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Abbreviations: AWC = available water capacity; DTOL = tolerances to drought; EQ = Ellenberg's climate quotient; EQm = modified EQ; ESDB = European soil database; LogEQm = decimal logarithm from EQm; RSC = relative site constancy; SA = summer aridity; SDM = species distribution model; STOL = tolerances to shade; SNS = soil nutrient status

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Abstract

Based on macroecological data, we test the hypothesis whether European tree species of temperate and boreal distribution maintain their water and nutrient supply in the more arid southern margin of their distribution range by shifting to more fertile soils with higher water storage than in their humid core distribution range. To answer this question, we gathered a large dataset with more than 200,000 plots that we related to summer aridity (SA), derived from WorldClim data, as well as soil available water capacity (AWC) and soil nutrient status, derived from the European soil database. The soil compensatory effects on tree species distribution were tested through generalized additive models. The hypothesis of soil compensatory effects on tree species distribution under limiting aridity was supported in terms of statistical significance and plausibility. Compared to a bioclimatic baseline model, inclusion of soil variables systematically improved the models' goodness of fit. However, the relevance measured as the gain in predictive performance was small, with largest improvements for *P. sylvestris*, *Q. petraea* and *A. alba*. All studied species, except *P. sylvestris,* preferred high AWC under high SA. For *F. sylvatica*, *P. abies* and *Q. robur*, the compensatory effect of soil AWC under high SA was even more pronounced on acidic soils. Soil compensatory effects might have decisive implications for tree species redistribution and forest management strategies under anthropogenic climate change. Therefore, soil compensatory effects deserve more intensive investigation, ideally, in studies combining different spatial scales to reduce the uncertainty associated with the precision of soil information.

Introduction

Contemporary forest management planning increasingly relies on projections from tree species distribution models (SDMs) under future climate conditions (Attorre et al., 2011; Falk and Mellert, 2011; Hlásny et al., 2014; Hanewinkel et al., 2014; Mellert et al., 2015; Zimmermann et al. 2013). SDMs (Guisan and Zimmermann 2000) usually predict the probability of species occurrence or abundance. However, to avoid misspecification (e.g. due to model extrapolations), SDMs should not only be calibrated across the entire species range to ensure that climatic limits are properly covered by the data (Mellert et al., 2011, Beauregard and de Blois 2014), but tree SDMs should also consider soil properties (Thuiller, 2013; Diekmann et al., 2015). As soil data at the location of species occurrence are not available at the continental scale of our study, we tested soil effects in SDMs based on geodata (Panagos et al., 2012).

Soil is a key compartment for forest productivity (Cajander, 1949; Barnes et al., 1982; Bailey 1987). Both water and nutrient availability in soils matter for tree growth (e.g. Mellert and Ewald 2014) and may exert compensatory effects under limiting climatic conditions, especially at the warm and dry edge of their distribution. Yet soil variables are still rarely used in tree SDMs (but see Bertrand et al., 2012; Brus et al. 2011; Coudun et al., 2006; Piedallu et al., 2013; Dolos et al., 2015; Piedallu et al., 2016) and the few studies accounting for soil conditions in SDMs or niche models for trees have all been limited in their spatial extents to countries (Leuschner et al. 2009, Piedallu et al., 2016) or a single biogeographic region(e.g. Dullinger et al. 2012, Nieto-Lugilde et al., 2015). Hitherto, the use of soil variables in tree SDMs of continental extent has been hindered by the lack of soil data at continental to global scales (Ewald and Hédl, 2014). Previous SDMs for plants relied on qualitative soil data (e.g. soil type, Brus et al., 2011; Dolos et al., 2015) as indirect environmental factors in the sense of Austin (1980) or considered only topsoil properties (e.g. Dubuis et al., 2013) which are less relevant for deeper rooting trees than for herbs (Beauregard and Bois, 2014). Therefore, SDMs for tree species should use information from the entire soil profile.

In a temperate and (sub)mediterranean climate available water capacity (AWC) is an important component of the soil water supply (Blume et al., 2015; Latron et al. 2009). Most importantly, AWC is a crucial buffer that allows trees to survive dry periods (Bréda et al., 2006). This is especially relevant at the rear edge of their distribution. Soil nutrient status (SNS) is an important proxy for nutrient availability (Binkley and Vitousek, 1989). Both factors were mentioned in the formulation of the “relative site constancy” (RSC) hypothesis by Walter (1973). The RSC hypothesis asserts that many plants originating from relatively humid climates prefer moister soils and/or humid microclimates under dryer macroclimatic conditions. Accordingly, higher AWC in the soils should compensate for a more arid macroclimate while higher soil nutrient availability in the soils is expected to improve water use efficiency (e.g. Bradbury and Malcolm, 1977). Thus, the RSC hypothesis predicts a shift of the probability of occurrence of temperate trees towards soils with high AWC under high summer aridity (SA). We further assume that this preference for high AWC should be more pronounced on oligotrophic soils, where more water has to be transpired to transport the same amount of nutrients.

The RSC hypothesis implies that sustainable forest management planning cannot only rely on regional data (or local expert knowledge) but must also include insights from broad scale SDMs that incorporate climate and soil information from the entire species range, including the margins.

The central aim of our study is to test whether temperate trees maintain their water and nutrient supply at the arid southern margin of their distribution range by shifting to more fertile soils with higher water storage. If this soil compensation is effective at the rear edge, it should be evident even based on coarse-gridded coarse-scale data. In testing this hypothesis, we compare statistical species responses with expert knowledge (Ellenberg 1988; Niinemets and Valladares, 2006).

Material and Methods

To test the macroecological question of soil compensatory effects at the drier climatic conditions at the rear edge, we combine a large dataset containing more than 270,000 vegetation plots from Central and Southern Europe with ca. 210,000 presence-absence records of temperate species with bioclimatic and edaphic variables derived from WorldClim (Hijmans et al., 2005) and the European Soil Database (ESDB, Panagos et al., 2012).

Target species

The study focuses on five temperate tree species of economic interest, most of them abundant and widespread in Europe: silver fir (*Abies alba* Mill.); European beech (*Fagus sylvatica* L.); Norway spruce (*Picae abies* (L.) H. Karst.); Scots pine (*Pinus sylvestris* L.); and sessile oak (*Quercus petraea* (Mattuschka) Liebl.) (*syn. Q. humilis*).

Species optima and tolerances to drought (DTOL) and shade (STOL) as well as the nutrient requirements, especially regarding base cation availability are summarized in Table 1. All five species tolerate a wide range of soil conditions from acidic to basic soils (physiological amplitude corresponding to the fundamental niche), while exhibiting narrower and more differentiated requirements in the field (ecological amplitude corresponding to the realized niche, Ellenberg 1988, and descriptions below). STOL is an important trait conveying competitive power (Niinemets and Valladares, 2006), which is negatively correlated to DTOL (Tab. 1). The supplementary material (p. 1) contains more detailed descriptions of species ecology.

Table 1: *Species traits*

Tree distribution data

To represent a gradient from humid to xeric macroclimatic conditions, we collected vegetation plots from Central to Southern Europe (Fig. 1). Cold range margins were represented by including continental ICP Forests data (Fischer et al. 2010) extending to Northern Europe. The resulting sample represents a gradient from subboreal and cold temperate to warm temperate and (sub)mediterranean climates (Table 2). Due to gaps in soil data, especially in Turkey, large areas in South-Eastern Europe could not be included in the analyses. In our analysis it is crucial to distinguish between presence-absence and presence-only data as several data sources (e.g. the European Phenological Database) did not report absence. While frequency distributions (Fig. 2) were extracted from a combination of presence-only (Fig. 1a) and presence-absence data, statistical modeling was solely based on presence-absence data reporting true absences (Fig. 1b). Maps showing an overview about the observed probability of occurrence of the five species in Europe can be found in the supplementary material (Fig. S1-S5).

