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## Soil water storage appears to compensate for climatic aridity at the xeric margin of European tree species distribution

Karl H. Mellert, Jonathan Roger Michel Henri Lenoir, Susanne Winter, Christian Kölling, Isabel Dorado-Liñán, Jean-Claude Gégout, Axel Göttlein, Daniel Hornstein, Matthias Jantsch, Nina Juvan, et al.

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1 **Soil water storage appears to compensate for climatic aridity at the**  
 2 **xeric margin of European tree species distribution**

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59 ecosystems, macroecology, soil nutrient status

60

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

66

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83

84 **Abstract**

85 Based on macroecological data, we test the hypothesis whether European tree  
86 species of temperate and boreal distribution maintain their water and nutrient  
87 supply in the more arid southern margin of their distribution range by shifting to  
88 more fertile soils with higher water storage than in their humid core distribution  
89 range. To answer this question, we gathered a large dataset with more than  
90 200,000 plots that we related to summer aridity (SA), derived from WorldClim  
91 data, as well as soil available water capacity (AWC) and soil nutrient status,  
92 derived from the European soil database. The soil compensatory effects on tree  
93 species distribution were tested through generalized additive models. The  
94 hypothesis of soil compensatory effects on tree species distribution under  
95 limiting aridity was supported in terms of statistical significance and plausibility.  
96 Compared to a bioclimatic baseline model, inclusion of soil variables  
97 systematically improved the models' goodness of fit. However, the relevance  
98 measured as the gain in predictive performance was small, with largest  
99 improvements for *P. sylvestris*, *Q. petraea* and *A. alba*. All studied species, except  
100 *P. sylvestris*, preferred high AWC under high SA. For *F. sylvatica*, *P. abies* and *Q.*  
101 *robur*, the compensatory effect of soil AWC under high SA was even more  
102 pronounced on acidic soils. Soil compensatory effects might have decisive  
103 implications for tree species redistribution and forest management strategies  
104 under anthropogenic climate change. Therefore, soil compensatory effects  
105 deserve more intensive investigation, ideally, in studies combining different  
106 spatial scales to reduce the uncertainty associated with the precision of soil  
107 information.

108

## 109 **Introduction**

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

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

140 In a temperate and (sub)mediterranean climate available water capacity  
141 (AWC) is an important component of the soil water supply (Blume et al., 2015;  
142 Latron et al. 2009). Most importantly, AWC is a crucial buffer that allows trees to  
143 survive dry periods (Bréda et al., 2006). This is especially relevant at the rear  
144 edge of their distribution. Soil nutrient status (SNS) is an important proxy for  
145 nutrient availability (Binkley and Vitousek, 1989). Both factors were mentioned  
146 in the formulation of the “relative site constancy” (RSC) hypothesis by Walter  
147 (1973). The RSC hypothesis asserts that many plants originating from relatively  
148 humid climates prefer moister soils and/or humid microclimates under dryer  
149 macroclimatic conditions. Accordingly, higher AWC in the soils should  
150 compensate for a more arid macroclimate while higher soil nutrient availability  
151 in the soils is expected to improve water use efficiency (e.g. Bradbury and  
152 Malcolm, 1977). Thus, the RSC hypothesis predicts a shift of the probability of  
153 occurrence of temperate trees towards soils with high AWC under high summer  
154 aridity (SA). We further assume that this preference for high AWC should be  
155 more pronounced on oligotrophic soils, where more water has to be transpired  
156 to transport the same amount of nutrients.

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

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

168

169 **Material and Methods**

170 To test the macroecological question of soil compensatory effects at the  
171 drier climatic conditions at the rear edge, we combine a large dataset containing  
172 more than 270,000 vegetation plots from Central and Southern Europe with ca.  
173 210,000 presence-absence records of temperate species with bioclimatic and  
174 edaphic variables derived from WorldClim (Hijmans et al., 2005) and the  
175 European Soil Database (ESDB, Panagos et al., 2012).

176

#### 177 *Target species*

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

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

193

#### 194 **Table 1: Species traits**

195

#### 196 *Tree distribution data*

197 To represent a gradient from humid to xeric macroclimatic conditions, we  
198 collected vegetation plots from Central to Southern Europe (Fig. 1). Cold range  
199 margins were represented by including continental ICP Forests data (Fischer et  
200 al. 2010) extending to Northern Europe. The resulting sample represents a



201 gradient from subboreal and cold temperate to warm temperate and  
202 (sub)mediterranean climates (Table 2). Due to gaps in soil data, especially in  
203 Turkey, large areas in South-Eastern Europe could not be included in the  
204 analyses. In our analysis it is crucial to distinguish between presence-absence  
205 and presence-only data as several data sources (e.g. the European Phenological  
206 Database) did not report absence. While frequency distributions (Fig. 2) were  
207 extracted from a combination of presence-only (Fig. 1a) and presence-absence  
208 data, statistical modeling was solely based on presence-absence data reporting  
209 true absences (Fig. 1b). Maps showing an overview about the observed  
210 probability of occurrence of the five species in Europe can be found in the  
211 supplementary material (Fig. S1-S5).

212

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

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

215

#### 216 *Climate data*

217 We used long-term aggregated climate data (1950-2000) on precipitation and  
218 mean temperature from the WorldClim data portal (Hijmans et al., 2005)  
219 providing climatic grids at 30 arc-seconds (~1 km) resolution (in WGS 1984  
220 coordinate system). Similar to Rasztovits (2012), we computed a modified  
221 Ellenberg climate quotient (EQ) to represent summer aridity (SA). EQ was  
222 originally defined as the ratio of July temperature (in °C) to annual precipitation  
223 (in mm) multiplied by 1000. Despite its simplicity, EQ is a good proxy for climatic  
224 drought (Fang and Lechovicz, 2006; Czúcz et al., 2011; Mátyás et al., 2010;  
225 Stojanovic et al. 2013) with equal explanatory power in SDMs (Mellert et al.,  
226 2016) compared to climatic water balance (cf. Piedallu et al. 2013). For focusing  
227 this index on the most limiting summer period (Bréda et al. 2006), we slightly  
228 modified the index (EQ<sub>m</sub>) by using the ratio of mean temperature during the  
229 warmest quarter (BIO10) to precipitation during the warmest quarter (BIO18)  
230 (<http://worldclim.org/bioclim>). As very low summer precipitation in some  
231 regions leads to large numbers, we used the logarithm (LogEQ<sub>m</sub>) in our analyses.

