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Using ecological and life-history characteristics for projecting species' responses to climate change

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Abstract. Assessing the impact of climate change on range dynamics is difficult in the absence of large-extent distribution data. We developed a novel two-step approach as an instrument for biodiversity risk assessment. First, we established relationships between modelled loss of occupied grid cells ('range loss', $R^2=0.29$), or gain of currently unoccupied grid cells ('range gain', $R^2=0.30$), for 195 plant species with distributional data under the A1FI climate change scenario up to 2080, and ecological and life history traits (life form, leaf persistence, ecological strategy, pollen vector, Ellenberg indicator values and characteristics derived from species' ranges). Secondly, we used the resulting coefficients to predict climatic sensitivity for 688 plant species without spatially explicit distributional information. The models predicted range losses of $34\pm 20\%$ (mean \pm standard deviation) and range gains of $3\pm 4\%$. Specifically, measures of species' distribution, such as range size, were significantly related to both range loss and range gain. Other traits associated with range loss (e.g. life form, number of floristic zones) were not necessarily related to range gain (instead related to Ellenberg temperature indicator), indicating that two distinct sets of ecological processes govern range expansion and contraction. We found interaction effects between moisture indicator values and life form for range loss, and between moisture and temperature indicator values for range gain. The responses of species to climate change are complex and context dependent. Thus, our results highlight the importance of incorporating trait interactions in models to assess risks of climate change.

Keywords. climate change scenarios; species traits; Germany; life form; Ellenberg values, range loss; range gain; range size; strategy type

Introduction

Species distribution models (SDMs) have been successfully used to assess some potential consequences of climate change on plant distribution (e.g. Thuiller et al. 2005, Pompe et al. 2008). A wide range of correlative approaches is available (Thuiller et al. 2008, 2009), relating presence or presence/absence of species to different layers of environmental variables. Although these approaches have several limitations (e.g. Guisan and Theurillat 2000, Dormann et al. 2007, Guisan et al. 2007, Pöyry et al. 2008, Trivedi et al. 2008,

Thuiller et al. 2008, Dormann et al. 2012) they have been widely applied in biogeography and conservation biology. SDMs can be useful in obtaining information about environmental conditions that determine (or at least correlate with) species' distributions or co-occurring species (e.g. Schweiger et al. 2012, Hanspach et al. 2014). SDMs therefore have become an important component in assessing the risks for species arising from changing environmental conditions. Unfortunately, it is not possible to parameterize SDMs for most European plant species because of insuffi-

cient data. The Atlas Florae Europaea (AFE, Jalas et al. 1972 ff., Kurtto et al. 2004), the most comprehensive distribution data base for plants in Europe and the most widely used source for model calibration, currently contains only c. 20% of the European flora. For Germany this results in projections for only 845 species based on AFE distributions (cf. Pompe et al. 2008) from a total number of ca. 3600 plant species (Klotz et al. 2002).

In contrast, many national data bases give a more complete picture of plant distributions (e.g. FloraWeb¹ for Germany). However, models trained on data that do not cover the full distribution range of the species under study (e.g. Trivedi et al. 2008, Ashcroft et al. 2009) tend to underestimate the species' climatic niche and hence might overestimate the impact of climate change. Thus, a more realistic projection of species' distributions under changing environmental conditions requires model calibration with distribution data that cover preferably the (almost) complete environmental gradient inhabited by a species (Pompe et al. 2008, Barbet-Massin et al. 2010). However, for a comprehensive European risk assessment it would be desirable to provide an estimate of risk also for those species for which little or no spatial information is available. This is of special importance since families for which detailed distribution data are lacking (e.g. Poaceae, Fabaceae, Lamiaceae) include species of high ecological and economic importance.

In this paper, we advocate a tool that uses qualitative data to quantify species' risks arising from global change, which only depends on the availability of information on the full geographical and thus environmental gradient for a (small) subset of species.