Figure 1: *Plot density in Central and Southern Europe*

Table 2: *Data overview – Number of plots by countries*

Climate data

We used long-term aggregated climate data (1950-2000) on precipitation and mean temperature from the WorldClim data portal (Hijmans et al., 2005) providing climatic grids at 30 arc-seconds (~1 km) resolution (in WGS 1984 coordinate system). Similar to Rasztovits (2012), we computed a modified Ellenberg climate quotient (EQ) to represent summer aridity (SA). EQ was originally defined as the ratio of July temperature (in °C) to annual precipitation (in mm) multiplied by 1000. Despite its simplicity, EQ is a good proxy for climatic drought (Fang and Lechovicz, 2006; Czúcz et al., 2011; Mátyás et al., 2010; Stojanovic et al. 2013) with equal explanatory power in SDMs (Mellert et al., 2016) compared to climatic water balance (cf. Piedallu et al. 2013). For focusing this index on the most limiting summer period (Bréda et al. 2006), we slightly modified the index (EQm) by using the ratio of mean temperature during the warmest quarter (BIO10) to precipitation during the warmest quarter (BIO18) (http://worldclim.org/bioclim). As very low summer precipitation in some regions leads to large numbers, we used the logarithm (LogEQm) in our analyses.

Within the range of presences of each species LogEQm values were categorized into three different summer ardity levels (SA1-3) by using the 1st and 9th deciles, as done by Alonso-Ponce et al. (2010). The range below the 1st decile represents the humid margin, the interdecile between the 1st and 9th deciles characterizes intermediate or mesic SA conditions (SA2), and the range above the 9th decile represents the most xeric conditions under which the focal species occurs (cf. the xeric margin, SA3) (Fig. 2). This stratification allows for testing and visualizing possible compensatory soil effects by modeling the response of the species along soil gradients under different climatic conditions (see Leuschner et al. 2009 for a similar approach). SA3 values of the study species were highly correlated (Spearman’s r = 0.9, p < 0.05) to their drought tolerance (DTOL, Table 1).

Figure 2: *Boxplot for LogEQm*

Soil data

Soil properties were derived from the European soil database (ESDB, Panagos et al. 2012). Available soil water capacity (AWC, derived according to Hiederer, 2013) was downloaded from the ESDB website (http://eusoils.jrc.ec.europa.eu/content/european-soil-database-derived-data). Both maps are at a scale of 1:1,000,000. The qualitative map of soil types (soil mapping units, SMU) is available as vector data, while AWC data is available as raster data with 1 km resolution. For explanatory modelling (see below), AWC was stratified into bins of 5 mm width across the range of AWC values (40-60 mm) for which plot density was high (> 15,000 plots), and into bins of 20 mm width across the range of AWC values for which plot density was lower, resulting in a total of 8 bins (<20, 20-40, 40-45, 45-50, 50-55, 55-60, 60-80, >80 mm).

Soil nutrient status (SNS) variable was defined as an ordinal variable with 6 levels characterizing the availability of macro- and micro nutrients in the entire soil profile (Table 3) along a gradient from strongly acidic to calcareous or alkaline soils. Due to acidification and/or substrate stratification chemical properties exhibit characteristic vertical gradients in soil profiles (Kölling et al., 1996), resulting in corresponding vertical profiles of nutrient supply (Blume et al., 2016). The soil types derived from the ESDB (Table T1 in the supplementary material) were ordered based on typical chemical properties (Table 3). For soil types with high chemical variation (e.g. Cambisols) parent material and physical properties of the ESDB soil mapping unit were used as auxiliary criteria. In the first step we grouped strongly acidic soils with free aluminium in the soil solution (i), intermediate, moderately acidic soil (ii) and neutral to basic soils with free carbonate in the soil solution (iii). The nutrient supply is unbalanced at the opposite positions of acidity gradient (i and iii) and tends to be optimal on intermediate soils (ii). Each of these three groups was further divided into two subclasses (1+2, 5+6), in order to differentiate weakly and strongly unbalanced nutrient supply, or in the case of the moderately acidic soils, to distinguish between soil with a higher (4) or lower (3) nutrient release rate through weathering. The availability of phosphorous (P) and most trace elements is optimal within the intermediate classes (3+4). Thus, soils with intermediate SNS often combine low base saturation in the topsoil with high base saturation in the subsoil (e.g. most Luvisols), which usually provides a balanced nutrient supply for optimal tree growth (Mellert and Göttlein, 2013).

***Table 3:** Classification of soil nutrient status*

Data aggregation

To avoid pseudoreplication and spatial autocorrelation of samples (Kühn, 2007), we based our analysis on data aggregated in environmental space. Instead of considering each vegetation plot as an independent observation contributing one degree of freedom per record, we averaged data based on the classes (bins) for SA, AWC and SNS as described above. By doing so, replicated plot observations in geographic space occurring under similar environmental conditions are converted to binary counts in a matrix cell defined by classes of environmental conditions. In this way we can model the probability of occurrence in a structured space of environmental parameters without inflating the degrees of freedom by pseudoreplicates in geographic space (cf. Austin, 1990). The resulting bins were only considered with a minimum number of 20 plots. The stratification leads to a considerable reduction of sample size and degrees of freedom (number of plots ~ 213,900; number of bins 8 (AWC) x 6 (SNS) x 3 (SA) total 144 less bins with no observations results in a N between 105 for P. abies and N = 115 for P. sylvestris), but eliminates the risk of type I error (falsely rejecting the null hypothesis of no effect) (Kühn, 2007).

Statistical modelling

All statistical analyses were computed using the free statistical software R (R Core Team, 2015). Besides using the packages “mgcv” and “PresencesAbsence” (Freeman and Moisen, 2008), we also used the “raster” package for handling gridded data (Hijmans and Etten, 2014).

We tested the relative site constancy (RSC) hypothesis within a gradient analytic perspective on SDMs (Halvorsen et al., 2012). The probability of species occurrence (P_{occ}) based on presence-absence data (target variable) was modeled based on the soil variables (AWC and SNS) at the three summer aridity (SA) levels. The response to soil factors at different SA levels was examined by applying spline functions with constrained complexity. Therefore, the degrees of freedom (parameter k in the gam() function from the “mgcv” package in R (R core team 2015, Wood, 2006, 2017)) was restricted to a maximum of four (cf. Mellert et al., 2011) to obtain reasonable and smooth response curves of P_{occ} along soil gradients, which can be linear, unimodal, or take an u-shaped or sigmoid/saturated form.

We used GAM as implemented in R (R core team 2015, Wood, 2006, 2017). The “mgcv” algorithm follows the law of parsimony with smoothness selection by the generalized cross validation (GCV) (gam-function arguments: method="GCV.Cp, select=TRUE") criterion resulting in the simplest significant relationship (Wood, 2006, 2017). The overall formula for modeling P_{occ} of each species is as follows:

$$\text{logit}(P_{occ}) = \beta_0 + \beta_1{*}SA1 + \beta_2{*}SA3 + f(AWC){*}SA1 + f(AWC){*}SA2 + f(AWC){*}SA3 + f(SNS){*}SA1 + f(SNS){*}SA2 + f(SNS){*}SA3$$

(Equation 1)

Consequently, the model estimates are composed of six smooth functions and three linear parameters β_0– β_2, where β_0 is the intercept value, and SA2 (medium aridity) is the reference category.