232           Within the range of presences of each species LogEQm values were  
233 categorized into three different summer aridity levels (SA1-3) by using the 1st and  
234 9th deciles, as done by Alonso-Ponce et al. (2010). The range below the 1st  
235 decile represents the humid margin, the interdecile between the 1st and 9th  
236 deciles characterizes intermediate or mesic SA conditions (SA2), and the range  
237 above the 9th decile represents the most xeric conditions under which the focal  
238 species occurs (cf. the xeric margin, SA3) (Fig. 2). This stratification allows for  
239 testing and visualizing possible compensatory soil effects by modeling the  
240 response of the species along soil gradients under different climatic conditions  
241 (see Leuschner et al. 2009 for a similar approach). SA3 values of the study  
242 species were highly correlated (Spearman's  $r = 0.9$ ,  $p < 0.05$ ) to their drought  
243 tolerance (DTOL, Table 1).

244

245

**Figure 2: Boxplot for LogEQm**

246

*Soil data*

248 Soil properties were derived from the European soil database (ESDB, Panagos et  
249 al. 2012). Available soil water capacity (AWC, derived according to Hiederer,  
250 2013) was downloaded from the ESDB website  
251 (<http://eusoils.jrc.ec.europa.eu/content/european-soil-database-derived-data>).  
252 Both maps are at a scale of 1:1,000,000. The qualitative map of soil types (soil  
253 mapping units, SMU) is available as vector data, while AWC data is available as  
254 raster data with 1 km resolution. For explanatory modelling (see below), AWC  
255 was stratified into bins of 5 mm width across the range of AWC values (40-60  
256 mm) for which plot density was high (> 15,000 plots), and into bins of 20 mm  
257 width across the range of AWC values for which plot density was lower, resulting  
258 in a total of 8 bins (<20, 20-40, 40-45, 45-50, 50-55, 55-60, 60-80, >80 mm).

259           Soil nutrient status (SNS) variable was defined as an ordinal variable with 6  
260 levels characterizing the availability of macro- and micro nutrients in the entire  
261 soil profile (Table 3) along a gradient from strongly acidic to calcareous or  
262 alkaline soils. Due to acidification and/or substrate stratification chemical  
263 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).

282

283

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

284

285 Data aggregation

286 To avoid pseudoreplication and spatial autocorrelation of samples (Kühn,  
287 2007), we based our analysis on data aggregated in environmental space. Instead  
288 of considering each vegetation plot as an independent observation contributing  
289 one degree of freedom per record, we averaged data based on the classes (bins)  
290 for SA, AWC and SNS as described above. By doing so, replicated plot  
291 observations in geographic space occurring under similar environmental  
292 conditions are converted to binary counts in a matrix cell defined by classes of  
293 environmental conditions. In this way we can model the probability of  
294 occurrence in a structured space of environmental parameters without inflating

295 the degrees of freedom by pseudoreplicates in geographic space (cf. Austin,  
296 1990). The resulting bins were only considered with a minimum number of 20  
297 plots. The stratification leads to a considerable reduction of sample size and  
298 degrees of freedom (number of plots ~ 213,900; number of bins 8 (AWC) x 6  
299 (SNS) x 3 (SA) total 144 less bins with no observations results in a N between 105  
300 for *P. abies* and N = 115 for *P. sylvestris*), but eliminates the risk of type I error  
301 (falsely rejecting the null hypothesis of no effect) (Kühn, 2007).

302

### 303 Statistical modelling

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

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

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

325

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

(Equation 1)

329

330 Consequently, the model estimates are composed of six smooth functions  
331 and three linear parameters  $\beta_0$ –  $\beta_2$ , where  $\beta_0$  is the intercept value, and SA2  
332 (medium aridity) is the reference category.

333 Model adequacy was evaluated using the Akaike information criterion (AIC)  
334 and the GCV criterion. GCV was also used for GAM calibration within the “mgcv”  
335 algorithm. Golub et al. (1979) introduced GCV as a variant of leave-one-out cross  
336 validation. As with AIC, lower values of the GCV score indicate better explanatory  
337 power and its values are not linearly related to the proportion of explained  
338 variance. Predictive accuracy was evaluated by the area under the curve (AUC)  
339 statistic, which is a standard criterion to characterize the fit of binary SDMs  
340 (Franklin, 2010) and the true skill statistic (TSS), another criterion that is gaining  
341 acceptance in SDMs (Barbet-Massin et al. 2012). TSS ranges from –1 to +1, where  
342 +1 indicates perfect agreement and values of zero or less indicate a performance  
343 no better than random (Allouche et al. 2006). Both criteria measure for the  
344 ability of a model to classify a species correctly as present or absent in a given  
345 data set. While AUC is threshold-independent, TSS relies on a threshold of  
346 occurrence (Peterson et al. 2011). We used the prevalence of the species as a  
347 threshold as this is a simple and meaningful baseline method (Liu et al. 2005).

348 As an additional aspect to hypothesis testing, the relevance of soil effects  
349 was assessed by comparing the performance of the full model (Equ. 1) to the  
350 reference or baseline model only including summer aridity (SA). This validation  
351 was carried out based on a resampling of the binned data. In a leave-one-out  
352 procedure, one bin was left out in each iteration. So the number of iterations  
353 equals the number of bins (e.g. 115 for *P. sylvestris*). AIC and GCV of all resulting  
354 models were stored for model validation. The predictive performance (AUC and  
355 TSS) was computed using the “PresencesAbsence” package in R (R Core Team,  
356 2015) based on the original (unbinned) data set split into the same portions as

357 the binned data set (e.g. 1/115 for *P. sylvestris*). Differences in validation criteria  
358 between the full and the baseline model were tested by a T-Test.

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

363

## 364 **Results**

### 365 *Modeling results*

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

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

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

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

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

412

413 **Figure 3: Species responses at different SA levels**

414

415 Accuracy of the full models (Equ. 1) was fair to good according to the AUC  
 416 classification of Swets (1988) (Table 4). Compared to the purely bioclimatic  
 417 baseline model inclusion of soil parameters significantly improved the  
 418 explanatory power (AIC and GCV score) and predictive accuracy (AUC and TSS

419 score) of all five studied species ( $p < 0.05$ ). Relative improvements in model  
 420 quality criteria (% , AIC, GCV, TSS, AUC) are as follows: *Abies alba* (40.6, 30.0, 1.2,  
 421 5.0); *Fagus sylvatica* (21.9, 15.9, 3.2, 3.9); *Picea abies* (15.4, 11.3, 0.3, 2.6) *Pinus*  
 422 *sylvestris* (47.8, 43.6, 16.3, 9.9); and *Quercus petraea* (36.8, 26.8, 6.7, 5.7).

423

424 **Table 4: Model evaluation**

425

426 **Discussion**

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

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

444 Further, a major uncertainty of our study is the influence of former  
 445 management interventions on species distribution patterns. As there is no way of  
 446 reconstructing those interventions at the scale of our study, effects of  
 447 management history remain hidden in unexplained variation. Similarly,  
 448 Leuschner et al. (2009) were unable to take management effects into account in  
 449 their test of the RSC-hypothesis, comparing distribution centre (Lower Saxony,



450 Germany) and eastern margin (Slovakia). Marginal populations did not prefer  
451 moister and more fertile soils at the eastern margin, where, however, annual  
452 temperature and precipitation were rather similar to the central distribution  
453 area. Therefore Leuschner et al. (2009) hypothesized that cold winters and late  
454 frost are more important limiting factors than summer drought at the  
455 continental margin.

