

# The Iberian Peninsula as a potential source for the plant species pool in Germany under projected climate change

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**Abstract** The application of niche-based modelling techniques to plant species has not been explored for the majority of taxa in Europe, primarily due to the lack of adequate distributional data. However, it is of crucial importance for conservation adaptation decisions to assess and quantify the likely pool of species capable of colonising a particular region under altered

future climate conditions. We here present a novel method that combines the species pool concept and information about shifts in analogous multidimensional climate space. This allows us to identify regions in Europe with a current climate which is similar to that projected for future time periods in Germany. We compared the extent and spatial location of climatically analogous European regions for three projected greenhouse gas emission scenarios in Germany for the time period 2071–2080 (+2.4°C, +3.3°C, +4.5°C average increase in mean annual temperature) to those of the recent past in Europe (1961–90). Across all three scenarios, European land areas which are characterised by climatic conditions analogue to those found in Germany decreased from 14% in 1961–1990 to ca. 10% in 2071–2080. All scenarios show disappearing current climate types in Germany, which can mainly be explained with a general northwards shift of climatically analogous regions. We estimated the size of the potential species pool of these analogous regions using floristic inventory data for the Iberian Peninsula as 2,354 plant species. The identified species pool in Germany indicates a change towards warmth and drought adapted southern species. About one-third of the species from the Iberian analogous regions are currently already present in Germany. Depending on the scenario used, 1,372 (+2.4°C average change of mean annual temperature), 1,399 (+3.3°C) and 1,444 (+4.5°C) species currently not found in Germany, occur in Iberian regions which are climatically analogous to German 2071–80 climate types. We believe

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that our study presents a useful approach to illustrate and quantify the potential size and spatial distribution of a pool of species potentially colonising new areas under changing climatic conditions.

**Keywords** Analogous climates · Climate scenarios · Distribution · Flora · Species pool theory

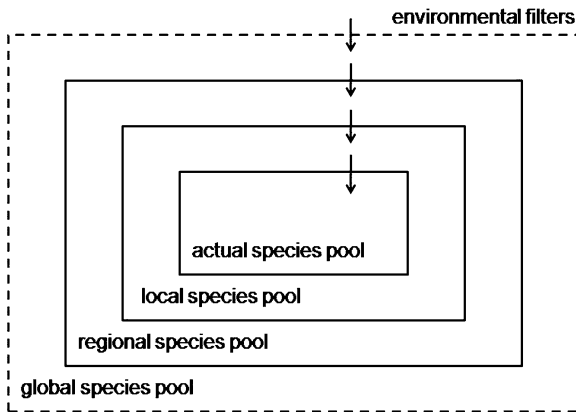
## Introduction

Species ranges and species assemblages have shifted in response to changing climatic conditions in the past (Huntley 1991; Pitelka 1997) and there are several well-documented examples for range shifts in response to recent climate change (Hughes 2000; Walther et al. 2002; Hickling et al. 2006). Recent results indicate that Europe is likely to experience major environmental changes and that climate conditions will shift northwards (Ohlemüller et al. 2006a; Metzger et al. 2008). For instance, climates similar to those of Mediterranean environments are projected to expand into Central Europe. A key risk for regional species occurrence is therefore disappearing current climate. The introduction of new species to new regions challenges further the assessment of the potential impacts. Global temperatures are projected to increase by ca. 2–4°C by 2100 (IPCC 2007). In combination with changes in other bioclimatic variables such as precipitation, this will affect regional bioclimatic conditions and is likely to lead to alterations of species ranges (e.g. Thuiller et al. 2005a; Pompe et al. 2008). Future climate change is therefore likely to promote the formation of novel species associations (Williams et al. 2007). The degree of climatic suitability in potentially new areas can be deduced from currently occupied environments of a species (e.g. through niche-based modelling approaches; Huntley et al. 2004; Pearson and Dawson 2003; Thuiller et al. 2009). The degree to which a species will be affected by climate change depends on the change of climatic suitability in current locations, its environmental tolerance (Ohlemüller et al. 2006b) and its dispersal capacity to new areas that may become climatically suitable. Species with a broader tolerance of climate conditions (i.e. species with a wide climatic niche breadth occurring under different climate types) may be less vulnerable to climate change (Thuiller et al. 2005b). Several studies have identified potential

range shifts for many European species, potentially leading to severe impacts on local species pools (e.g. Thuiller et al. 2005a; Araújo et al. 2006; Huntley et al. 2007; Pompe et al. 2008; Settele et al. 2008) and these predicted range shifts give an indication of the magnitude of potential future biological invasions (Walther et al. 2009).