Model adequacy was evaluated using the Akaike information criterion (AIC) and the GCV criterion. GCV was also used for GAM calibration within the “mgcv” algorithm. Golub et al. (1979) introduced GCV as a variant of leave-one-out cross validation. As with AIC, lower values of the GCV score indicate better explanatory power and its values are not linearly related to the proportion of explained variance. Predictive accuracy was evaluated by the area under the curve (AUC) statistic, which is a standard criterion to characterize the fit of binary SDMs (Franklin, 2010) and the true skill statistic (TSS), another criterion that is gaining acceptance in SDMs (Barbet-Massin et al. 2012). TSS ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al. 2006). Both criteria measure for the ability of a model to classify a species correctly as present or absent in a given data set. While AUC is threshold-independent, TSS relies on a threshold of occurrence (Peterson et al. 2011). We used the prevalence of the species as a threshold as this is a simple and meaningful baseline method (Liu et al. 2005).

As an additional aspect to hypothesis testing, the relevance of soil effects was assessed by comparing the performance of the full model (Equ. 1) to the reference or baseline model only including summer ariditiy (SA). This validation was carried out based on a resampling of the binned data. In a leave-one-out procedure, one bin was left out in each iteration. So the number of iterations equals the number of bins (e.g. 115 for P. sylvestris). AIC and GCV of all resulting models were stored for model validation. The predictive performance (AUC and TSS) was computed using the “PresencesAbsence” package in R (R Core Team, 2015) based on the original (unbinned) data set split into the same portions as the binned data set (e.g. 1/115 for P. sylvestris). Differences in validation criteria between the full and the baseline model were tested by a T-Test.

Although residuals of binary models contain very little information useful for model checking (Wood 2017), we were able to check residuals of our models as they are based on grouped data. These checks generally showed no hints for a serious violation of modelling assumptions.

Results

Modeling results

The result of modeling is shown in the mosaic plot in Fig. 3, where species define rows and summer aridity levels (SA1-SA3) columns. In each single graph, the effect of the soil physical (AWC, x-axis) and chemical gradients (SNS, y-axis) on the probability of occurrence (P_{occ}, z-axis) at a specific summer aridity level is shown as response surface. Generally, the level of P_{occ} was higher at intermediate summer aridity (SA2, reference category) compared sites with a higher summer aridity (SA3). However, *A. alba*, *P. abies* and *F. sylvatica*, as typical species of mixed mountain forests, showed similar P_{occ} under humid (SA1) as under intermediate summer aridity (SA2). Accordingly, P_{occ} of *A. alba* and *F. sylvatica* was not significantly different under both conditions, while P_{occ} of the boreal *P. abies* was even higher ($p<0.05$) under humid conditions (SA1) compared to intermediate aridity (SA2). As a result, the overall effects of the three SA levels on species occurrence were significant ($p < 0.05$) in 13 of 15 cases.

The soil effects on P_{occ} can be recognized as the modification of the general level of P_{occ} depending on the soil gradients along the x-axis (AWC) and y-axis (SNS) in Fig. 3, where deviations from a flat surface indicate soil effects. For instance the P_{occ} level of *P. sylvestris* was not significantly affected by soil nutrient status at humid sites (SA1). Generally, under humid climatic conditions (SA1) soil effects were most variable, significant for *A. alba, F. sylvatica* and *Q. petraea*, only partially for *P. abies* (AWS) and generally insignificant for *P. sylvestris*.

In contrast, soil compensation effects at high summer aridity levels (SA3, right column) were significant ($p < 0.05$) for all species except the nutrient effect (SNS) on *P. sylvestris*. Similarly, soil effects at mesic sites (SA2) were all significant except for AWC on *P. abies.*

For all studied tree species except *Q. petraea*, the response surfaces took quite different shapes depending on the level of SA (Fig. 3). Under mesic conditions (SA2), soil-related response surfaces were unimodal (*Q. petraea*), plateau- (*P. abies*) and or u-shaped (*A. alba*, *P. sylvestris*). *F. sylvatica* peaked at intermediate AWC and was invariant to SNS. Response surfaces under mesic conditions (SA2) corresponded to assumed ecological preferences (Table 1) of *F. sylvatica*, *P. abies* and *Q. petraea*, but not of *P. sylvestris* and *A. alba*. In accordance with expert knowledge (Table 1), *P. abies* and *F. sylvatica* were quite invariant to SNS at intermediate climatic conditions. In contrast, at the xeric margin (SA3), responses of all three drought intolerant species clearly supported a compensatory effect of AWC. In addition, *P. abies* preferred acidic sites with high water storage and avoided calcareous sites at its xeric margin (SA3).

The drought tolerant tree species, *P. sylvestris* and *Q. petraea*, showed lower P_{occ} under low summer aridity (SA1) compared to the intermediate aridity level (SA2). Under mesic conditions (SA2), *P. sylvestris* occurred most frequently under extreme soils conditions (low and high AWC, low and high SNS). In contrast, at the xeric margin (SA3), its optimum was shifted towards intermediate AWC. *Quercus petraea* was the only species that showed consistent preference for more acidic soils by avoiding calcareous sites with high AWC at all aridity levels, however, most pronounced at SA3.

Figure 3: *Species responses at different SA levels*

Accuracy of the full models (Equ. 1) was fair to good according to the AUC classification of Swets (1988) (Table 4). Compared to the purely bioclimatic baseline model inclusion of soil parameters significantly improved the explanatory power (AIC and GCV score) and predictive accuracy (AUC and TSS score) of all five studied species ($p < 0.05$). Relative improvements in model quality criteria (%, AIC, GCV, TSS, AUC) are as follows: *Abies alba* (40.6, 30.0, 1.2, 5.0); *Fagus sylvatica* (21.9, 15.9, 3.2, 3.9); *Picea abies* (15.4, 11.3, 0.3, 2.6) *Pinus sylvestris* (47.8, 43.6, 16.3, 9.9); and *Quercus petraea* (36.8, 26.8, 6.7, 5.7).

Table 4: *Model evaluation*

Discussion

We found that all studied species except *P. sylvestris* prefer high soil water storage (AWC) under xeric conditions (SA3) (Fig. 3), which suggests a compensatory effect of soil under limiting climatic conditions at the southern margin of temperate tree species distribution, thus supporting the relative site constancy (RSC) hypothesis (Walther, 1973). We are not aware of another macroecological study reporting soil compensatory effects for tree species distribution under limiting climatic aridity at the European scale. These findings might have important implications for expected range shifts of tree species under anthropogenic climate change, including potential lagging effects (cf. extinction lags) (Lenoir and Svenning, 2015) at the trailing edge.

However, the generality of compensatory soil effects is still not entirely clear. Descriptive statistics based on all observed presences showed only few extreme occurrences indicating that high soil water storage allows species to effectively extend their distribution area in arid climates (Fig. 2). This finding is supported by observations from Lopez-Senespleda and Montero (2015), who used a subsample of the Spanish NFI data for which water-holding capacity was estimated.

Further, a major uncertainty of our study is the influence of former management interventions on species distribution patterns. As there is no way of reconstructing those interventions at the scale of our study, effects of management history remain hidden in unexplained variation. Similarly, Leuschner et al. (2009) were unable to take management effects into account in their test of the RSC-hypothesis, comparing distribution centre (Lower Saxony, Germany) and eastern margin (Slovakia). Marginal populations did not prefer moister and more fertile soils at the astern margin, where, however, annual temperature and precipitation were rather similar to the central distribution area. Therefore Leuschner et al. (2009) hypothesized that cold winters and late frost are more important limiting factors than summer drought at the continental margin.