456 Our study lends partial support to nutrient effects. Although compensatory  
457 effects of AWC were most pronounced at oligotrophic sites (SNS=1), observed  
458 minima of this effect did not correspond to suggested physiological maxima  
459 under well balanced nutrient supply (SNS 3-4) (Ellenberg, 1988; Niinemets and  
460 Valladares, 2006), except for *A. alba*.  $P_{occ}$  of *P. sylvestris* and *Q. petraea* under  
461 xeric climate appeared to reflect ecological rather than physiological preferences  
462 (Ellenberg 1988), lending further support to the importance of biotic interactions  
463 (Leuschner et al., 2009; Meier et al., 2010) at the rear edge. This finding is  
464 underpinned by demographic studies (e.g. Lakatos and Molnár, 2009; Benito-  
465 Garzon et al., 2013) as well as by comparisons between SDMs and process-based  
466 models (e.g. Serra-Diaz et al., 2013). Apparently, shade tolerant temperate tree  
467 species such as *F. sylvatica* (Ellenberg, 1988) loose competitive power close to  
468 their xeric sub-Mediterranean limits, allowing more light-demanding oaks and  
469 pines to occupy more favorable soils (higher AWC and SNS). This result is in  
470 accordance with Serra-Diaz et al. (2013), who found a positive correlation of  $P_{occ}$   
471 and productivity of *P. sylvestris* in Spain, which is not found in Central Europe  
472 (Ellenberg, 1988). Consistent to our findings on species ranges along the summer  
473 aridity gradient (Fig. 2), recent studies (Ligot et al., 2013; Tegel et al., 2014;  
474 Sánchez-De Dios et al. 2016) show that the drought tolerance of *F. sylvatica*  
475 might have been underestimated in earlier literature (Niinemets and Valladares,  
476 2006; Table 1).

477 *Quercus petraea* can also occupy soils with high AWC in a xeric climate, but  
478 avoids carbonate soils (see Table 1, physiological and ecological optima). This  
479 distribution can be related to niche partitioning between *Q. petraea* (acidic) and  
480 *Q. pubescens* (basic soils) at dry sites (Ellenberg, 1988). Besides competition,

481 southern limits of temperate species can be co-determined by pests, e.g. by *Ips*  
482 *typographus* or *Heterobasidion annosum* for *P. abies* (Caudullo et al., 2016). The  
483 response of *P. abies* supports Central European expert opinion (Falk et al., 2013)  
484 that this boreal species is endangered by *H. annosum* infestations on carbonate  
485 soils under warm conditions (> 7.5 °C in mean annual temperature). The  
486 examples of *P. abies* preferring acidic soils with high AWC and *P. sylvestris*  
487 preferring intermediate AWC at high summer aridity (SA3) show that, at the xeric  
488 margin, soil compensation may lead to habitat preferences considerably  
489 different from Central European experience, as laid down in Ellenberg ecograms  
490 (Ellenberg, 1988).

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

503

## 504 **Conclusions**

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

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

518

### 519 **References**

- 520 Alonso-Ponce R, López Senespleda E, Sánchez Palomares O (2008) A novel application of  
 521 the ecological field theory to the definition of physiographic and climatic potential  
 522 areas of forest species. *Eur J Forest Res* 129:119–131.
- 523 Attorre F, Alfò M, Sanctis M de *et al* (2011) Evaluating the effects of climate change on  
 524 tree species abundance and distribution in the Italian peninsula. *Appl Veg Sci*  
 525 14:242–255
- 526 Austin MP (1980) Searching for a model for use in vegetation analysis. *Vegetatio* 42:11–  
 527 21.
- 528 Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative  
 529 niche: environmental niches of five *Eucalyptus* species. *Ecol Monogr* 60:161–177
- 530 Bailey RG (1987) Suggested hierarchy of criteria for multi-scale ecosystem mapping.  
 531 *Landscape Urban Plan* 14:313–319
- 532 Barbet-Massin M, Jiguet F, Albert CH *et al* (2012) Selecting pseudo-absences for species  
 533 distribution models: how, where and how many? *Methods Ecol Evol* 3:327–338
- 534 Barnes BV, Pregitzer KS, Spies TA *et al* (1982) Ecological Forest Site Classification. *J*  
 535 *Forest* 80:493–498
- 536 Beauregard F, Blois S de (2014) Beyond a climate-centric view of plant distribution:  
 537 edaphic variables add value to distribution models. *PloS one* 9:e92642
- 538 Benito-Garzón M, Ruiz-Benito P, Zavala MA (2013) Interspecific differences in tree  
 539 growth and mortality responses to environmental drivers determine potential  
 540 species distributional limits in Iberian forests. *Global Ecol Biogeogr* 22:1141–1151
- 541 Bertrand R, Perez V, Gégout J-C (2012) Disregarding the edaphic dimension in species  
 542 distribution models leads to the omission of crucial spatial information under  
 543 climate change: the case of *Quercus pubescens* in France. *Glob Change Biol* 18:2648–  
 544 2660

- 545 Binkley D, Vitousek P (1989) Soil nutrient availability. In: Pearcy RW, Ehleringer JR,  
546 Mooney HA et al (eds) Plant Physiological Ecology. Field methods and  
547 instrumentation. Springer Netherlands, Dordrecht, pp 75–96
- 548 Blume H-P, Brümmer GW, Fleige H *et al* (2015) Scheffer/Schachtschabel soil science.  
549 Springer
- 550 Bohn U, Neuhäusl R, Gollub G, Hettwer C, Neuhäuslova Z, Raus T, Schlüter H, Weber H  
551 (2003) Map of the natural vegetation of Europe, scale 1:2500000. Parts 1–3.  
552 Landwirtschaftsverlag, Münster-Hiltrup
- 553 Bradbury IK, Malcolm DC (1977) The effect of phosphorus and potassium on  
554 transpiration, leaf diffusive resistance and water-use efficiency in Sitka spruce (*Picea*  
555 *sitchensis*) seedlings. J Appl Ecol:631–641
- 556 Bréda N, Huc R, Granier A *et al* (2006) Temperate forest trees and stands under severe  
557 drought. A review of ecophysiological responses, adaptation processes and long-  
558 term consequences. Ann For Sci 63:625–644
- 559 Brus DJ, Hengeveld GM, Walvoort DJ *et al* (2011) Statistical mapping of tree species over  
560 Europe. Eur J Forest Res 131:145–157.
- 561 Bussotti F, Pollastrini M (2017) Observing climate change impacts on European forests:  
562 what works and what does not in ongoing long-term monitoring networks. Front  
563 Plant Sci 8.
- 564 Cajander AK (1949) Forest types and their significance. Acta Forestalia Fennica 56:1–71
- 565 Caudullo, G., Tinner, W., de Rigo, D. (2016) *Picea abies* in Europe: distribution, habitat,  
566 usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston  
567 Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU,  
568 Luxembourg, pp. e012300+.
- 569 Coudun C, Gégout J-C, Piedallu C *et al* (2006) Soil nutritional factors improve models of  
570 plant species distribution. An illustration with *Acer campestre* (L.) in France. J  
571 Biogeogr 33:1750–1763
- 572 Czúcz B, Gálhidy L, Mátyás C (2011) Present and forecasted xeric climatic limits of beech  
573 and sessile oak distribution at low altitudes in Central Europe. Ann For Sci 68:99–  
574 108.
- 575 Diekmann M, Michaelis J, Pannek A (2015) Know your limits – The need for better data  
576 on species responses to soil variables. Basic Appl Ecol 16:563–572