Traits are widely used to study the response of plant and animal species to environmental factors, or change therein, and the impacts on community composition, ecosystem functions and ecosystem services (e.g. McKenzie et al. 2007, Küster et al. 2010, 2011, Douma et al. 2012). Analyses based on SDMs have shown an association of species' ecological and life-history charac-

teristics with modelled range shifts (Thuiller et al. 2005, Broenniman et al. 2006, Pöyry et al. 2008, Pearson et al. 2014). These studies indicate that species with small ranges, or those that can be related to specific (single) habitat, may therefore be more endangered than others under climate change. An important question is whether there are certain plant traits that make plants more resilient or more responsive to climate change, or whether species with specific range characteristics are more sensitive to climate change, i.e. show more or less either range loss or gain. For example, cold-adapted species in Central Europe have been shown to be potentially more threatened by increased temperatures at their current growth locations than other species (Thuiller et al. 2005).

However, relationships between climate and species' traits are often more complex and are due to interactions between different climatic elements and/or traits (e.g. Chapin et al. 1993, Broennimann et al. 2006). For example, range expansion can be attributed to general climate warming but also changes with different climate extremes and/or effective dispersal or high competitive ability of species. To cope with the challenge of identifying species' traits that determine the response to climate change, past studies (e.g. Behrens et al. 2009) used Ellenberg indicator values to make a qualitative risk assessment classifying sensitivity by ranges of indicators and expected positive or negative reactions by species.

We need to select representative as well as simple ecological and biological characteristics that are useful for assessing changes quantitatively and that are also ecologically meaningful (cf. Foden et al. 2013). Suitable ecological and biological characteristics for such an approach are those related to ecological performance, competitive ability, dispersal ability, stages in life history or persistence during a disturbance (e.g. Bernhardt-Römermann et al. 2008 and references therein, Wellstein et al. 2011):

- Strategy type, shoot phenology or life forms (see Raunkjær 1934, Grime et al. 1988, Klotz et al. 2002) are associated with adaptations to disturbance or seasonal changes in climatic parameters.

¹ <http://www.floraweb.de/>, last accessed 19/09/2104

- Range-related variables (e.g. geographic distribution), correlate with environmental conditions under climate change (Broennimann et al. 2006).
- Ellenberg indicator values such as temperature, continentality and moisture respond to abiotic conditions (Diekmann 2003).
- Response to climate or different environments is associated with variability in traits or suites of traits, e.g. life form, leaf traits, root traits (cf. Lavorel et al. 2007).

Certain changes in climate may therefore favour certain traits in a community or assemblage (Violle and Jiang 2009, Küster et al. 2011) or species that possess these traits (Lososová et al. 2008). Also, it is well known that life-form spectra differ largely among different types of climates and environments (see Wellstein et al. 2011). Thus one would expect various life forms, strategy types, dispersal strategies or leaf structures to be favoured under climate change. Changes in the composition of traits may affect ecosystem functioning (Küster et al. 2011). Overall, recent studies suggest that the responses of species cannot be predicted sufficiently well from a single plant trait; one must use several traits in combination (Barboni et al. 2004, Küster et al. 2008). This means that species with a single common trait characteristic may show different responses to climate change depending on other traits. In other words, it is probable that considering interactive effects between different traits can explain range changes due to climate change more precisely than main effects alone.

In this study, we address the question how the climate-change tolerance of plants relates to plant species' traits and how this relationship can be translated into predictions of risks for species in the absence of distributional data. Thus, we are interested in how ecological and life-history characteristics can be employed as correlates of performance under climate change projections (Thuiller et al. 2004) and as extension of data-limited species distribution models. Understanding of these patterns can be important in vulnerability assessments (Pearson et al. 2014). In comparison to the approach explored by Pearson and

colleagues (2014) our method does not require the availability of so much biogeographical information for the target species.

The goal of our study can be summarized as follows: (i) identification of empirical relationships among ecological and life-history characteristics and projected range loss and gain under climate change; and (ii) extrapolation to a large number of species (lacking large-scale distribution data), based on the empirical relationships derived from (i).

To this end, we relate two datasets, namely results from recent species distribution modelling, using one high-emission scenario for the late 21st century (Pompe et al. 2008, +3.8 °C) and data on eight biological and ecological characteristics of plant species in Central Europe (Ellenberg et al. 1991, Klotz et al. 2002).