Our study lends partial support to nutrient effects. Although compensatory effects of AWC were most pronounced at oligotrophic sites (SNS=1), observed minima of this effect did not correspond to suggested physiological maxima under well balanced nutrient supply (SNS 3-4) (Ellenberg, 1988; Niinements and Valladares, 2006), except for *A. alba*. P_{occ} of *P. sylvestris* and *Q. petraea* under xeric climate appeared to reflect ecological rather than physiological preferences (Ellenberg 1988), lending further support to the importance of biotic interactions (Leuschner et al., 2009; Meier et al., 2010) at the rear edge. This finding is underpinned by demographic studies (e.g. Lakatos and Molnár, 2009; Benito-Garzon et al., 2013) as well as by comparisons between SDMs and process–based models (e.g. Serra-Diaz et al., 2013). Apparently, shade tolerant temperate tree species such as *F. sylvatica* (Ellenberg, 1988) loose competitive power close to their xeric sub-Mediterranean limits, allowing more light-demanding oaks and pines to occupy more favorable soils (higher AWC and SNS). This result is in accordance with Serra-Diaz et al. (2013), who found a positive correlation of P_{occ} and productivity of *P. sylvestris* in Spain, which is not found in Central Europe (Ellenberg, 1988). Consistent to our findings on species ranges along the summer aridity gradient (Fig. 2), recent studies (Ligot et al., 2013; Tegel et al., 2014; Sánchez-De Dios et al. 2016) show that the drought tolerance of *F. sylvatica* might have been underestimated in earlier literature (Niinemets and Valladres, 2006; Table 1).

Quercus petraea can also occupy soils with high AWC in a xeric climate, but avoids carbonate soils (see Table 1, physiological and ecological optima). This distribution can be related to niche partitioning between *Q. petraea* (acidic) and *Q. pubescens* (basic soils) at dry sites (Ellenberg, 1988). Besides competition, southern limits of temperate species can be co-determined by pests, e.g. by *Ips typographus* or *Heterobasidion annosum* for *P. abies* (Caudullo et al., 2016). The response of *P. abies* supports Central European expert opinion (Falk et al., 2013) that this boreal species is endangered by *H. annosum* infestations on carbonate soils under warm conditions (> 7.5 °C in mean annual temperature). The examples of *P. abies* preferring acidic soils with high AWC and *P. sylvestris* preferring intermediate AWC at high summer aridity (SA3) show that, at the xeric margin, soil compensation may lead to habitat preferences considerably different from Central European experience, as laid down in Ellenberg ecograms (Ellenberg, 1988).

Our findings supporting the RSC hypothesis question the traditional assumption that tree species distribution at the continental extent can be estimated from climatic variables alone (Whittaker 1970), but supports the more recent finding that soil properties matter for macroecology (Thuiller, 2013; Diekmann et al., 2015). The relatively modest improvements in model performance can be related to (1) the coarse spatial resolution of the soil grid, leading to an underestimation of predictive capacity, and (2) to the interference of biotic interactions (competition and pests, see below) and human impacts (especially forest management). These remaining uncertainties and limitations could be addressed based on the ICP Forests monitoring network (Seidling 2016, Bussotti and Pollastrini 2017), if complemented by rear edge populations of important European tree species, at best in a spatially nested design.

Conclusions

With respect to available water content, macroecological analysis supports the relative site constancy hypothesis in terms of statistical significance and plausibility of soil compensatory effects on tree species distribution under limiting climatic conditions. The inclusion of soil significantly improves explanatory power and predictive performance of models. The contribution of soil parameters is most obvious for *P. sylvestris*, *Q. petraea* and *A. alba*.

Our findings imply that tree species ecology cannot be understood from isolated case studies at the rear edge. Therefore, work is needed to expand our knowledge on the importance of soil compensatory effects to a larger number of tree species using models that do also account for biotic interactions and human impacts. Combining studies of continental extent with high-resolution species occurrence and environmental information remains a considerable challenge. This study points to opportunities and current limits of such an approach.

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Table 1: *Tree species-related information on shade tolerance (STOL), drought tolerance (DTOL) according to Niinemets and Valladares (2006), physiological optimum with respect to soil acidity according to Ellenberg (1988) and the corresponding approximate range of the soil nutrient status (SNS) (see Table 3).*

Species	**Tolerance**		**Physiological optimum in the soil gradient**		**Ecological optimum**	
	Shade (STOL)	**Drought (DTOL)**	according to Ecogram	approx. SNS range	according to Ecogram	approx. SNS range
Aalba	4.6	1.81	base rich	2-6	not specified	
Fsylv	4.56	2.4	base rich	2-6	invariant	1-6
Pabie	4.45	1.75	intermediate	2-5	not specified	
Psylv	1.67	4.34	intermediate	2-4	calcareous; acidic	1, 6
Qpetr	2.73	3.02	base rich	2-5	acidic	1-3

Table 2: *Sample regions, data sources, and numbers of plots.*

Region	Number of plots	Data Source	Institution	Contact persons/References	URL
Alps	10276	GIVD[1], AVD: EU-00-014[2]	UPJV[3]	Lenoir et al. (2012)	www.givd.info/ID/EU-00-014
Austria	10048	NFI[4] Austria	BFW[5]	Markus Neumann	http://bfw.ac.at/
Europe	422	Provenance database	ASP[6]	Monika Konnert	www.asp.bayern.de
Europe	8687	PEP725[7]	TUM Ecoclimatology[8]	Annette Menzel	www.pep725.eu
Europe	256	BeFoFU[9] database	TUM Geobotany[10]	Alexey Zharov, Susanne Winter	http://www.biogeo.org/ASJ/BeFoFu.html
Europe	33014	GBIF[11]			www.gbif.org
Europe	7322	Level-I database	ICP Forests[12]	Fischer et al. (2010), Walter Seidling	www.icp-forests.org
Europe	103	ITRDB[13]	TUM Ecoclimatology[8]	Isabel Dorado-Liñán	http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring
France	51211	NFI[4] France	IGN[14]	Jonathan Lenoir	http://inventaire-forestier.ign.fr/spip/
Germany	51699	NFI[4] Germany	TI[15]	Heino Polley	https://www.thuenen.de/en/wo/fields-of-activity/forest-monitoring/national-forest-inventory/
Germany	367	KLIP12[16]	TUM Geobotany[10]	Matthias Jantsch	http://geobotanik.wzw.tum.de/index.php?id=43
Greece	640	GIVD, EU-GR-007[17]	Uni Thessaloniki[18]	Tsiripidis et al. (2012)	http://www.givd.info/ID/EU-GR-007
Hungary	9139	NFI[4] Hungary	NEBIH[19]	György Solti	http://portal.nebih.gov.hu/
Italy	2171	GIVD[1], EU-IT-011[20]	Uni Rome[21]	Fabio Attorre	http://www.givd.info/ID/EU-IT-011
Serbia	19235	NFI[4] Serbia	ILFE[22]	Dejan Stojanovic	www.ilfe.org
Slovenia	794	GIVD[1], EU-SI-001[23]	ZRCSAZU[24]	Andraž Čarni, Nina Juvan, Aleksander Marinšek	http://www.givd.info/ID/EU-SI-001
Spain	74430	NFI[4] Spain	MAGRAMA[25]	Roberto Vallejo Bombín	http://www.magrama.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3.aspx

No.	Institution (Abbreviation)	Data Source (Abbreviation)	Full names of Institution / Data source
1		GIVD	Global Index of Vegetation-Plot Databases
2		AVD: EU-00-014	The Alps Vegetation Database
3	UPJV		Université de Picardie Jules Verne (Amiens, France)
4	Diverse Institution	NFI[4]	National Forest Invetory
5	BFW	NFI Austria	Bundesforschungszentrum für Wald
6	ASP	Provenance database	Bayerisches Amt für forstliche Saat- und Pflanzenzucht
7		PEP725	European Phenological Database
8	TUM Ecoclimatology		Technische Universität München, Professorship of Ecoclimatology
9	TUM Ecoclimatolog	BeFoFU database	European Beech Forests for the Future
10	TUM Geobotany		Technische Universität München, Professorship of Geobotany
11		GBIF	Global Biodiversity Information Facility
12	ICP Forests	Level-I database	International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests
13		ITRDB	International Tree-Ring Data Bank
14	IGN	NFI France	Institut National de l'Information Géographique et Forestière (Paris, France)
15	TI	NFI Germany	Thünen Institute of Forest Ecosystems
16		KLIP12	Klimaprogramm Bayern
17		EU-GR-007	Hellenic Beech Forest Database
18	Uni Thessaloniki	NFI Spain	Aristotle University of Thessaloniki
19	NEBIH	NFI Hungary	National Food Chain Safety Office
20		EU-IT-011	Vegetation Plot Database Sapienza University of Rome
21	Uni Rome		Sapienza University of Rome
22	ILFE		Institute of Lowland Forestry and Environment, University of Novi Sad
23		EU-SI-001	Vegetation Database of Slovenia
24	ZRCSAZU		Research Center of the Slovenian Academy of Sciences and Arts
25	MAGRAMA		Ministerio de Agricultura, Alimentación y Medio Ambiente