There are some comprehensive national digital databases with a nearly complete coverage of plant distributions (e.g. FLORKART, FloraWeb URL: <http://www.floraweb.de/>, Germany; BSBI Distribution Maps, <http://www.bsbi.org.uk/html/atlas.html>, UK), however, the availability of data across large environmental gradients is still limited (Yesson et al. 2007). For the majority of species, it is therefore difficult to quantify distribution-climate relationships and to deduce the suitable climate space across the entire range of a species. The most comprehensive plant distribution data at the European continental scale are the *Atlas Florae Europaeae* (AFE; Jalas and Suominen 1972–1994; Jalas et al. 1996, 1999; Kurtto et al. 2004). It contains ca. 20% of the European flora. Modelling of possible future responses of plants as well as climate risk assessment are therefore restricted to this number of exemplar taxa (Thuiller et al. 2005a). For many other taxa (except terrestrial vertebrates and butterflies) data are even more limited. Risk assessments based on distribution models of individual species suffer from lack of appropriate data for many species and from limited general applicability. We here present an additional measure using the species pool concept that allows a more general climate change risk assessment which can help to identify the potential invading species pool of a region.

Under the assumption that each species has its own “ecological fingerprint”, the general form of the species pool in theory can be described by nested pools on different scales (Fig. 1). Species ranges are determined by large-scale climate conditions. Hence, the local flora (i.e. the flora at smaller scales) is usually presented as a specific list of plants distributed in a certain area (Mueller-Dombois and Ellenberg 1974 after Zobel 1997) and determined by the number of available species at the next larger scale (Fig. 1, Zobel 1992, 1997). Species adapted to conditions at the smaller scale are therefore a subsample of the larger-scale species pool. Climate change may therefore act as a filter, removing species that belong to a current local flora but lack the characteristics necessary in the future (e.g. climatic



**Fig. 1** The hierarchical species pool concept, modified after Zobel 1997. At each level, the species pool is a reduced subset of the level above due to environmental filters excluding species of the superordinate species pool

tolerance, Zobel 1997). Further filters such as dispersal, migration, competition and adaptation determine which species will actually succeed in establishing at new locations (Zobel 1997).

In this study, we investigate the extent to which the future German climate space is present in Europe under current climatic conditions and how this may result in the appearance of non-native species in Germany. To this end, we combine an analysis of analogous climate space with the species pool concept. Our first assumption is that those large-scale ecological properties such as climate explain which species occur where they do. Most current species distributions are the result of historical as well as current climatic conditions leading to spatiotemporal heterogeneity in distribution patterns (Zobel 1997; Huntley 1991), however, several studies have shown that a substantial proportion of the variation in species distributions can be explained by current climate alone (Thuiller et al. 2005a). Recent studies compared extent and distribution of analogous and non-analogous climates to quantify risks for European plant species (Ohlemüller et al. 2006a). We now apply this rationale to a comparison of projected climatic conditions in Germany (2071–80) with climatically analogous regions of the recent past in Europe (1961–90). Using this approach, the pool of species potentially able to establish in Germany in the future can be quantified by identifying current climatically analogous regions in Europe. We now focus on the Iberian Peninsula and its potential to act as a source region for new species arrivals into Germany under future climate change.

## Methods

### Identification of climatically analogous regions

Regions in Europe with current climatic conditions which are analogous to future conditions in Germany were identified using climate data from the recent past (1961–90) and one future decadal time slice (2071–2080). Current and potential future European climate was quantified on a 10' (arcminutes) grid from interpolated observed (Mitchell et al. 2004) and future simulated climate data using five biologically relevant variables that are widely used in bioclimatic studies (Woodward 1987; Thuiller et al. 2005a): mean annual temperature ( $^{\circ}\text{C}$ ), mean temperature of the coldest month ( $^{\circ}\text{C}$ ), growing degree days  $>5^{\circ}\text{C}$  ( $^{\circ}\text{C}$ ), annual precipitation (mm) and annual water deficit (mm). Future projections were based on three alternative scenarios (Spangenberg 2007), developed for the European project ALARM ([www.alarmproject.net](http://www.alarmproject.net), Settele et al. 2005): the moderate SEDG scenario (Sustainable Europe Development Goal, climate derived from IPCC SRES scenario B1), the intermediate BAMBU (Business As Might Be Usual, A2) and the severe GRAS (GRowth Applied Strategy, A1FI). The three scenarios are illustrations of possible futures, exploring the trends and interactions of different factors like climate, economic growth and political and administrative decisions, including those on biodiversity management (Spangenberg 2007). Looking at the climatic boundaries for the 1,865 grid cells in Germany selected in our analysis from the 10' grid, the average increases in annual mean temperature between reference and the three scenario periods were 2.4, 3.3 and 4.5 $^{\circ}\text{C}$  for SEDG, BAMBU and GRAS, respectively. Values for the temperature of the coldest month showed greater increase from 3.3, 4.4 $^{\circ}\text{C}$  up to 5.0 $^{\circ}\text{C}$  for scenarios. By 2080 annual precipitation increased by 163 mm (SEDG), 186 mm (BAMBU) and 181 mm (GRAS), whereby maximum values of precipitation showed increases of ca. 200 mm averaged across all grid cells.