Materials and methods

Species' distribution model

We used plant distribution data from the database of the Atlas Florae Europaeae maintained by the Botanical Museum, University of Helsinki at a resolution of 50 km × 50 km (Lahti and Lampinen 1999) for the 550 plant species that are currently recorded in Germany¹ (see Pompe et al. 2008 for a detailed description of the SDMs). We used generalized linear models (GLMs) within the R-based BIOMOD framework (Thuiller et al. 2009) to downscale and project species distribution to Germany (10' × 6', degree-minutes resolution grid, n=2995 grid cells). To this end we merged the environmental data from the 50km × 50km grid (Europe) with information available for Germany at the 10' × 6' resolution, including percentages of soil types and land-use classes (forest, grassland, cropland and urban landscape) and physiologically relevant climate variables (Table S1; Pompe et al. 2008, 2010). The models were trained on a random subset of the original data (70%) and evaluated on the remaining 30% using Cohen's kappa statistic (Thuiller et al. 2009, Kappa coefficients were 0.63 ± 0.13, (mean ± s.d.)). The fitted models were projected to the 10' × 6' grid using current (1961–90) and scenario conditions resulting from climate and land use change projections for the reference period 2051–80, assuming stability in

Table 1. Species' traits and distribution characteristics (cf. Klotz et al. 2002, Ellenberg et al. 1991) related to range changes in response to climate-change scenarios in Germany.

Traits	Description
Range size	Proportion occupied of the 2995 grid cells (10' longitude × 6' latitude, i.e. approx. 12km × 11km grid resolution) in Germany (www.floraweb.de)
Number of floristic zones	Number of floristic zones occupied globally by the species was used to characterize species' large-scale versatility across geographic range (Kühn and Klotz, pp. 227–239 in Klotz et al. 2002)
Number of habitats	Number of the main terrestrial habitats (n=10) occupied by a plant species was used to characterize species local-scale versatility. It is based on the system of Haeupler and Muer (2000). The species are assigned up to 10 main terrestrial habitats, ranging from woodlands T1, bush- and shrublands, clearings T2, tall herb communities, bushes, and turfs near or above treeline T3, dwarf scrub communities below alpine areas T4, boulder and scree habitats without wood species T5, poor grasslands T6, meadows and pastures T7, forbs communities, forest grassland ecotones, and tall herb slopes outside flood-plains T8, plant cultures (except meadows, pastures, forests) T9 and urban-industrial and other commercially influenced formations T10. (Haeupler, pp. 247–272 in Klotz et al. 2002)
Ellenberg indicator values	Indicators for temperature, soil reaction, continentality, moisture
Life-form	therophyte – summer annuals, which can only reproduce by means of generative diaspores; geophyte – resting buds are subterranean, often on storing organs protected within the soil; hemicryptophyte – resting buds are situated on herbaceous shoots close to the soil surface protected by foliage or dead leaves; chamaephyte – resting buds are situated on herbaceous or only slightly lignified shoots some centimetres above the soil surface protected by parts of the plant itself and/or by a snow cover (especially cushion plants); phanerophytes (resting buds are situated on (woody) shoots above the soil surface) including: nanophanerophyte – resting buds are situated on woody shoots, which form a stemless shoot system with strong basal ramification, i.e. trees and shrubs; hemiphanerophyte – resting buds are situated on woody, basally ramified shoots up to a height of ca. 50 cm (dwarf shrub) or on the only basally lignified parts of higher shoots, which do not become lignified in their upper parts but die down periodically; macrophanerophyte – resting buds are situated on woody shoots, the medial and apical ramifications of a woody trunk form a crown; two forms: species related to two life-forms were summarized into one category to explain potential versatility (Krumbiegel, pp. 93–118 in Klotz et al. 2002)
Ecological strategy	7 classes following Grime (1979): competitors, competitors/ruderals, competitors/stress-tolerators, competitors/stress-tolerators/ruderals, ruderals, stress-tolerators, stress-tolerators/ruderals (Klotz and Kühn, pp. 197–201 in Klotz et al. 2002).
Leaf persistence	4 classes: spring green, summer green, overwintering green, persistent green (Klotz and Kühn, pp. 119–126 in Klotz et al. 2002).
Pollen vector	Pollen vector or type of pollen transfer. Applicable types were 'wind', 'insects', 'selfing'; species with two categories were summarized into one separate category 'two' (i.e. selfing/wind, insect/selfing) to explain versatility (Durka, pp. 133–175 in Klotz et al. 2002).