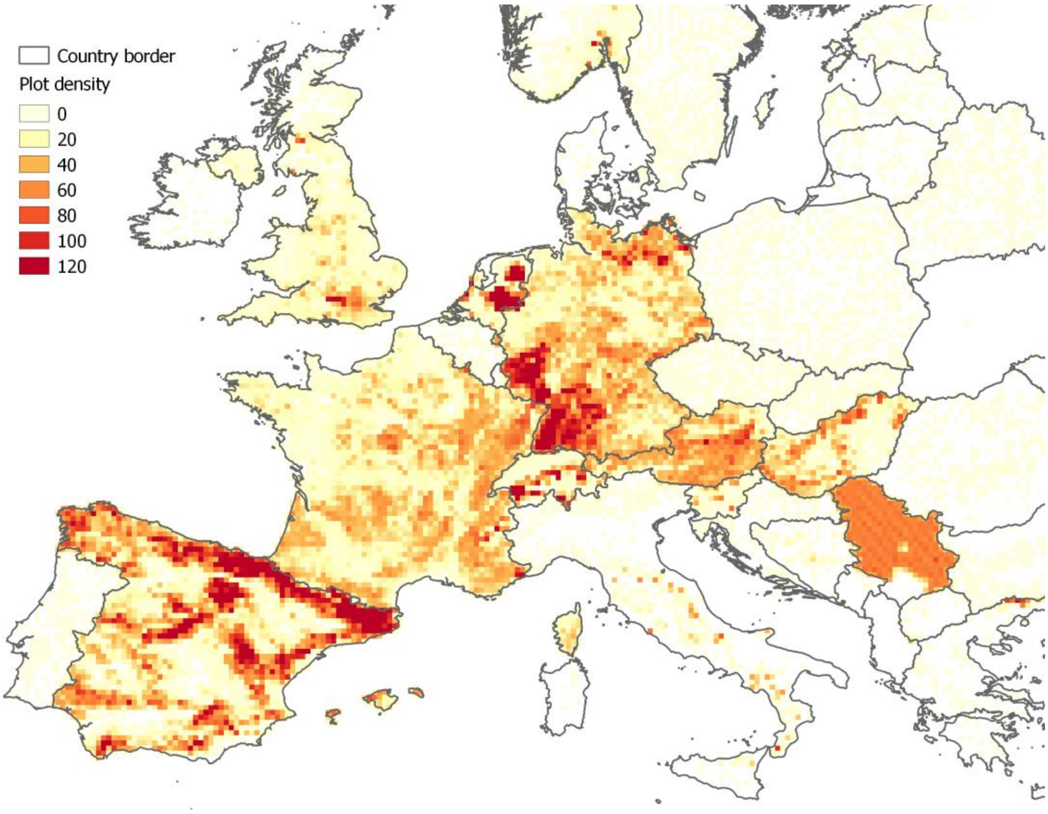
Table 3: *Soil chemical properties used for classification of the soil nutrient status (SNS) of terrestrial soil types of the European Soil Database (ESDB, Panagos 2012). For classification of soil types see Table T1 in the supplementary material.*

Index number	Soil nutrient status (SNS)	Short characteristic determining the nutrition status	Soil reaction	Base saturation and ionic strenght	Typical nutrient deficiencies for not adapted plants
1	oligotrotrophic	unbalances nutrition with free aluminum	moderately to strong acid	low	P, Ca, Mg, partly N
2	meso-oligotrophic				
3	mesotrophic	balanced nutrition without a dominating cation or anion in soil solution or induced nutrition deficiency	moderately acid to neutral	Intermediate to high	no deficiencies
4	eutrophic				
5	calcareous meso-oligotrophic	unbalances nutrition with free carbonate	slightly acid to slightly neutral	high	P, K, Fe, Mn, partly N
6	calcareous oligotrophic				

***Table 4** Results of the model evaluation involving the Akaike information criterion (AIC), the generalized cross validation criterion (GCV) the true skill statisitic (TSS) and the area under the curve statistic (AUC). The validation is based on a leave-one-out resampling of the binned data. The table entries show the mean ± standard deviation of model quality criteria. For all species criteria are statistically different for 'SA only' and 'Full models' (p < 0.05).*

Species	**Model**	**AIC**	**GCV**	**TSS**	**AUC**
Aalba	SA only	7829.793 ±1.33e+02	73.673 ±1.33e+00	0.594 ±2.55e-02	0.801 ±1.32e-02
	Full	4652.257 ±1.26e+02	51.604 ±1.35e+00	0.601 ±2.13e-02	0.841 ±1.16e-02
Fsylv	SA only	14215.162 ±2.51e+02	130.175 ±2.41e+00	0.473 ±1.81e-02	0.741 ±9.49e-03
	Full	11101.638 ±2.6e+02	109.523 ±2.66e+00	0.488 ±1.92e-02	0.77 ±1.23e-02
Pabie	SA only	15593.006 ±3.39e+02	153.214 ±3.45e+00	0.681 ±1.5e-02	0.848 ±7.21e-03
	Full	13189.302 ±3.01e+02	135.91 ±3.05e+00	0.683 ±1.87e-02	0.87 ±9.4e-03
Psylv	SA only	15784.848 ±4.25e+02	138.681 ±3.89e+00	0.276 ±2.27e-02	0.648 ±1.18e-02
	Full	8247.45 ±3.2e+02	78.167 ±2.85e+00	0.321 ±2.8e-02	0.712 ±1.45e-02
Qpetr	SA only	12454.258 ±1.95e+02	110.706 ±1.81e+00	0.388 ±2.99e-02	0.703 ±1.45e-02
	Full	7864.95 ±1.95e+02	81.027 ±1.83e+00	0.414 ±2.42e-02	0.743 ±1.37e-02

***Figure 1:** Plot density of presence-only records (Figure 1a upper panel) and plot density of presence-absence recods (Figure 1b lower panel)   in Southern and Central Europe as well as adjacent regions in a 16x16 km grid. In Northern Europe the plots density is constantly low (ca. 1 plot per grid cell, light grey).*



