespitosa* (L.) P. Beauv., *Lamium flavidum* F. Herm. and *Polystichum aculeatum* (L.) Roth, and similarly for *Galium rotundifolium* L., *Lysimachia nemorum* L., *Ranunculus nemorosus* DC., *Salvia glutinosa* L., *Solidago virgaurea* L., the bryophytes *Dicranodontium denudatum* (Brid.) E. Britton and *Pterigynandrum filiforme* Hedw. Decreasing habitat suitability was also obtained for *Aposeris foetida* (L.) Less., *Carex alba* Scop., *Hieracium murorum* L., *Phyteuma spicatum* L., *Polygonatum verticillatum*, *Sanicula europaea* L. and *Sorbus aucuparia* L. Strong habitat reductions could be also projected for *Cardamine enneaphyllos* (L.) Crantz, *Homogyne alpina* (L.) Cass., *Knautia dipsacifolia* Kreutzer, *Polygala chamaebuxus* L., *Sesleria albicans* Kit. ex. Schult., *Valeriana montana* L. and *Veronica urticifolia* Jacq.

However, two herbaceous species might profit from increasing temperature: the non-native *Impatiens parviflora* (Figure 6h) and *Vicia sepium* L. Furthermore, the suitable habitat of *Quercus petraea* might increase in beech forests (Figure 6i) exactly into those areas which might be lost for the distribution of *Picea abies*, as the lower boundary by

7.3 °C of *Q. petraea* coincides with the upper boundary of *P. abies* (Table 3). Suitable habitats will also increase for *Carpinus betulus* (Figure 6j) as well as for *Prunus avium* (Figure 6k). Also *Acer campestre* (Figure 6l), *Hedera helix* L. and *Lathyrus vernus* (L.) Bernh., showing the same increasing habitat suitability, and *Juglans regia* and *Sorbus torminalis* (L.) Crantz, showing a similar pattern, might belong to the winners of global warming in beech forests on base-rich substrate.

DISCUSSION

We revealed many beech forest plant species that showed a clear sensitivity to temperature and we were able to localize the potential future suitable habitat under a changing temperature regime. Most of these species show a clear preference for lower temperatures and consequently the models predict shrinking habitat suitability for the future. Mainly tree and other woody species have their preferred habitat in warmer beech or beech mixed forests and for these species we forecast increasing habitat suitability in the future.

As expected, the results are usually coincident with the general ecology of these species already described in the literature (e.g. temperature preference according to Oberdorfer, 1994; numerical temperature indicator values of Ellenberg, 2001) or with their main altitudinal distribution in beech forests in Europe (Dierschke & Bohn, 2004; Marinšek et al., 2013). We also found a preference for lower temperatures which has not yet been described in the literature for *Carex ovalis*, *Deschampsia cespitosa*, *Mercurialis perennis* L., *Phyteuma spicatum*, *Ranunculus nemorosus* and *Solidago virgaurea*. The found preference for higher temperatures of *Vicia sepium* corresponds with its main distribution to planar and submontane forests (Dierschke & Bohn, 2004).

In the Jura Mountains of France and Switzerland, a decrease of the cold-adapted species *Prenanthes purpurea*, *Senecio ovatus* and *Solidago virgaurea* as well as an increase of the warm-adapted species *Quercus petraea* could be determined over the period 1989-2007 (Lenoir et al., 2010). This could be evidence for a climatic driven change, because also in the present study we obtained good models for these species showing the same trend for the future in Bavaria. The increase of *Impatiens parviflora*, which was already found in different phytosociological studies in central Europe over the last decades (Carraro et al., 1999; Lysik, 2008; Schmidt et al., 2008; Kowarik, 2010; Huwer & Wittig, 2012; Jantsch et al., 2013), could also be an effect of temperature increase according to our models showing increasing habitat suitability for this species in the future.

Temperature has an important influence on species number on base-rich substrate. The plots with the highest number of species and lower temperatures are found on base-rich substrate and all are located in the Alps. Most plant species growing there are adapted to lower temperatures. Indeed, on the base-rich substrate in the Alps nearly all plant species preferring acidic substrate also occur because of the acidification of the topsoil by coniferous trees and high precipitation rates (e.g. *Vaccinium myrtillus*). Vice versa, base-rich substrate preferring species are generally missing on acidic substrate independent of the temperature. Hence, almost all species of beech forests were encountered in the Alps. Additionally, the Alps are a unique natural area characterised by a high diversity of habitats and soils, resulting in a high species number (Ewald & Fischer, 1993). The higher altitude (>800 m) of the Alps also implies lower mean annual temperatures (<6.5°C). Therefore the found correlation might not be caused only by the temperature but by the high number of species in the Alps. Summarizing, the species composition of the mixed beech forests in the Alps seems to be endangered by increasing temperatures, but it is not totally clear if temperature is the most important reason for the spatial distribution of species in the Alps.