soil types. We used a scenario that assumes a world geared to economic growth up to 2080 (GRowth Applied Strategy GRAS, for which the climate change scenario is derived from the IPCC SRES A1FI scenario, HadCM3 model run; Fronzek et al. 2012, Spangenberg et al. 2012). Data were provided by the EU-project ALARM: Assessing LARge-scale environmental Risks for biodiversity with tested Methods (Settele et al. 2005, Reginster et al. 2010, Settele et al. 2012). The simulated future annual mean temperature in Germany for 2051–80 was 3.8°C higher than in the reference period 1961–90 (Pompe et al. 2008). The probability surfaces for current and future projections were transformed into presence/absence maps using thresholds maximizing Cohen's Kappa. We calculated the numbers of 10' × 6' grid cells potentially lost ('range loss') and gained ('range gain') by each species, relative to the modelled current distribution, and converted these to percentages of the number of cells currently occupied. We did this using the scenario projections for Germany, applying two migration scenarios: unlimited dispersal for range gain and no dispersal for range loss (Pompe et al. 2008).

Explanatory variables

Explanatory variables covered data on life-history traits, ecological traits, Ellenberg indicator values (Ellenberg et al. 1991) and characteristics derived from the species' geographical distribution (i.e. number of occupied grid cells in Germany from FloraWeb, number of occupied floristic zones, number of occupied habitats for species in Germany). Information was derived from the BioFlor database (Klotz et al. 2002 and references therein) except for indicator values (Table 1; Ellenberg et al. 1991). Here, we used the term 'trait' for all the plant characteristics described in Table 1, although only life-history traits are traits in a strict sense as defined by Violle et al. (2007). Since complete trait information was available for only 195 species, we used these to model the relationship between traits and projected species' responses to climate change.

To explore whether species' traits in combi-

nation could explain range loss and range gain we used linear models on arcsine square root-transformed (cf. Crawley 2007) percentage range loss and log10-transformed percentages of observed grid cells in Germany ($n=2995^3$). We used the logarithm of the continuous explanatory variables to reduce the influence of outliers and to achieve linearization. We assessed collinearity and redundancy in the set of variables by performing hierarchical variable clustering using the complete linkage agglomeration method on squared Spearman's rank correlation coefficients as similarity measures (Harrell, 2001). Although selected variables were obviously interrelated, our analyses showed that none of them provided strongly redundant information (squared Spearman's rank correlation coefficient ≤ 0.37). We limited the interactions to two way-interactions, based on the rule of thumb that no more than $n/10$ variables should be included to avoid a modelling bias (Harrell, 2001). We applied backward selection, removing variables that were not statistically significant. Insignificant main effects were kept if interactions were significant. F-ratio statistics for the effects in the minimal adequate model were based on Type III sums of squares (Table 2) calculated using R software (version R2.13.0, R Development Core Team²). In the case of significant relationships for categorical variables, we performed post-hoc tests using the function `glht` (General Linear Hypotheses, package `multcomp`) and ran pair-wise multiple comparisons computing the contrast matrix (Bretz et al. 2010).

The resulting transfer functions (for range loss and range gain) were used to project sensitivity to climate change based on the selected variables for 688 species that occur in Germany but for which currently European distribution maps are not available within the Atlas Florae Europaeae. We validated the results by rebuilding the model 100 times, randomly excluding 30% of the 195 species, which were then subsequently used for evaluation. We calculated the mean (\pm s.d.) for range loss and range gain projections of those plant species that were selected for the models: (i) projections from SDMs ($n=195$), i.e.

² <http://www.R-project.org>, last accessed 19/09/2014

Table 2. Summary of the regression results (estimates and standard error) and analysis of covariance (see also Table S3) of the effects of species' characteristics for range loss and range gain under climate change scenarios in Germany for 195 selected species (minimum adequate model derived using error probability). Range loss: R^2 adjusted = 0.22, R^2 multiple = 0.29 ($p < 0.001$), (arcsin square-root transformation of response variable range loss); range gain: R^2 adjusted = 0.29, R^2 multiple = 0.30 ($p < 0.001$), (log10 transformation of response variable range gain). Empty cells: predictors are not selected for the minimal adequate model by backward selection ($p \leq 0.050$ (*), $p < 0.010$ (**), and $p < 0.001$ (***)).