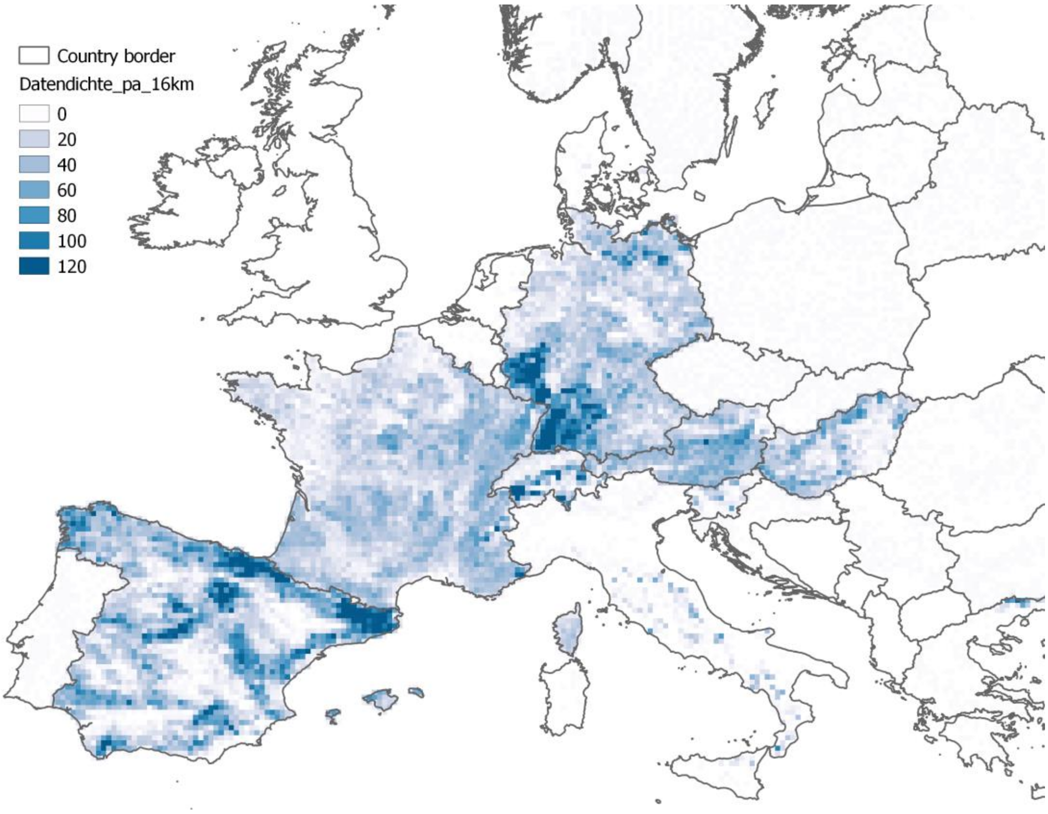

Country border
Datendichte_pa_16km
0
20
40
60
80
100
120

Figure 2: *Frequency distribution of the modified Ellenberg's quotient (LogEQm) indicating summer aridity for five major forest tree species of Central Europe (Abies alba = Aalba, Fagus sylvatica = Fsylv, Picea abies = Pabie, Pinus sylvestris = Psylv, Quercus petraea = Qpetr). Boxplots represent data as stratified for the analysis: Values between the lower and upper whiskers represent range of the second decile to the 9th decile (SA2). Accordingly, points below the lower whisker represent the 1st decile (SA1, humid climatic conditions) and points above the upper whisker represent the 10th decile (SA3, xeric climatic conditions). Red squares in the boxplots of tree species indicate sites under high summer aridity where species only occur under a high available water capacity of the soil (> 50 mm). Total number of plots usable as presence-only records = 278,814.*

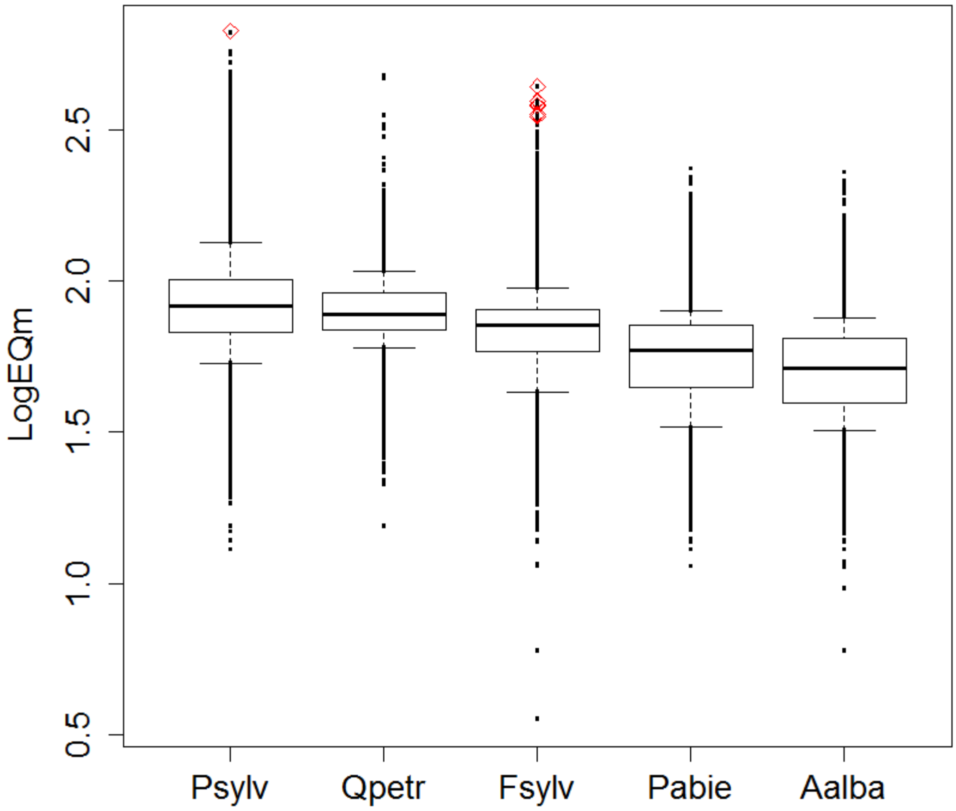
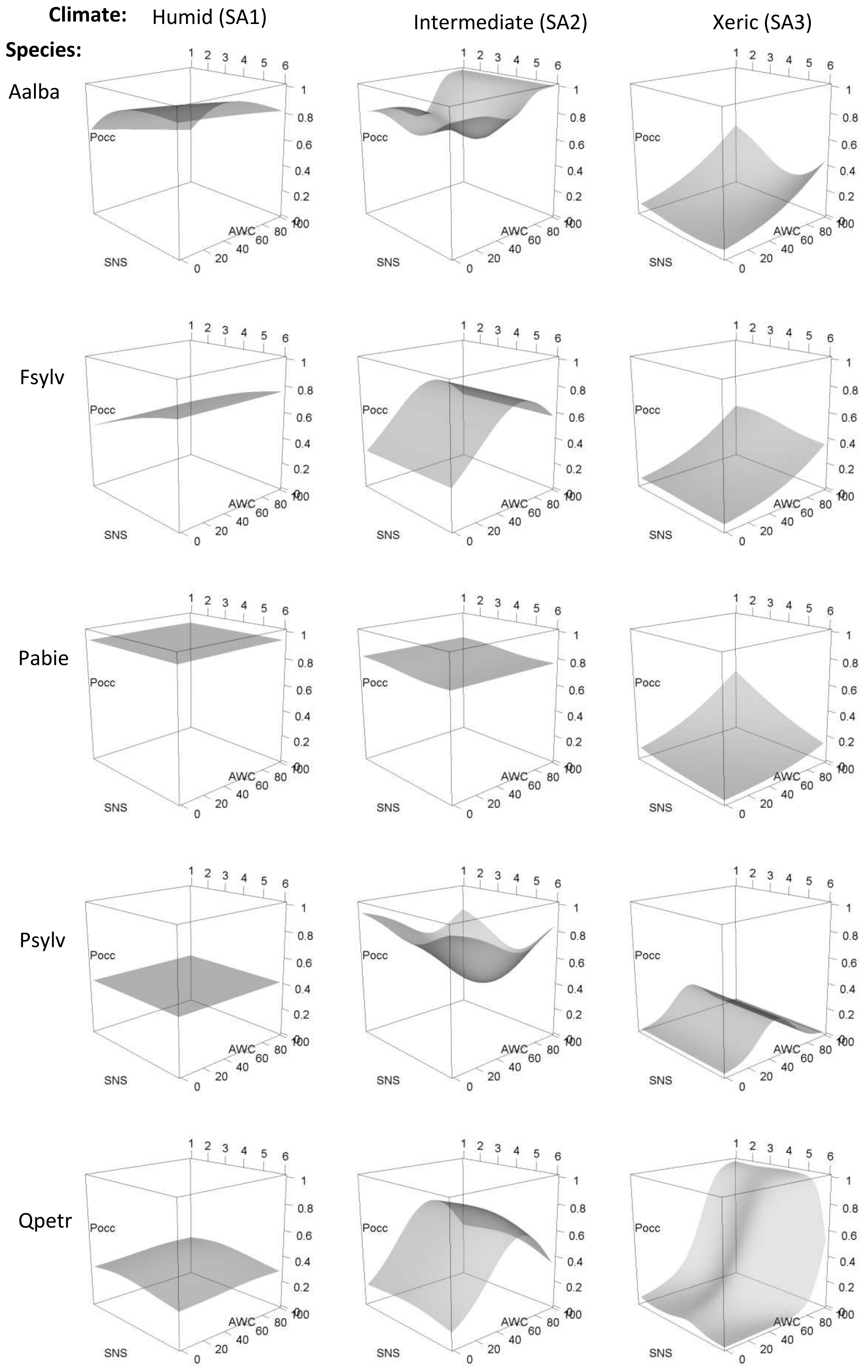