In order to identify major climate types (i.e. clusters) within Germany, we grouped the 1,865 German 10' grid cells using agglomerative hierarchical cluster analysis of the standardised climate variables based on Euclidean distance and Ward's linkage method (Fovell 1997; Legendre and Legendre 1998). We opted for a six-cluster cut-off as this resulted in a meaningful level

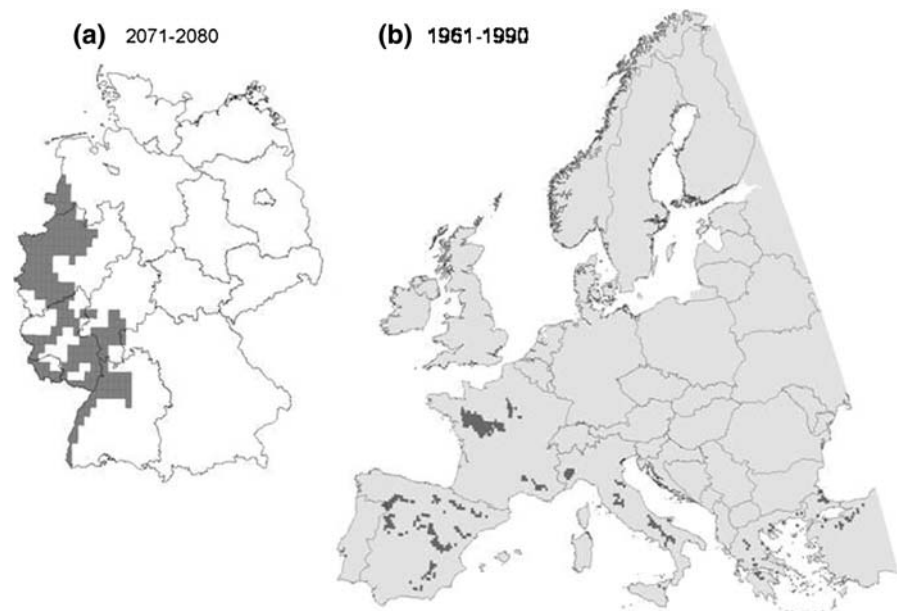
of detail in climatic variation of the German climate space and reflects the main biogeographical units (after Federal Agency for Nature Conservation, [www.bfn.de](http://www.bfn.de)). A separate cluster analysis was performed for each of the three future scenario climate datasets of the 2071–80 period. In each cluster, for each of the three scenarios we calculated the climatic boundaries (minimum and maximum value of the five climate variables). We then determined climatically analogous regions in Europe in 1961–90, by checking for each European grid cell whether the 1961–1990 climate conditions of all five variables were within the range of the minimum and maximum value of each climate variable for each cluster (see supplementary material, Table S1–S4 and Fig. S1a–d). If so, the 1961–1990 climate conditions of that grid cell were considered analogous to the conditions of a particular German cluster in 2071–2080 (see Fig. 2). For comparison, we did the same using the baseline climate (1961–1990) in Germany and identified the climatically analogous grid cells elsewhere in Europe using the range of the variables from the clusters in 1961–90 (Fig. 3). This is similar to a BIOCLIM approach in that the climatic limits of each cluster are defined by hard minimum/maximum boundaries (Nix 1986; Finch et al. 2006). In order to analyse the extent of climatically analogous regions for each European country, we computed the absolute and relative number of grid cells per country (see Table S5). Each grid cell could have more than one

future analogous climate cluster. We quantified the number of analogous grid cells that overlapped for each pair of climate types under SEDG, BAMBU and GRAS in Europe, and calculated the overlap of analogous regions between the three scenarios (see Table S6 and S7). All cluster analyses were performed in S-Plus 6.2, overlays of climate grid and country files were done in ArcGIS 9.1.