- 577 Dolos K, Bauer A, Albrecht S (2015) Site suitability for tree species. Is there a positive  
578 relation between a tree species' occurrence and its growth? *Eur J Forest Res*  
579 134:609–621.
- 580 Dubuis A, Giovanettina S, Pellissier L *et al* (2013) Improving the prediction of plant  
581 species distribution and community composition by adding edaphic to topo-climatic  
582 variables. *J Veg Sci* 24:593–606
- 583 Ducouso A, Bordacs S (2004) EUFORGEN technical guidelines for genetic conservation  
584 and use for pedunculate and sessile oaks. *Quercus robur* and *Q. petraea*
- 585 Dullinger S, Gatttringer A, Thuiller W *et al* (2012) Extinction debt of high-mountain plants  
586 under twenty-first-century climate change. *Nat Clim Change* 2:619–622
- 587 Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen*. Verlag Eugen  
588 Ulmer, Stuttgart
- 589 Ellenberg H (1988) *Vegetation ecology of central Europe*. Cambridge University Press,  
590 Cambridge
- 591 Ewald J, Hédli R (2014) Spatial Modeling of Vegetation Potential. An Introduction. *Folia*  
592 *Geobot* 49:309–312
- 593 Falk W, Mellert K, Bachmann-Gigl U *et al* (2013) Bäume für die Zukunft: Baumartenwahl  
594 auf wissenschaftlicher Grundlage. *LWF aktuell* 94:8
- 595 Falk W, Mellert KH (2011) Species distribution models as a tool for forest management  
596 planning under climate change: risk evaluation of *Abies alba* in Bavaria. *J Veg Sci*  
597 22:621–634
- 598 Fang J, Lechowicz MJ (2006) Climatic limits for the present distribution of beech (*Fagus*  
599 L.) species in the world. *J Biogeogr* 33:1804–1819
- 600 Fischer R, Lorenz M, Granke O *et al* Forest condition in Europe: 2010 technical report of  
601 ICP forests
- 602 Franklin J (2010) *Mapping Species Distributions: Spatial Inference and Prediction*.  
603 Cambridge University Press, Cambridge
- 604 Freeman EA, Moisen G (2008) PresenceAbsence: An R package for presence absence  
605 analysis
- 606 Golub GH, Heath M, Wahba G (1979) Generalized cross-validation as a method for  
607 choosing a good ridge parameter. *Technometrics* 21:215–223
- 608 Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol*  
609 *Model* 135:147–186

- 610 Halvorsen R (2012) A gradient analytic perspective on distribution modelling.  
611 Sommerfeltia 35:1–165
- 612 Hanewinkel M, Cullmann DA, Michiels H-G *et al* (2014) Converting probabilistic tree  
613 species range shift projections into meaningful classes for management. J Environ  
614 Manage 134:153–165
- 615 Hiederer R (2013) Mapping soil properties for Europe—spatial representation of soil  
616 database attributes. Publications Office of the European Union, EUR26082EN  
617 Scientific and Technical Research series. Luxembourg
- 618 Hijmans RJ, Cameron SE, Parra JL *et al* (2005) Very high resolution interpolated climate  
619 surfaces for global land areas. Int J Climatol 25:1965–1978
- 620 Hijmans RJ, van Etten J (2014) raster: Geographic data analysis and modeling. R package  
621 version 2.2-31.
- 622 Hlásny T, Mátyás C, Seidl R *et al* (2014) Climate change increases the drought risk in  
623 Central European forests: What are the options for adaptation? Forestry Journal  
624 60:5–18
- 625 Kölling C, Hoffmann M, Gulder H-J (1996) Bodenchemische Vertikalgradienten als  
626 charakteristische zustandsgrößen von waldökosystemen. Z Pflanz Bodenkunde  
627 159:69–77
- 628 Kühn I (2007) Incorporating spatial autocorrelation may invert observed patterns. Divers  
629 Distrib 13:66–69
- 630 Lakatos F, Molnár M (2009) Mass mortality of beech (*Fagus sylvatica* L.) in South-West  
631 Hungary. Acta Silvatica et Lignaria Hungarica 5:75–82
- 632 Latron J, Llorens P, Gallart F (2009) The hydrology of Mediterranean mountain areas.  
633 Geography Compass 3:2045–2064
- 634 Leibundgut H (1984) Unsere Waldbäume. Eigenschaften und Leben. Huber, Frauenfeld
- 635 Lenoir J, Hattab T, Pierre G (2017) Climatic microrefugia under anthropogenic climate  
636 change: implications for species redistribution. Ecography 40:253–266
- 637 Lenoir J, Svenning J-C (2015) Climate-related range shifts—a global multidimensional  
638 synthesis and new research directions. Ecography 38:15–28
- 639 Lenoir J, Svenning J-C, Dullinger S *et al* (2012) The Alps Vegetation Database—a geo-  
640 referenced community-level archive of all terrestrial plants occurring in the Alps.  
641 Biodiversity and Ecology 4:331–332