Pinus sylvestris was mainly introduced into anthropogenic devastated beech forest stands in the last centuries in areas of lower altitude. Thus the preference of this species for higher temperatures might be critically viewed because this species is also well adapted to lower temperatures. This is evidenced by its presence in the Alps up to 1600 m (Oberdorfer, 1994) as well as its occurrence even in northern Scandinavia. For *Larix decidua* Mill., a subalpine tree species, the apparent preference for a warmer climate is implausible. The tree has been planted by foresters mainly in the warmer parts of our study area and we found it in only one plot within its natural distribution range in the Alps. Even in the Bavarian Alps, which is the natural distribution range of *L. decidua*, its occurrence is quite restricted spatially (Aas, 2012) and beech forests tend to be unsuitable for a shade-intolerant species like *L. decidua*, which largely precludes natural regeneration. For *Fagus sylvatica* we could not assume changes in its studied range, as the occurrence of beech was a prerequisite for plot selection.

For such bryophyte species preferring rocks and dead wood, the modelling might be indecisive because rock coverage and dead wood proportion were not equal in all studied forests and these features might be more important than temperature. Mountain areas have generally a higher proportion of rock and dead wood than lowland forests. Hence the occurrence of these bryophytes in areas with a colder climate, as indicated by our analyses, might not really be dependent on the temperature, but on the local geology and forest structure. The species *Fissidens dubius* P. Beauv., *Tortella tortuosa* (Hedw.) Limpr. and *Ctenidium molluscum* (Hedw.) Mitt. prefer calcareous rocks (Nebel & Philippi, 2001a;b), which occur more frequently in the mountainous parts of the Alps than in the lower base-rich areas, but do not show a clear preference for climate according to literature (Nebel & Philippi, 2001a,b). In contrast *Paraleucobryum longifolium* prefers siliceous rocks in mountain areas (Nebel & Philippi, 2001a) such as those widely found in the mountainous parts of the Bavarian Forest. These areas are at higher altitudes with lower temperatures, providing a good match for our temperature model. However, the question is whether the presence of the silicatic rocks might be more important for the further occurrence of the species than lower temperatures.

Lophocolea heterophylla has its main distribution area in coniferous rich mountain forests with dominating acidic substrate, but is also widely distributed in forests at lower altitudes (Nebel & Philippi, 2001c). An obvious preference for lower temperatures is not conclusive for this species. *Dicranodontium denudatum* is a bryophyte, preferring areas with high precipitation and more acidic conditions (Nebel & Philippi, 2001a). *Pterigynandrum filiforme* prefers to grow on the bark and roots of trees in mountainous areas (Nebel & Philippi, 2001b). Our models predict a preference for lower temperatures for these species. Accordingly, for the bryophytes, favouring lower temperatures might be an indirect indicator of their preference for higher precipitation rates. In this case decreasing precipitation rates might be more critical for the species survival than increasing temperatures. Temperature and precipitation are strongly correlated (0,8) in most cases in our dataset, i.e. high altitudes have low temperatures and high precipitation amounts, and low altitudes have higher temperatures and lower precipitation amounts.

Generally, we have to mention that the modelled potential habitat suitability should not be taken as the recent distribution of the species (e.g. Schönfelder & Bresinsy, 1990; BIB, 2012) as known. Our models show only *potential* suitable habitats for species in beech forests and show where the species could occur across Bavaria with a high probability if (mixed) beech forests would be there. The response of the same plant species to changing temperatures might be different in other ecosystems or for the whole distribution area. *Maianthemum bifolium*, for example, is a widely distributed forest plant species in Bavaria (Schönfelder & Bresinsky, 1990; BIB, 2012) with no clear temperature preference (Ellenberg, 2001), but according to our models it is clearly adapted to cold habitats in beech forests.

A strong accordance between our models and temperature driven changes in beech forests in Bavaria might be given for the higher temperature preferring species *Juglans regia* and the cold-adapted *Senecio ovatus*. Both species in our study showed well performing GLMs, and in another study a strong correlation with winter temperature values (Jantsch et al., 2013). In that study *Juglans regia* increased significantly in frequency, and *Senecio ovatus* decreased significantly in the studied beech forests over the last decades.

Bavaria will be affected strongly by the temperature increase in the future. Consequently, we can expect strong shifting rates of the plant species. But the persistence of cold-adapted plant species under increasing temperatures as well as the ability of other plant taxa to spread into new areas (Thuiller et al., 2008) should also be considered.