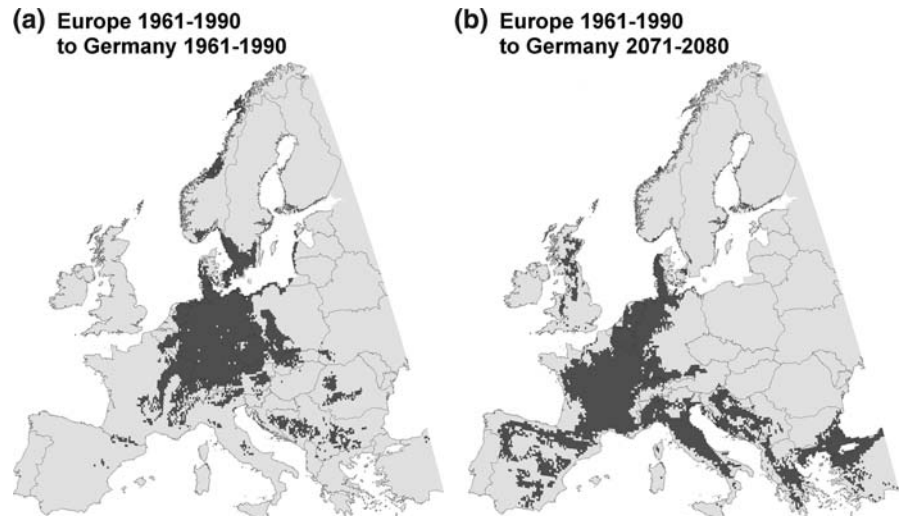
### The potential species pool

After having identified areas in Europe which currently have a climate analogous to at least one of the six future German climate types, we compiled data from regional European floristic data sources to quantify the species pools of these areas. After checking the available literature, we focussed our species pool approach on the Iberian Peninsula. The *Flora Iberica* (Castroviejo et al. 1986–2006) is probably the most recent, most complete and geographically best resolved flora of those regions climatically analogous to projected future German climate conditions. France has an incomplete floristic database, Italy provides nearly complete species distribution information but not at a spatial resolution suitable for this analysis. Countries from the Balkan Peninsula largely lack sufficient published species distribution information. We therefore used all published volumes I–VIII, X, XIV and XXI of the *Flora Iberica* to compile complete species

**Fig. 2** **a** An example of a German 2071–80 climate type (*cluster*) under the moderate SEDG scenario. **b** Areas in Europe with current (1961–90) climate conditions analogous to those found in the German cluster shown in **(a)**



**Fig. 3** Spatial extent of regions with current (1961–90) climate conditions which are analogous to those found in Germany in (a) the 1961–90 period and (b) the 2071–80 period for all the three scenarios combined (see methods for details)



lists for each of the Iberian provinces. The Iberian provinces were then overlaid with the climatically analogous areas on the 10' grid using ArcGIS 9.1 and only provinces containing more than four climatically analogous grid cells were used for further analyses (Fig. S2). Within these provinces species occurrences were collated and summarised in a database (including species' altitudinal limits) to identify the species pool of the future analogous climate regions. In order to refine our species pool, we used altitude as an additional environmental filter and combined information of the altitudinal limits of the plants from the *Flora Iberica* and the elevation information for the 10' grid cell (Haase et al. 2007). We only selected species for which the altitudinal range limit matched up with that of the climatically analogous grid cells. In order to quantify the species pools selected (i.e. for each scenario and cluster), we combined species information for the *Flora Iberica* and the German plant distribution database *FLORKART* (FloraWeb URL: <http://www.floraweb.de/>). Following the taxonomic checklist and list of synonyms given in Wisskirchen and Haeupler (1998), we counted species which are already present in Germany and/or which may have the potential to colonise Germany in the future based on the species pool of the climatically analogous areas. Ellenberg indicator values (Ellenberg et al. 1991) were used to test whether the selected species information provide ecologically plausible results. We used Mann–Whitney-*U*-tests to assess differences in Ellenberg values between the species pools under the three different scenarios and the species already

recorded in Germany in the *FLORKART* database for the following indicator values: moisture (F), temperature (T), continentality (K), soil reaction (R), light (L), fertility (N) and salinity (S). These values were only available for species currently occurring in Central Europe, i.e. not for those exclusively found on the Iberian Peninsula. In order to determine how many of the Iberian species are found in other parts of Europe, we combined information on species occurrence from our study with species distribution data of the *Atlas Florae Europaeae* (AFE, Jalas and Suominen 1972–1994; Jalas et al. 1996, 1999; Kurtto et al. 2004). Calculations and statistical analysis were done using the R software package (R Development Core Team 2006) and Sigma Stat 3.0.1.