- 642 Leuschner C, Köckemann B, Buschmann H (2009) Abundance, niche breadth, and niche  
643 occupation of Central European tree species in the centre and at the margin of their  
644 distribution range. *Forest Ecol Manag* 258:1248–1259
- 645 Ligot G, Balandier P, Fayolle A *et al* (2013) Height competition between *Quercus petraea*  
646 and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *Forest*  
647 *Ecol Manag* 304:391–398
- 648 Lopez-Senespleda E, Montero G Tipificación Ecológico-Selvícola de las Principales  
649 Especies Forestales Españolas, Madrid, Spain
- 650 Mátyás C, Ackzell L, Samuel CJA (2004) EUFORGEN technical guidelines for genetic  
651 conservation and use for Scots pine (*Pinus sylvestris*). Bioversity International
- 652 Mátyás C, Berki I, Czúcz B *et al* (2010) Future of beech in Southeast Europe from the  
653 perspective of evolutionary ecology. *Acta Silvatica et Lignaria Hungarica* 6:91–110
- 654 Meier ES, Kienast F, Pearman PB *et al* (2010) Biotic and abiotic variables show little  
655 redundancy in explaining tree species distributions. *Ecography* 33:1038–1048
- 656 Mellert KH, Ewald J (2014) Nutrient limitation and site-related growth potential of  
657 Norway spruce (*Picea abies* [L.] Karst) in the Bavarian Alps. *Eur J Forest Res* 133:433–  
658 451
- 659 Mellert KH, Fensterer V, Küchenhoff H *et al* (2011) Hypothesis-driven species  
660 distribution models for tree species in the Bavarian Alps. *J Veg Sci* 22:635–646
- 661 Mellert KH, Göttelein A (2013) Identification and validation of thresholds and limiting  
662 nutrient factors of Norway spruce by using new nutritional levels and modern  
663 regression. *Allg Forst Jagdztg* 184:197–203
- 664 Mellert KH, Deffner V, Küchenhoff H *et al* (2015) Modeling sensitivity to climate change  
665 and estimating the uncertainty of its impact. A probabilistic concept for risk  
666 assessment in forestry. *Ecol Model* 316:211–216
- 667 Mellert KH, Ewald J, Hornstein D *et al* (2016) Climatic marginality: a new metric for the  
668 susceptibility of tree species to warming exemplified by *Fagus sylvatica* (L.) and  
669 Ellenberg's quotient. *Eur J Forest Res* 135:137–152
- 670 Nieto-Lugilde D, Lenoir J, Abdulhak S *et al* (2015) Tree cover at fine and coarse spatial  
671 grains interacts with shade tolerance to shape plant species distributions across the  
672 Alps. *Ecography* 38:578–589
- 673 Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of  
674 temperate northern hemisphere trees and shrubs. *Ecol Monogr* 76:521–547

- 675 Panagos P, van Liedekerke M, Jones A *et al* (2012) European Soil Data Centre: Response  
 676 to European policy support and public data requirements. *Land Use Policy* 29:329–  
 677 338
- 678 Piedallu C, Gégout J, Perez V *et al* (2013) Soil water balance performs better than  
 679 climatic water variables in tree species distribution modelling. *Glob Ecol and Biogeogr*  
 680 22:470–482
- 681 Piedallu C, Gégout J-C, Lebourgeois F *et al* (2016) Soil aeration, water deficit, nitrogen  
 682 availability, acidity and temperature all contribute to shaping tree species  
 683 distribution in temperate forests. *J Veg Sci*:387–399
- 684 Rasztoivits E, Moricz N, Berki I *et al* (2012) Evaluating the performance of stochastic  
 685 distribution models for European beech at low-elevation xeric limits. *Idojárás*  
 686 116:173–194
- 687 Sánchez De Dios R, Hernández L, Montes F *et al* (2016) Tracking the leading edge of  
 688 *Fagus sylvatica* in North-Western Iberia: Holocene migration inertia, forest  
 689 succession and recent global change. *Perspect Plant Ecol* 20:11–21
- 690 Serra-Diaz JM, Keenan TF, Ninyerola M *et al* (2013) Geographical patterns of congruence  
 691 and incongruence between correlative species distribution models and a process-  
 692 based ecophysiological growth model. *J Biogeogr* 40:1928–1938
- 693 Stojanović DB, Kržič A, Matović B *et al* (2013) Prediction of the European beech (*Fagus*  
 694 *sylvatica* L.) xeric limit using a regional climate model. An example from southeast  
 695 Europe. *Agr Forest Meteorol* 176:94–103
- 696 Tegel W, Seim A, Hakelberg D *et al* (2014) A recent growth increase of European beech  
 697 (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress.  
 698 *Eur J Forest Res* 133:61–71.
- 699 Thuiller W (2013) On the importance of edaphic variables to predict plant species  
 700 distributions – limits and prospects. *J Veg Sci* 24:591–592
- 701 Tsiripidis I, Bergmeier E, Fotiatidis G *et al* (2012) Hellenic Beech Forests Database (Hell-  
 702 Beech-DB)
- 703 Walter H (1973) *Vegetation of the earth in Relation to Climate and the Eco-Physiological*  
 704 *Conditions*. English Universities Press
- 705 Whittaker RH (1970) *Communities and ecosystems*. Macmillan, London
- 706 Wolf H (2003) *EUFORGEN Technical Guidelines for genetic conservation and use for for*  
 707 *silver fir (Abies alba)*. Bioersivity International



- 708 Wood S (2006) Generalized additive models: an introduction with R. CRC press, Boca  
709 Raton
- 710 Wood S (2017) Mixed GAM Computation Vehicle with Automatic Smoothness  
711 Estimation. R-reference manual.
- 712 Zimmermann NE, Jandl R, Hanewinkel M *et al* (2013) Chapter 4 Potential future ranges  
713 of tree species in the Alps. In: Cerbu GA, Hanewinkel M, Gerosa G, Jandl R (eds)  
714 Management Strategies to Adapt Alpine Space Forests to Climate Change Risks,  
715 InTech, Chapters published August 28, 2013 under CC BY 3.0 license DOI:  
716 10.5772/56933

717 **Table 1:** Tree species-related information on shade tolerance (STOL), drought  
 718 tolerance (DTOL) according to Niinemets and Valladares (2006), physiological  
 719 optimum with respect to soil acidity according to Ellenberg (1988) and the  
 720 corresponding approximate range of the soil nutrient status (SNS) (see Table 3).  
 721

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

722

723

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

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

<b>No.</b>	<b>Institution (Abbreviation)</b>	<b>Data Source (Abbreviation)</b>	<b>Full names of Institution / Data source</b>
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 <sup>4</sup>	National Forest Inventory
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

726

727

728 **Table 3:** Soil chemical properties used for classification of the soil nutrient status (SNS) of terrestrial soil types of the European Soil  
 729 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	oligotrophic	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				