	Range loss		Range Gain	
	Estimate (Std. Error)	F-value	Estimate (Std. Error)	F-value
Intercept	1.225 (0.423)*	8.393	-4.968 (2.219)*	5.013
Range size	-0.321 (0.095)***	11.358	-1.616 (0.192)***	66.576
Life form		2.642		
Geophytes	0.363 (0.297)			
Hemikryptophytes	-1.260 (0.706)			
Phanerophytes	0.225 (0.222)			
Therophytes	0.997 (0.300)**			
Two life forms	-0.286 (0.328)			
Number of floristic zones	-2.14 (0.755)**	8.057		
Ellenberg indicator value temperature			7.846 (2.842)**	7.622
Ellenberg indicator value moisture	0.031 (0.477)	0.004	8.158 (3.208)*	6.466
Ellenberg indicator value continentality	0.429 (0.182)*	5.578		
Ellenberg indicator value soil reaction	-0.584 (0.22)*	6.523		
Number of floristic zones × Ellenberg indicator value moisture	2.467 (1.092)*	5.107		
Life form × Ellenberg indicator value moisture		2.790		
Geophytes × moisture	-0.586 (0.467)			
Hemikryptophytes × moisture	1.704 (0.947)			
Phanerophytes × moisture	-0.368 (0.318)			
Therophytes × moisture	-1.367 (0.411)**			
Two life forms × moisture	0.911 (0.555)			
Ellenberg indicator temperature × Ellenberg indicator value moisture			-10.695 (4.163)*	6.601

calibration, (ii) predictions for the 195 species using the resulting transfer function, i.e. evaluation, (iii) projections for the 688 species using the transfer functions based on ecological and life-history traits. We calculated the coefficient of variation (cv, as ratio of standard deviation to the mean) of the different projections.

Results

Range loss

The minimal adequate trait-based model (TBM) for range loss (195 species, projection with no dispersal, Table 2, Table S3) showed significant negative relationships with the observed range ($p < 0.001$), the number of occupied floristic zones