## Results

### Climatically analogous regions

We identified six German climate types for each of the three future climate scenarios and the corresponding regions in Europe which currently have climatic conditions analogous to those of these climate types (Fig. 2, see also supplementary material). Under current conditions (reference period 1961–1990), Germany and some bordering regions were identified as having climatic conditions analogous to those of Germany in the period 1961–1990 (Fig. 3a, Table S5). There is a generally projected decrease of climatically analogous regions in Europe up to 2080 of ca. 14% in

the recent past to ca. 10% under the GRAS scenario (10% under SEDG and 11% under BAMBU). Between 64% (SEDG) and 94% (GRAS) of German grid cells under current climate conditions had no analogous grid cell in Germany under projected future climate conditions (Table 1; Fig. 3). Using projected future German climate types, climatically analogous regions were found at some distance and mainly in Central and South Europe such as the Iberian Peninsula and the Balkan region, the North of Greece and Turkey, Mediterranean maritime areas including North and Central Italy and the coastal region of France (Fig. 3b).

We quantified the number of analogous grid cells for current and scenario projections at the European level. The projected future climate of some regions (i.e. climate types) in Germany was currently more widespread in Europe than that of others. For instance, scenario SEDG climate type 2 has 1,129 analogous grid cells in Europe, whereas climate type 6 only has 68 analogous grid cells (Table 1, see also supplementary material). Largest climatically analogous regions were found in France (Table S5, >50% gain of climatically analogous grid cells under BAMBU scenario). Whilst the number of analogous grid cells increased from moderate SEDG to intermediate BAMBU to severe GRAS in Italy and Spain, we found decreasing numbers under GRAS in France (Table S5). The mean ( $\pm$  standard deviation) for the ratio of overlapping

analogous grid cells between climate types was  $4.9 \pm 6.0\%$  (SEDG),  $3.9 \pm 5.6\%$  (BAMBU) and  $6.0 \pm 10.5\%$  (GRAS), respectively, whereas 40% (SEDG), 47% (BAMBU) and 47% (GRAS) of the pairs of climate types did not show an overlap (Table S6). Nearly half of the identified grid cells that were analogous grid cells in Europe under the +2.4°C scenario (SEDG) also were analogous under the more severe scenarios BAMBU and GRAS (Table S7). The current climate of the Iberian Peninsula did not represent all conditions found in Germany in 2080. There was no analogous region (grid cell) anywhere on the Iberian Peninsula for two German climate types under the SEDG scenario, one type under BAMBU and two types under the GRAS scenario (Fig. 4). The mean ( $\pm$  standard deviation) for the number of identified analogous grid cells from all clusters was  $70 \pm 83$  (SEDG),  $80 \pm 57$  (BAMBU) to  $100 \pm 93$  (GRAS). Maximum values were obtained under BAMBU and SEDG with nearly 230 Iberian grid cells being climatically analogous to projected future German climate conditions (Table S5).

#### Extended species pool approach

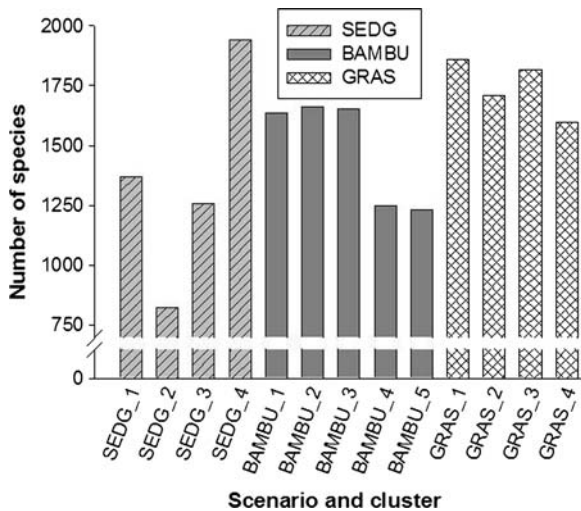
Overall, more than 2,700 plant species occurred in the identified Iberian analogous regions. After adding the altitudinal filter this number was reduced to 2,354 species. Among the three scenarios the number of species differed marginally between 2,227 plants in scenario SEDG, 2,250 plants in BAMBU and 2,297 plants in GRAS. The three species pools based on the three scenarios shared ca. 95% of the species. About one-third of these species were listed in the German distribution database *FLORKART*, namely 855 in SEDG, 851 in BAMBU and 853 in GRAS. From the plants already occurring in Germany, again ca. 95% were identical among the different species pools in the three scenarios.