730

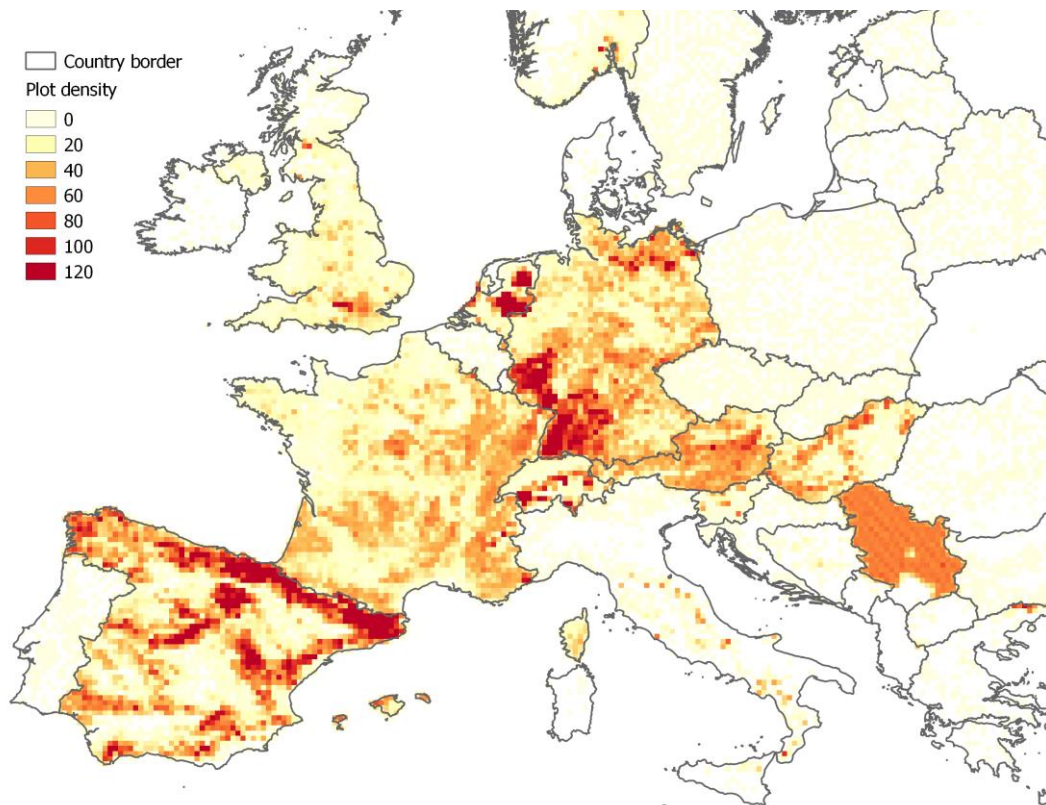
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732 **Table 4** Results of the model evaluation involving the Akaike information criterion (AIC), the generalized cross validation criterion  
 733 (GCV) the true skill statistic (TSS) and the area under the curve statistic (AUC). The validation is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

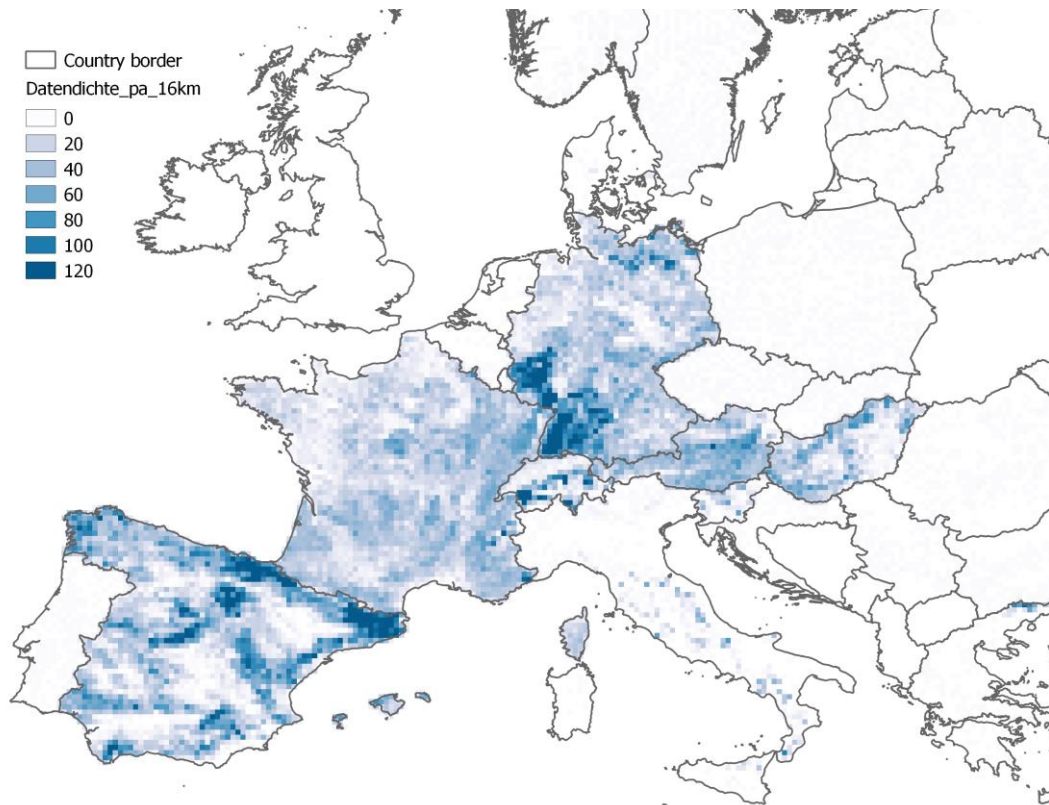
Species	Model	AIC	GCV	TSS	AUC
Aalba	SA only	7829.793 $\pm$ 1.33e+02	73.673 $\pm$ 1.33e+00	0.594 $\pm$ 2.55e-02	0.801 $\pm$ 1.32e-02
	Full	4652.257 $\pm$ 1.26e+02	51.604 $\pm$ 1.35e+00	0.601 $\pm$ 2.13e-02	0.841 $\pm$ 1.16e-02
Fsylv	SA only	14215.162 $\pm$ 2.51e+02	130.175 $\pm$ 2.41e+00	0.473 $\pm$ 1.81e-02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

736

737 **Figure 1:** Plot density of presence-only records (Figure 1a upper panel) and plot  
738 density of presence-absence records (Figure 1b lower panel) in Southern and  
739 Central Europe as well as adjacent regions in a 16x16 km grid. In Northern Europe  
740 the plots density is constantly low (ca. 1 plot per grid cell, light grey).  
741