***Figure 3:** Results of the model for the five tree species from the top in alphabetical order (Aalba to Qpetr, species abbreviations see Figure 1). All graphs show the response surface of the probability of occurrence (P_{occ}) against available water capacity (AWC) and soil nutrient status (SNS). First column: Mean P_{occ} at the summer aridity level at 1^{st} decile (humid climate, SA1); Second column: Mean P_{occ} at 2.-9. decile (intermediate climate, SA2); Third column: Mean P_{occ} at the summer aridity level at 10th decile (xeric climate, SA3). Number of presence-absence records ~213,900 are reduced by data aggregation to 107 (Aalba), 112 (Fsylv), 105 (Pabie), 115 (Psylv), 114 (Qpetr). All main effects of the models are significant ($p < 0.05$), except β_1 for SA1 of Aalba* and *Fsylv (see Equ. 1). AWC and SNS effects in a xeric climate (SA3, right column) indicating possible compensation by the soil are significant for all species except SNS for Psylv.*


Climate:
Humid (SA1)
Intermediate (SA2)
Xeric (SA3)
Species:
Aalba
Fsylv
Pabie
Psylv
Qpetr
Pocc
SNS
AWC
1 2 3 4 5 6
0 0.2 0.4 0.6 0.8 1
0 20 40 60 80 100

Supplementary material

1. Species description

A. alba distribution is restricted to the montane belt, where it commonly grows in mixed stands, mostly with *F. sylvatica* and *P. abies* (element of the Central European mountain flora, Walter 1973) and thrives best on soils with high moisture availability (Wolf 2003; Ellenberg and Leuschner, 2010). The species is very shade tolerant, grows under a wide range of soil pH conditions from acidic to basic and is moderately drought-sensitive.

F. sylvatica is widely distributed and often dominant in Central and Western Europe (Ellenberg, 1988) and forms extensive stands in Mediterranean mountain ranges. *F. sylvatica* can grow on soils with widely variable nutrient conditions but favours mesic soils, where root penetration is not constrained by stagnant water (Ellenberg and Leuschner, 2010). Within its range, *F. sylvatica* tends to dominate other tree species by shading due to rapid crown expansion. However, according to Niinemets and Valladares (2006), *F. sylvatica* is only moderately tolerant to drought.

P. abies is a boreal tree species that also occurs naturally in the montane and subalpine belts of temperate Europe. It grows mostly in mixtures with other conifers or deciduous trees up to the tree line (Ellenberg and Leuschner, 2010). However, due to its important economic value, the species has been distributed far beyond its natural range, where it was frequently planted in pure stands. Although, *P. abies* is a shade-tolerant tree species that tolerates a wide range of soil types its growth can be limited by soil chemistry (Mellert and Ewald 2014). Its optimum is on mesic soils with balanced nutrient supply (intermediate SNS).

P. sylvestris is widely distributed throughout Eurasia. *P. sylvestris* is a light-demanding weak competitor (Niinemets and Valladares ,2006). Although the species tolerates all kinds of site conditions it grows best on fertile soils (intermediate SNS, Ellenberg, 1988; Leibundgut, 1984), where, however, it is outcompeted by *P. abies* or broad-leaved tree species such as *F. sylvatica* (Ellenberg and Leuschner, 2010). Consequently, the species occurs mainly on poor, sandy soils, rocky outcrops or peat bogs, i.e. at sites where most other tree species are unable to thrive (Mátyás et al., 2004).

Q. petraea is widely distributed in Europe from northern Spain to southern Scandinavia and from Ireland to Ukraine. *Q. petraea* occupies a very broad range of soil pH conditions (3.5 to 9) and climate conditions from xeric to hygric (Ducousso and

Bordacs, 2004). It is a light-demanding deciduous tree and more drought tolerant than *F. sylvatica* (Niinemets and Valladares, 2006). In Central Europe, it is preferably found on dry acidic soils (Ellenberg and Leuschner, 2010).

2. Observed probability of occurrence

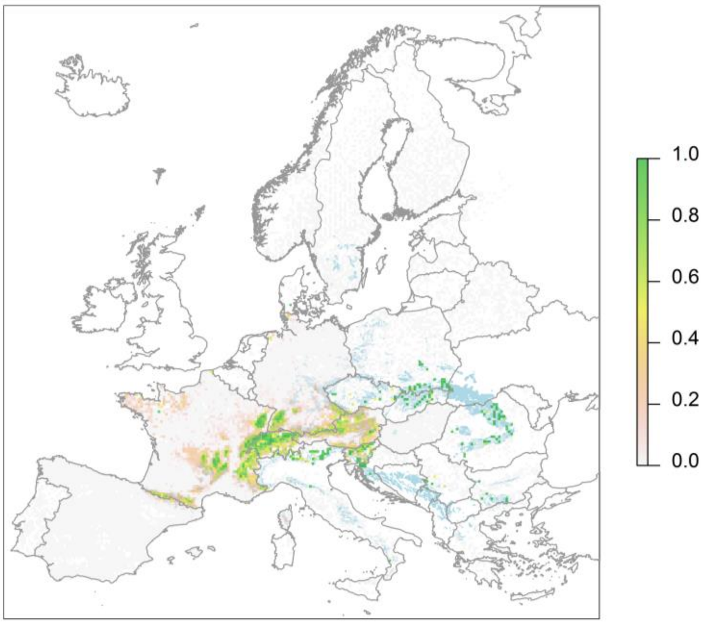


Fig. S1 Probability of occurrence of *Abies alba* observed within a 16 km raster of Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is displayed in bluish background colors.

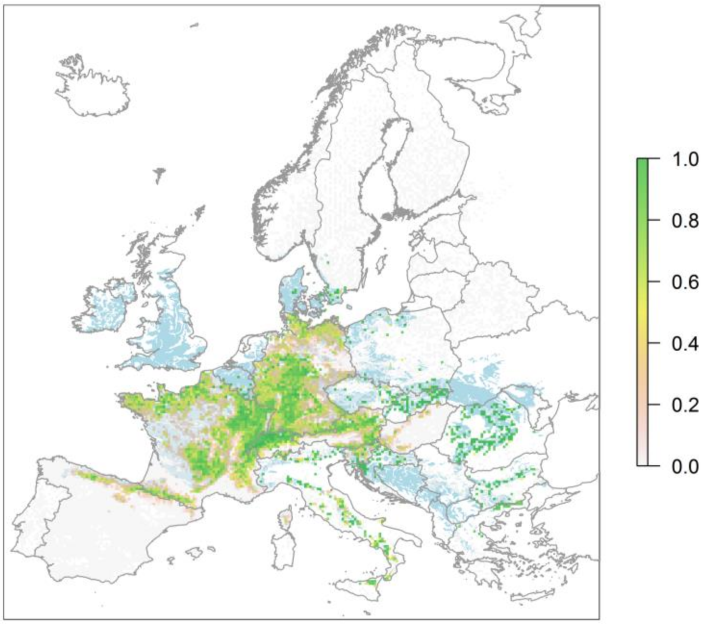


Fig. S2 Probability of occurrence of *Fagus sylvatica* observed within a 16 km raster of Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is displayed in bluish background colors.