The number of species occurring in the identified climate types differed markedly between scenarios from 824 (SEDG, cluster 2) to 1,941 (SEDG, cluster 4; Fig. 4). Under the scenarios BAMBU and GRAS, the range of species numbers differed less than that under SEDG (Fig. 4): SEDG  $1,348 \pm 460$  (mean  $\pm$  standard deviation), BAMBU  $1,486 \pm 223$  and GRAS  $1,745 \pm 119$ . Overall, including the altitude filter we found 1,372 species using SEDG, 1,399 species using BAMBU and 1,444 species using GRAS currently not

**Table 1** Number of European climatically analogous grid cells for the recent past (1961–90) and three alternative scenarios (2071–80, moderate SEDG, intermediate BAMBU, severe GRAS, see methods for details): the number of analogous grid cells per climate type, the absolute and relative number of analogous grid cells

Climate type	Current	SEDG	BAMBU	GRAS
1	1,313	873	978	660
2	828	1,129	1,784	1,279
3	1,233	629	428	575
4	1,078	400	155	530
5	607	277	280	133
6	371	68	122	93
N analogous	4,491	3,069	3,465	2,960
N analogous [%]	14.42	9.85	11.13	9.50
Analogous lack [%]	1.39	64.07	81.29	94.26

See Fig. S1 for the spatial distribution of each climate type for each of the three scenarios. Analogous lack [%]: relative number of grid cells which have no analogous region (grid cell) in Germany under the scenarios SEDG, BAMBU and GRAS



**Fig. 4** Number of species by analogous regions (applying altitude as filter) in the Iberian provinces for climate type 1 to 4 of scenarios SEDG (moderate) and GRAS (severe) and for climate type 1 to 5 for scenario BAMBU (intermediate). Note that cluster numbers refer to different climate types for each scenario (see supplementary material Fig. S1a). Climate types not shown here had no analogous grid cell in the Iberian Peninsula

observed in Germany (Table 2). Their relative numbers between the different climate types range from 48–61% (SEDG), 51–60% (BAMBU) and 53–61% (GRAS), respectively (Table 2). Overall, all climate types and scenarios shared 622 species, with 246 of these being currently not found in Germany.

Analyses of Ellenberg indicator values for moisture showed significantly smaller values for the species occurring in Germany as well as in Spain than for the exclusive FLORKART (i.e. Germany) species under all

**Table 2** Number of species (absolute, relative to the number of species N per scenario) selected by analogous regions (applying altitude filter, cf. Fig. 4) currently not observed in

Scenario	SEDG		BAMBU		GRAS	
	Absolute	Relative [%]	Absolute	Relative [%]	Absolute	Relative [%]
1	664	48	871	53	1,138	61
2	381	46	870	52	903	53
3	814	65	976	60	1,082	60
4	1,191	61	731	58	944	60
5	–	–	626	51	–	–
6	–	–	–	–	–	–
N	1,372		1,399		1,444	

Note that numbers refer to different climate types for each scenario (see supplementary material Fig. S1a). Climate types with no data have no analogous grid cell in areas for which species information for the Iberian Peninsula was available

scenarios (SEDG, BAMBU and GRAS, all  $P < 0.05$ ) (Fig. 5, Mann–Whitney test). This indicates that the species from the Iberian species pool prefer drier conditions than those from the pool already present in Germany. For the BAMBU ( $P = 0.045$ ) and the GRAS ( $P = 0.031$ ) scenario, temperature indicator values were significantly higher for the species that are common between *Flora Iberica* and FLORKART (Fig. 5). Under all scenarios, indicator values for light and continentality were significantly lower for identical species ( $P < 0.001$ ). Salinity, soil reaction and fertility indices showed no significant group differences. Approximately 7% (163 spp.) of plant species from identified Iberian species pools were listed in the *Atlas Florae Europaeae* (AFE). Most of these (more than two-thirds; data not shown) were also found in countries like France (80%), Italy (72%) or Portugal (66%).