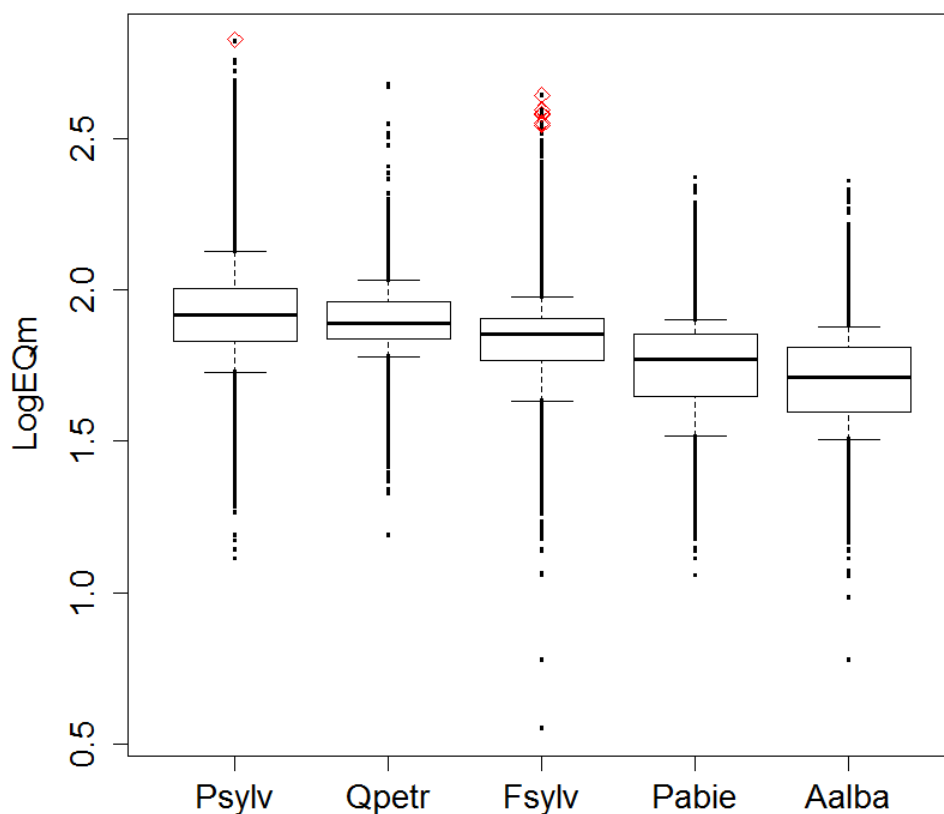
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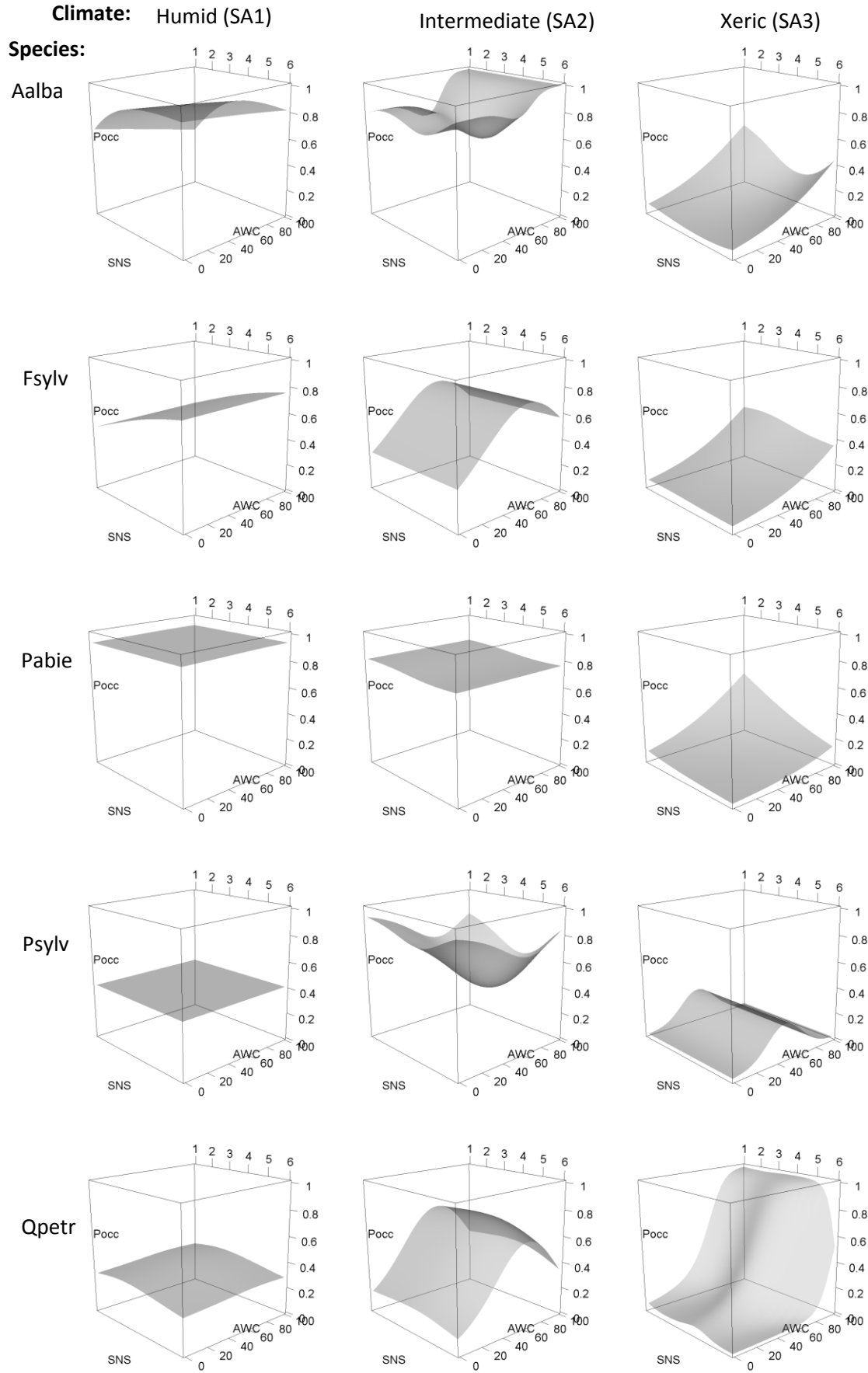


745 **Figure 2:** Frequency distribution of the modified Ellenberg's quotient (LogEQm)  
 746 indicating summer aridity for five major forest tree species of Central Europe  
 747 (*Abies alba* = Aalba, *Fagus sylvatica* = Fsylv, *Picea abies* = Pabie, *Pinus sylvestris* =  
 748 Psylv, *Quercus petraea*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



756

757 **Figure 3:** Results of the model for the five tree species from the top in  
758 alphabetical order (Aalba to Qpetr, species abbreviations see Figure 1). All graphs  
759 show the response surface of the probability of occurrence ( $P_{occ}$ ) against available  
760 water capacity (AWC) and soil nutrient status (SNS). First column: Mean  $P_{occ}$  at  
761 the summer aridity level at 1<sup>st</sup> decile (humid climate, SA1); Second column: Mean  
762  $P_{occ}$  at 2.-9. decile (intermediate climate, SA2); Third column: Mean  $P_{occ}$  at the  
763 summer aridity level at 10th decile (xeric climate, SA3). Number of presence-  
764 absence records ~213,900 are reduced by data aggregation to 107 (Aalba), 112  
765 (Fsylv), 105 (Pabie), 115 (Psylv), 114 (Qpetr). All main effects of the models are  
766 significant ( $p < 0.05$ ), except  $\beta_1$  for SA1 of Aalba and Fsylv (see Equ. 1). AWC and  
767 SNS effects in a xeric climate (SA3, right column) indicating possible  
768 compensation by the soil are significant for all species except SNS for Psylv.  
769  
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774