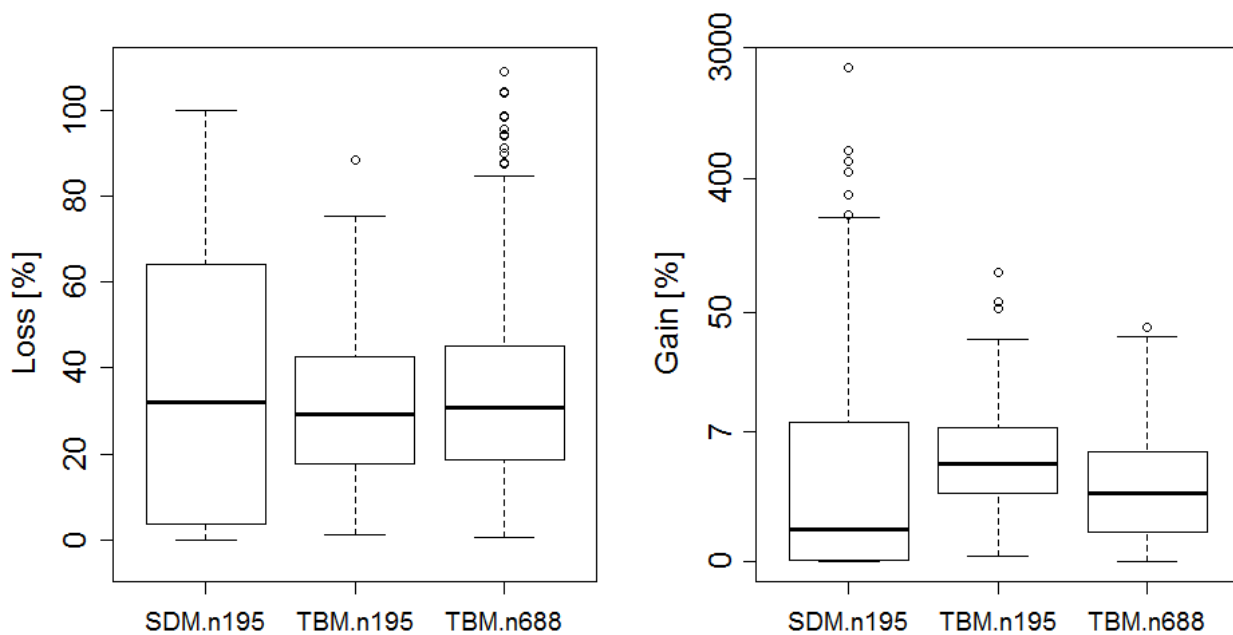


Figure 1. Modelled range loss (left) and range gain (right) under the unlimited migration assumption using species distribution models (SDM) for 195 species, extrapolating the trait-based model (TBM) for 195 species with European distribution and comprehensive trait data, and projection onto 688 European species for which European species' distribution information is not available. (Note: loss rates can exceed 100% in the TBMs).

($p=0.005$), and the Ellenberg indicator value for soil reaction ($p=0.012$). The Ellenberg indicator value for continentality ($p=0.019$) yielded a significant positive relationship. We found a significant interaction between the number of floristic zones and the Ellenberg moisture indicator value ($p=0.025$). Further, we found a significant relationship between life form (see Table 1 for the definition of life forms) and range loss ($p=0.025$). Therophytes (i.e. annuals) had a significantly lower rate of range loss (Fig. S1) than phanerophytes (i.e. trees) ($p=0.040$) and chamaephytes (i.e. cushion plants) ($p=0.026$). The interaction of the Ellenberg moisture value with life form was significantly ($p=0.019$) associated with range loss but the multiple comparison in post-hoc tests did not show significant differences between groups ($p>0.05$).

Range Gain

The minimal adequate TBM for range gain (195 species, projection with unlimited dispersal) showed significantly negative relations with observed range ($p<0.001$), and positive relations with the Ellenberg temperature indicator ($p=0.006$) and the Ellenberg moisture indicator

($p=0.012$). We found a significant interaction effect of the Ellenberg moisture indicator with the Ellenberg temperature indicator ($p=0.011$, Fig. S2).

Projections using ecological and life-history traits

The mean rate of range loss projected with TBMs for 688 species for which large-scale spatial information was not available was $34\pm 20\%$ ($cv=0.31$, $n=100$ cross-validations), while the projected mean rate of range gain was $3\pm 4\%$ ($cv=0.48$). The validation showed that TBM predictions were positively correlated with range loss ($\tau = 0.24$) and range gain ($\tau = 0.35$) projected with SDMs. TBM and SDM predictions were significantly correlated in 80% of the cross validation runs for range loss and in 100% of them for range gain.

Modelled species' sensitivity differed between projections from SDMs and projection based on TBM for the validation dataset ($n=195$, Fig. 1). We found significantly higher values for projections based on TBMs than on SDMs for range gain (Wilcoxon test, $p<0.01$). Range losses and gains showed a much larger variation based on SDMs compared with TBMs (cv : SDMs = 0.9, TBMs < 0.6 for range loss, SDMs=4.9, TBMs < 1.5 for range gain).

Discussion

Here, we present a novel approach to project species' responses to climate warming based on the characteristic relationship between their traits and climatic sensitivity. This method can help to assess potential distributional losses and gains in the absence of spatially explicit information on the distribution of a given species. Our results suggest that coarse-scale patterns of changes in species assemblages in Germany found in the previous analysis of Pompe et al. (2008, 2010) are underlain by specific patterns of species' traits.

As expected based on previous studies (Pompe et al. 2008, 2010), all current plant ranges undergo important changes under a high-emission scenario (+3.8 °C up to 2080). There are both beneficial and detrimental effects of climate warming. Prolonged vegetation period and lower risks of winter cold damage (e.g. frost) facilitate range expansion for species that are adapted to warm conditions (e.g. therophytes) or currently do not occur in Germany due to climatic limitations (Bergmann et al. 2010). Not surprisingly, we found that projected species' range changes were primarily related to warming. This is also supported by the results regarding Ellenberg indicator values. Thus, our results emphasize the effects of a rise in temperatures (temperature indicator value, lower loss rates for therophytes) on species' distributions, mostly via geographic range gain. Beyond that, species' traits were shown to be related to water availability under climate change by Küster et al. (2011), who found evidence of increasing proportions of species with sclero- and mesomorphic leaves under climate warming. We found interactions between moisture and other species characteristics (e.g. life form, temperature indicator values, number of floristic zones) to be significant in accounting for the expansion or contraction of ranges. One has to keep in mind that the species' moisture index is primarily characterized by soil moisture conditions and not classified by precipitation values (van der Veken et al. 2004, Ellenberg 1991). It is therefore not a physiological plant characteristic, but its use is helpful in large scale assessments. Our study empirically supports this because it indicates cor-