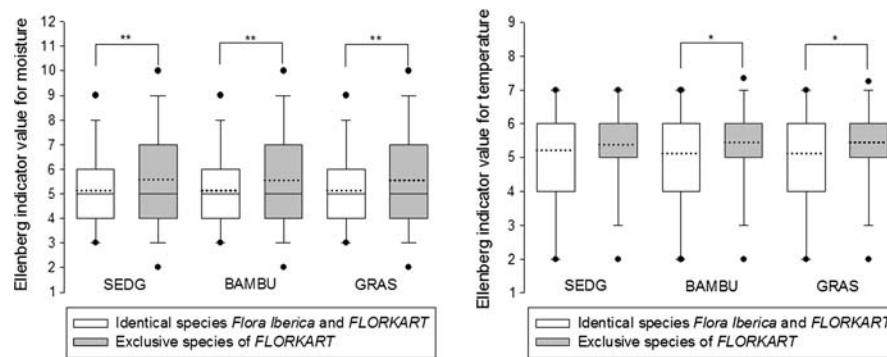
## Discussion

The aim of this study was to assess consequences of projected geographical shifts in climate on the size of the potential pool of species being able to establish in Germany under future climatic conditions. We believe that the approach presented here can be a valuable addition to niche-based modelling, in particular when detailed distribution data are not available.

### Climatically analogous regions

We identified areas in Europe with current climatic conditions which are analogous to those of the ranges

Germany (cf. [www.floraweb.de](http://www.floraweb.de)) for each climate type and the moderate SEDG, intermediate BAMBU and severe GRAS scenario



**Fig. 5** Comparison of Ellenberg indicator values between common species (i.e. Flora Iberica and FLORKART in Germany) (*white*) and exclusive species of FLORKART (*grey*) for the scenarios SEDG (moderate), BAMBU (intermediate) and GRAS (severe): moisture is significantly different (\*\*)

between the two selected species pools for all three scenarios (*left*), temperature is significantly different (\*) between the two selected species pools for the scenarios BAMBU and GRAS; *dotted line* mean; *solid line* median (Mann–Whitney test,  $P < 0.05$ )

of six projected climate types in Germany by 2080, using three emission scenarios (Figs. 2, 3, S1). Most of these analogous regions are located in southern and south-western Europe (e.g. France, Italy and Spain), indicating a general north-east shift in analogous climates across Europe up to 2080 (Ohlemüller et al. 2006a). Comparable climate conditions of Mediterranean regions are projected to shift northwards (Metzger et al. 2005). We observed a general trend of disappearing climate space from areas in Germany as well as in Europe overall (Table 1). Some climatic conditions widespread in the future in Germany may in fact not occur anywhere in Europe at present, indicating the creation of entirely novel climatic niches under future conditions (Williams et al. 2007). Range reductions of suitable or analogous climate space might have particularly detrimental consequences for rare species which generally occupy areas with rare climate conditions (Ohlemüller et al. 2008). Generally, higher temperatures in combination with expanding growing seasons will influence plant growth and we will therefore expect an expansion of plant species northwards (e. g. Walther et al. 2002). Therefore, we can expect not only changes in species diversity but also changes in species composition under changed climatic conditions (Thuiller et al. 2005a).

### Changing species pools in Germany

Most of the information on potential plant species' range shifts at the national level comes from studies of a

relatively small set of taxa (Pompe et al. 2008). Here, we illustrate the use of an extension of the species pool concept as an alternative or complementary technique to individual species bioclimatic modelling for assessing the extent of possible future species range shifts under climate change. In the absence of detailed range information for individual species, this approach provides a tool to infer the size and type of the potential future species pool from projected shifts in climate conditions. The identified climate-driven shifts can help to illustrate and quantify where local species composition is most likely to change and where resident species are likely to face the highest risk from colonising non-native species. Currently, mainly Atlantic-temperate as well as Euro-Siberian floristic elements occur in Germany (Walter and Straka 1970). In our study, the projected future German climate conditions were present in only a few and/or no climatically analogous regions for the baseline period 1961–90 in Germany, mainly to the South of Germany (Fig. 3, Table 1, Fig. S1). Conditions may become unsuitable for species at the location itself or dispersal to new areas of suitable climate might not be possible (Ohlemüller et al. 2006b). North-eastward shifts of climate conditions in Europe are therefore likely to pose a risk for the current species pool at any given location. Furthermore, these potential source regions harboured more than a thousand species which currently do not occur in Germany and have the potential to change the German species pool.