Some populations might be better adapted to higher temperatures and can ensure the species' persistence in beech forests and some species can spread more easily into new areas. Extinction might occur faster than expansion of new species as observed in shifting rates (Malcolm et al., 2002), especially for herbaceous plants (Bossuyt et al., 1999), which are much slower than would be necessary for a successful migration under climate change (Skov & Svenning, 2004; Loarie et al., 2009). Our 1,8 °C scenario shows strong changes in suitable habitats of forests species in beech forests. Changes might even be stronger under a 3 °C scenario, which can be seen as more realistic for the end of the 21st century. In consequence, strong changes are highly probable.

But there are also indications that the effect of temperature increase on vegetation shift is more complex than thought and that factors like a reduced intraspecific competition due to a higher mortality, an improved phenotypical plasticity, deteriorated life conditions for pest or pathogen species and other factors can stabilize the species persistence under a changed climate scenario (Lloret et al., 2012).

In the future large areas will have temperature values (>9 °C) which are currently only found in small parts of Bavaria and some areas will reach even higher temperature values (>11 °C) which are not present at all nowadays. Therefore the models are truncated on the warm side with the present data, and it is hard to predict the species' response to this temperature range. Other new species might arrive in the beech forests within the next decades, but it is difficult to predict which ones will arrive, and which niches in beech forests they will occupy. Species which might spread into beech forests in the future could be those found today in the parts of Europe which already represent the future temperatures of Bavaria (Bergmann et al., 2010). Suitable habitats might be created or may increase for evergreen woody species like *Buxus sempervirens* L., *Daphne laureola* L., *Ilex aquifolium*, *Ruscus aculeatus* L., present today in beech and beech mixed forests in areas with mild winters and warm summers (Bergmeier & Dimopoulos, 2001; Willner, 2002; Dierschke & Bohn, 2004; Di Pietro & Fascetti, 2005; Tsiripidis et al., 2007). This is equally valid for other woody species like *Carpinus orientalis* Mill., *Castanea sativa* Mill., *Fraxinus ornus* L., *Ostrya carpinifolia* Scop., *Quercus cerris* L., *Quercus frainetto* Ten., *Quercus pubescens* Willd. and *Staphylea pinnata* L. (Bergmeier & Dimopoulos, 2001; Willner, 2002; Dierschke & Bohn, 2004; Di Pietro &

Fascetti, 2005; Tsiripidis et al., 2007; Marinšek et al., 2013), and for herb species like *Cruciata glabra* (L.) Ehrend., *Melittis melissophyllum* L. and *Tamus communis* L. (Bergmeier & Dimopoulos, 2001; Willner, 2002; Dierschke & Bohn, 2004; Di Pietro & Fascetti, 2005; Tsiripidis et al., 2007; Marinšek et al., 2013), which have their main distribution in thermophilous mixed beech and adjacent deciduous forests. *Castanea sativa* saplings were indeed already present on three of our warmest plots and an increase of *Ilex aquifolium* was determined in a beech forest in northwest Germany over the last 30 years (Huwer & Wittig, 2012).

Increasing temperatures will likely promote the cultivation of additional forest tree species in today's beech dominated forests. The higher temperature-adapted forest tree species *Acer campestre*, *Carpinus betulus*, *Juglans regia*, *Prunus avium*, *Quercus petraea* and *Sorbus torminalis* might be more mixed with beech in the future instead of the lower temperature-adapted tree species *Acer pseudoplatanus* and *Picea abies*.

The strong fragmentation of forests in central Europe forms a barrier for the migration of typical forest plant species, and extinction and poor colonization of new areas is the consequence (Honnay et al., 2002; Skov & Svenning, 2004). Nature conservation has developed concepts and practices concerning how and where the current characteristic species composition of the beech forests should be preserved (Natura 2000 sites, nature and forest reserves, national parks, biosphere reserves). Shifting ranges might pose nature conservation with new tasks: namely how to deal with climate change induced alterations in species composition (Milad et al., 2012). At the very least the process of changing species composition must be accepted as part of a temperature-induced process which cannot be stopped by altering management plans (Fischer, 2008).

Conclusions

The trend towards "thermophilization" in beech forests is still limited (Jantsch et al., 2013). The reason is that species distribution areas will not "move" step by step with increasing mean annual temperatures, but suddenly with events of very high temperatures and very strong drought periods, respectively. This means that it will take some time until species fill up the new areas now becoming favourable for them. Nevertheless, the study clearly shows in which parts of a certain region the distribution areas of species may expand or decrease in the future.

Forestry will be confronted with changes concerning the traditional cultivation of forest trees, for instance, increasing problems with *Picea abies*, but it may generally benefit because more tree species could profit in beech forests from increasing temperatures than those which will suffer adverse effects. Nature conservation has to develop new concepts on how to deal with "moving" species under global warming.

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