relation with other traits related to plant strategies. Therefore, the index of moisture can be seen as a stress-related factor. Interaction between moisture index and temperature indicator values changes the typical interpretation of projected range change. In simple linear regression analyses we found no significant relationship between temperature or moisture indicator value and range gain (Fig. S2). Effects of climate change therefore differ at different values of the key predictors.

Broennimann et al. (2006) highlighted the idiosyncratic response of species. In their study the life forms annuals, geophytes, trees, perennials, shrubs, grasses and succulents were projected to consistently suffer under climate change under several IPCC SRES scenarios until 2050—especially geophytes, because precipitation was considered to be a critical factor. In contrast, in our study, geophytes benefit from climate change and show a weak trend for higher median range gain than other life-forms (Table S2). This might be explained by the fact that their main growing period is in spring and thus they are not as strongly influenced by the summer droughts common in the climate scenario used (Pompe et al. 2010; supplementary material). We found a negative impact on species confined to more acid soil conditions. This result probably indicates an interaction with the spatial distribution pattern of soils in Germany. Currently, micro-site conditions on more alkaline substrates in Germany tend to be drier and warmer (on average). However, most of the adaptation by species in Germany to calcareous habitats is due to ecological drift (Ewald 2003) after the last glacial period and the species are therefore pre-adapted to more Mediterranean-type climates (cf. overbalance of calcicoles in Central Europe, Wohlgemuth 2003).

Potential reorganisation of ecological communities under climate change (Pompe et al. 2010) is projected to lead to changes in trait composition. Van der Veken et al. (2004) predicted that climate warming will result in a higher proportion of hemicryptophytes, scleromorphic and stress-tolerant species. This will impact ecological networks and processes (e.g. nutrient cycling, intra- and interspecific interactions above or below

ground). Such indirect effects will probably have a stronger impact on ecosystems than the direct effects of the changing climate (Gilman et al. 2010). However, they are difficult to predict. To our surprise, life form (Raunkiær 1934) was the only one of the eight life-history traits (genuine traits *sensu* Violle et al. 2007) that was significantly associated with range loss. The role of life-history traits in our study may be hidden because the projected climate change includes a shift towards novel climates in Germany (Bergmann et al. 2010). Scenarios emphasize a general north-east shift of climatic conditions from the south (Mediterranean regions) to the north of Europe (Ohlemüller et al. 2006, Bergmann et al. 2010). Our results show a significant main effect of the continentality index for range loss. Species composition under climate change will therefore largely depend on geographical reorganization and immigration of new species (Pompe et al. 2008). In theory, species with broader ecological niche breadth are likely to spread into new regions, leading to changes in local species composition (Pompe et al. 2010).

Explained variation in SDM projections by TBM results was about 30% in our models using ecological and biological traits to account for range loss and gain. Comparing the variability between modelled range loss and gain using SDMs showed much larger variation in these than TBMs. The level of uncertainty around the projections, resulting from the repeated modelling of TBMs after SDMs is not analyzed separately. Some apparent problems relate to basic principles of either species distribution models or our new approach. Potential errors relate to the data themselves, underlying assumptions and statistical constructions in SDMs and TBMs. Limitations in data (e.g. coarse resolution, lack of data, biases of Atlas Florae Europaeae relating to sampling history and intensity varies per country [see Kalwij et al. 2014]) as well as shortcomings related to species' distribution models (e.g. using presence-absence data) are well documented in the literature (Dormann 2007, Rocchini et al. 2011, Rodríguez-Castañeda et al. 2012). Range changes are not only the result of limited climatic niche space (as

inferred from a SDM), but also are caused by population dynamics, genetics and stochasticity (Thuiller et al. 2010, Dormann et al. 2012). Small-scale climatic variability, i.e. the role of microclimate in providing small refuges that can buffer the impact of climate change (Randin et al. 2009, Scherrer and Körner 2011), can hardly be considered in our approach. The extrapolation of risks must therefore be used with care. Methods to propagate different sources of uncertainty in frequentist models are to the best of our knowledge not yet developed (for Bayesian approaches, see e.g. Draper 1995, Cressie et al. 2009).