According to the changing climate, a positive effect on warmth and drought adapted species is expected,

which is confirmed by our analysis of the Ellenberg indicator values. This further corroborates currently observed climate trends in Germany where a decreasing number of frost days is observed (Badeck et al. 2008). Hence, the extension of growing season as well as fewer cold days may be related to fewer cold-related deaths of warmth-adapted species. However, to what extent potential changes in species composition of ecosystems in Germany are realised will depend on the distance to new and remaining areas of suitable climate for these species. Quantifying dispersal/migration distances is difficult and the time lag between an area becoming climatically suitable and an area actually being colonised depends on the seed dispersal and migratory potential (including the dynamics of dispersal vectors), as well as the successes of germination and establishment (Pitelka 1997). In our analysis, for instance, species such as the Mediterranean tree *Quercus coccifera* L. (kermes oak) are projected to find climatic conditions in Germany in the future which are analogous to those where the species is found today. However, it is unclear whether this species will be able to disperse and establish itself in Germany by 2080. Past migration rates of tree species are far below the rates required under projected climate change, e.g. less than 100 km/yr (Davis and Shaw 2001; McLachlan et al. 2005). Furthermore, many species of the Mediterranean are limited in their range not due to current climate but as a legacy of the last glacial maximum (Svenning and Skov 2007). These species were therefore unable to trace the past warming and it will be even more unlikely that they will be able to trace the projected warming.

Species from the Iberian Peninsula have to disperse north-east, crossing barriers (e.g. the Pyrenees) which could prevent them from extending their ranges and keeping up with shifting climate space. Identified analogous regions of the Iberian Peninsula are far away from Germany; however, it is likely that some of the species of the Iberian species pool also occur in neighbouring countries such as France. This in turn would substantially reduce the distance the species would have to cover to reach this analogous climate space.

### Limitations

Our approach has several limitations, which are mostly in common with usually used species distribution models based on correlative methods. Ecological

projections of future novel climates are inherently extrapolative (Williams and Jackson 2007). Our analysis indicates the possible direction of climate change, but does not estimate the time at which a particular species may establish in Germany. Establishment of plants also depends on land management practices and the degree of habitat loss or fragmentation (Higgins et al. 2003). Similar to statistical niche-based models (i.e. envelope modelling), we ignored competition, community effects, further alternative migration processes (i.e. time lags) of species (Pearson and Dawson 2003; Huntley et al. 2004) or species interactions (Schweiger et al. 2008). Also, our approach does not avoid the ‘lack of equilibrium’ problem, because, similar to niche-based models, it assumes that species occur at a location because they are at equilibrium with the climatic conditions of that location. Furthermore, although climate provides the baseline conditions within each species can colonise, reproduce and establish viable populations, other factors related to species dispersal, competition and soil requirements will limit the number of colonising species from climatically analogous regions. Classifying climate or environmentally homogeneous regions depend on decisions by researchers with regard to the methods, variables and scenarios used (Metzger et al. 2005). Climatically analogous regions are therefore no trimmed blueprints of future species pools. Hence, our climate types were made up of puzzle pieces that could be rearranged using other climate variables, alternative reference periods or clustering procedures (e.g. Fovell 1997). Since the information on climate types in Germany was based on averages across larger regions, it is impossible to project high-resolution spatially explicit species ranges. In such regions, the species may be restricted to a few locations. Further climatic variables or different temporal or spatial scales may influence the spatial pattern and the distribution of climatically analogous regions (Bunce et al. 2002). However, our analyses showed a high consistency in estimates of the size of the potential species pool between scenarios. Our species pool approach might overestimate the number of potential new members of the species pool in Germany because of the way our model estimates the species pool: grid cells have different geographic extents than the floristic provinces and it is possible that species listed as occurring in a selected province may occur only in cells not observed in the selected analogous regions.

Additionally, we can only estimate species which will remain in the current German and Iberian flora or become new members of the regional species pool in Germany. We did not analyse potential members from other European or non-European-floras.

## Conclusions

Climate change will trigger not only the extinction of species at the local level but also the immigration of species currently not native to an area. We have provided an analysis of the distribution and the size of the potential species pool which could find suitable climate space in Germany under future climatic conditions. We see our study as an analysis of the baseline climate-driven potential species pool; other factors such as soil conditions, dispersal and competition will filter out a proportion of species from this climate-driven species pool. Species are likely to respond individually to changing environmental conditions, however, these individual responses happen in relation to those of neighbouring individuals and therefore have the potential to lead to altered species assemblages. From a conservation perspective, a proportion of Iberian plant species has the potential to impact upon species compositions on a regional level in Central European areas under future climate conditions and our study demonstrates a methodology which might help to identify these species.

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