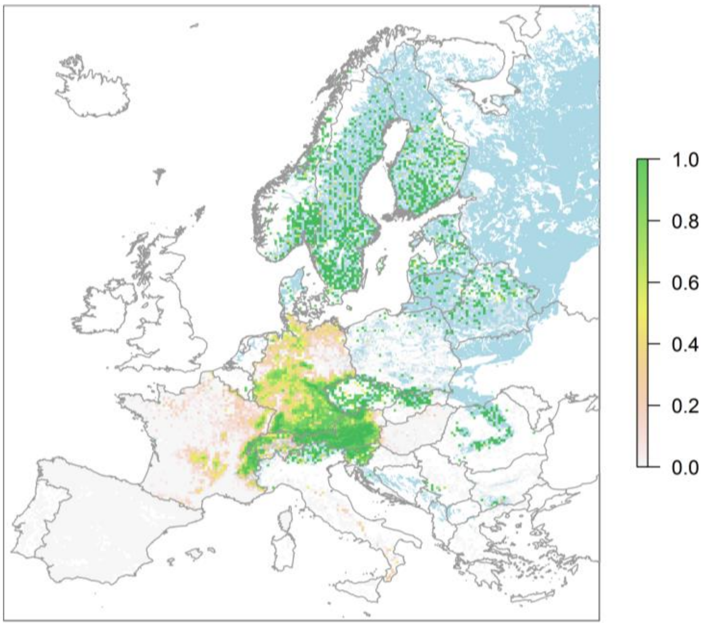


Fig. S3 Probability of occurrence of *Picea abies* observed within a 16 km raster of Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is displayed in bluish background colors.

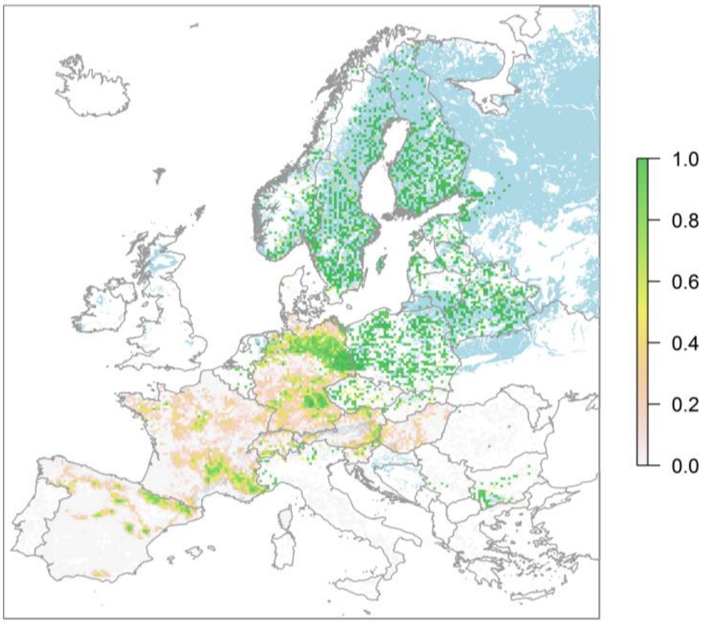


Fig. S4 Probability of occurrence of *Pinus sylvestris* observed within a 16 km raster of Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is displayed in bluish background colors.

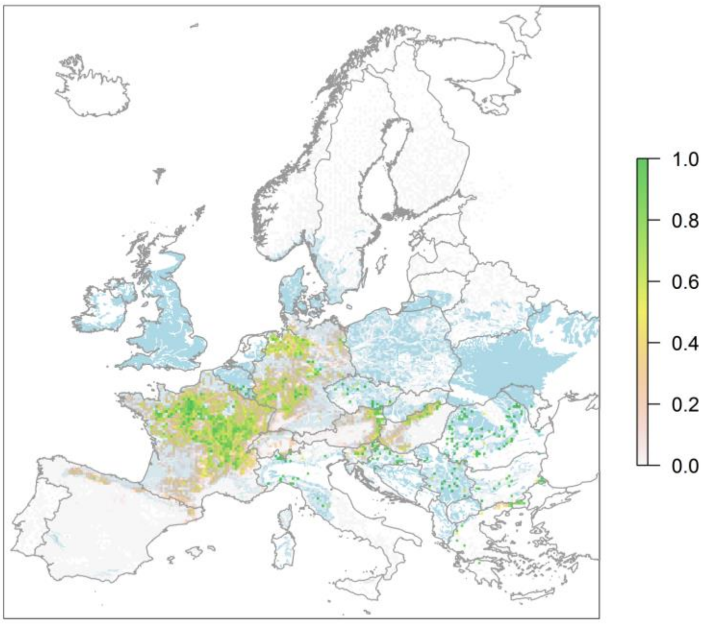


Fig. S5 Probability of occurrence of *Quercus petraea* observed within a 16 km raster of Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is displayed in bluish background colors.

Soil data

Table S1 Classification of the soil nutrient status (SNS) of terrestrial soil types adopted based on the European Soil Database (ESDB, Panagos 2006) using the soil types from FAO (1974).

Order	Trophic status	Soil types
1	Oligotrotrophic	Dystric Lithosol, Dystric Ranker, Dystric Regosol, Humic Podzol, Leptic Podzol, Orthic Podzol, Placic Podzol, Dystric Cambisol
2	meso-oligotrophic	Albic Arenosol, Cambic Arenosol, Dystric Cambisol, Dystric Gleysol; Dystric Luvisol, Eutric Lithosol, Ferric Gleysol, Ferric Luvisol, Gelic Regosol, Gleyic Acrisol, Gleyic Cambisol, Haplic Andosol, Haplic Arenosol, Lithosol, Ochric Andosol, Orthic Acrisol, Dystric Lithosol, Orthic Lithosol, Ranker
3	Mesotrophic	Albic Luvisol, Dystric Fluvisol, Dystric Planosol, Dystric Podsoluvisol, Eutric Cambisol, Dystric Gleysol, Eutric Gleysol, Eutric Planosol, Eutric Podsoluvisol, Eutric Regosol, Gelic Gleysol, Gleyic Podsoluvisol, Gleyic Podzol, Haplic Cambisol, Humic Gleysol, Luvic Arenosol, Luvic Chernozem, Mollic Planosol, Orthic Greyzem
4	eutrophic	Albic Cambisol, Eutric Cambisol, Calcaric Fluvisol, Calcaric Gleysol, Calcaric Phaeozem, Chromic Vertisol, Eutric Fluvisol, Gleyic Luvisol, Gleyic Phaeozem, Gleyic Vertisol, Haplic Phaeozem, Humic Chernozem, Luvic Gleysol, Luvic Phaeozem, Mollic Fluvisol, Mollic Gleysol, Ochric Phaeozem, Orthic Luvisol, Pellic Vertisol, Thionic Fluvisol, Thionic Gleysol, Vertic Cambisol, Vertic Luvisol
5	calcareous meso-oligotrophic	Calcaric Lithosol, Calcaric Regosol, Calcic Cambisol, Eutric Cambisol, Calcic Chernozem, Calcic Kastanozem, Calcic Luvisol, Chromic Cambisol, Chromic Luvisol, Haplic Kastanozem, Luvic Kastanozem, Cambic Rendzina, Orthic Rendzina, Rendzina
6	calcareous oligotrophic	Calcaric Lithosol, Cambic Rendzina, Orthic Rendzina, Rendzina