The first question we examined was how species' traits will help us to understand climate change impacts on plants. We tested the match between TBMs and SDMs obtained for one extreme future scenario and one statistical model. Errors that occur in SMDs are therefore passed on to the trait orientated approach. We discovered patterns related to species' traits. However there are potential pitfalls because we matched trait data to percentages of range loss and range gain under climate change, and not to abundances of species or populations. We did not address further correlations that are related to other traits and trait interaction because of limitation in data availability. In particular, range gain may largely depend on other ecological factors (e.g. filters for establishment, different migration rates) that we could not take into account, but our results indicate which traits are favoured and which processes are prone to facilitate species' immigration under changing conditions. The assessment of the immigration of species that currently do not occur in Germany (Pompe et al. 2010, Bergmann et al. 2010) may give further insights into the potential effects of species' characteristics.

Climatically induced stress will facilitate different pathways in different scenarios, and the improvement of models will require greater realism for different migration rates. To develop effective management strategies (for conservation, forestry, agriculture) it is hence necessary to adopt a more interdisciplinary approach comparing different methods.

We could show that multiple and interact-

ing aspects of species' biological and geographical characteristics are important in risk assessment (Fréville et al. 2007). When temperature increases it has different impacts on species that, on the one hand, share common traits (e.g. the same temperature indicator values) but, on the other hand, interact differently with other stressors (such as disturbance). Therefore, our results highlight the importance of trait interactions for characterizing species' responses to climate change (see also Pearson et al. 2014). In particular, relationships with range loss were complex in our study and considering only single predictors (e.g. single Ellenberg indicator values) might have led to misleading results (such as indicator values for temperature apparently being unimportant).

To improve the understanding of the relationship between climate change and species' traits it is necessary to analyse not only current niches of species but also niche shifts and intra-specific variability of species' traits (Violle and Jiang 2009, Hulme and Barret 2013). Thus our analyses can only be a first step that needs to be followed by more detailed analyses of, for example, species groups, such as native, ancient alien or recent alien species (cf. Küster et al. 2008, Poorter et al. 2014 and references therein), or among different regions due to within-trait heterogeneity or systematic changes across environmental gradients or life stages of a species (Cardillo et al. 2008, Violle and Jiang 2009). For instance, Küster et al. (2011) found that there are geographical differences in trait composition, which under climate change will change systematically. The recent progress in the development of trait databases (Kleyer et al. 2008, Lavorel et al. 2007, Kattge et al. 2011) will give the necessary support for conducting such analyses. The proposed method can potentially be applied to regions with scarce availability of biogeographical data. A concerted effort to determine a set of trait data for a substantial number of species would be the prerequisite for such an endeavor, as long as only relatively few species' distributions remain known.

Conclusion

Here, we present a new statistical method to ex-

plore the impact of climate change on plant species' ranges, on the basis of ecological characteristics and biological traits. To our knowledge, it is the largest assessment of this kind so far. One advantage of the approach is that it can be used without knowing the complete range distribution for all species. A measure of vulnerability to climate change, however, is needed for a subset of species (e.g. resulting from SDMs). We emphasize that its applicability is currently limited to regions with sufficient trait data availability (e.g. Europe, North America). The patterns we found suggest that there are general ecological processes that motivate further studies of predictive assessment of climate change impacts based on traits. We demonstrate that projections of species' vulnerability to climate change need to consider multiple traits and their interactions.

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Supplementary Materials

The following supplementary materials can be found online:

Table S1. Bioclimatic variables

Table S2. Estimates of range loss and range gain

Table S3. Analysis of covariance of the effects of species characteristics on range loss and range gain

Figure S1. Boxplot illustrating the range loss for different life forms under climate change scenario

Figure S2. Conditioning plot illustrating interactions

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