**Supplementary material****775 1. Species description**

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

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

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

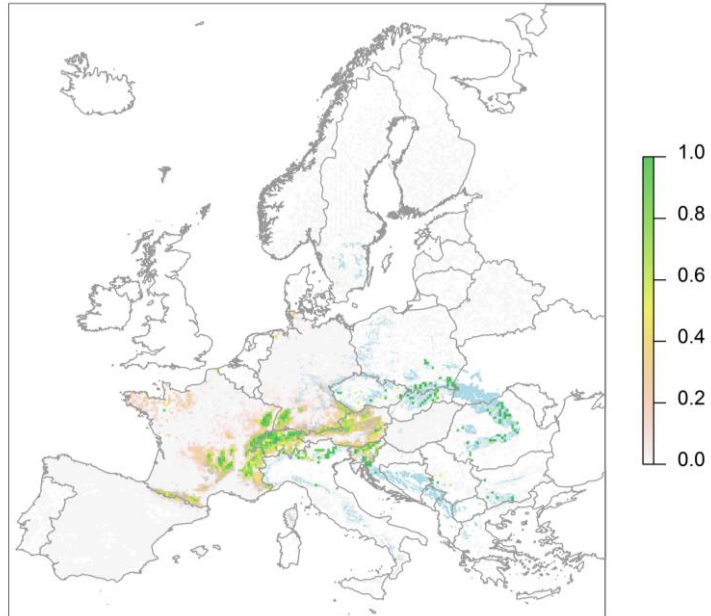
797 *P. sylvestris* is widely distributed throughout Eurasia. *P. sylvestris* is a light-  
798 demanding weak competitor (Niinemets and Valladares ,2006). Although the species  
799 tolerates all kinds of site conditions it grows best on fertile soils (intermediate SNS,  
800 Ellenberg, 1988; Leibundgut, 1984), where, however, it is outcompeted by *P. abies* or  
801 broad-leaved tree species such as *F. sylvatica* (Ellenberg and Leuschner, 2010).  
802 Consequently, the species occurs mainly on poor, sandy soils, rocky outcrops or peat  
803 bogs, i.e. at sites where most other tree species are unable to thrive (Mátyás et al.,  
804 2004).

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

808 Bordacs, 2004). It is a light-demanding deciduous tree and more drought tolerant than *F.*  
809 *sylvatica* (Niinemets and Valladares, 2006). In Central Europe, it is preferably found on  
810 dry acidic soils (Ellenberg and Leuschner, 2010).  
811

812 **2. Observed probability of occurrence**

813

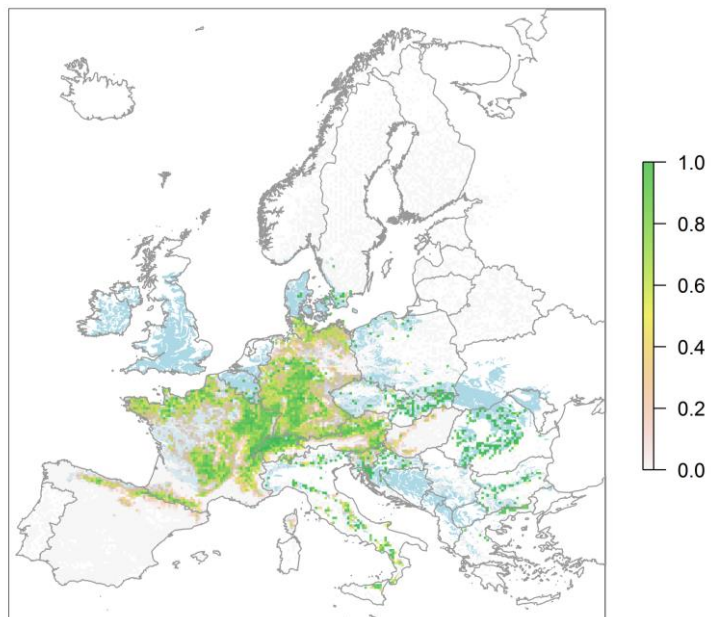


814

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

818

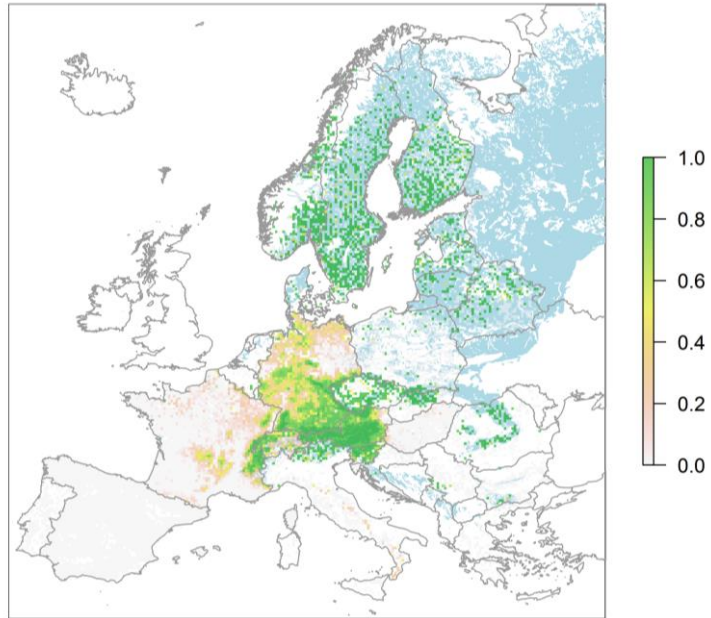
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820

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

824

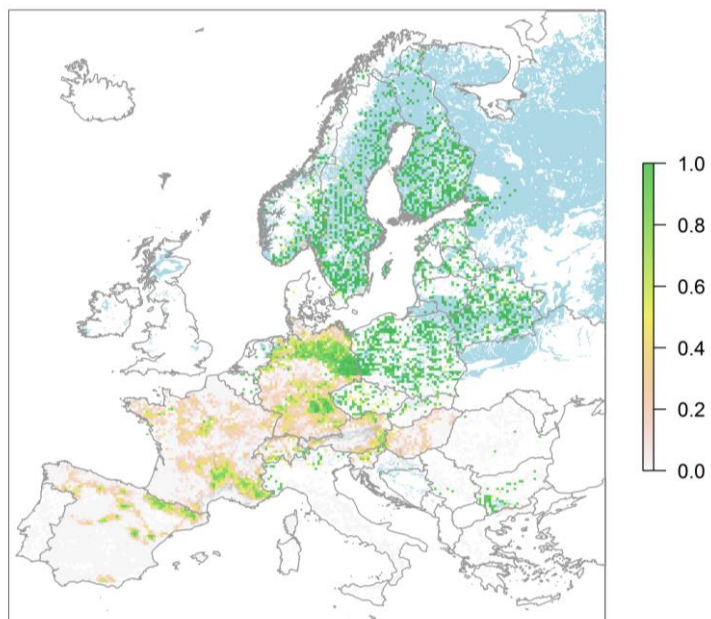


825

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

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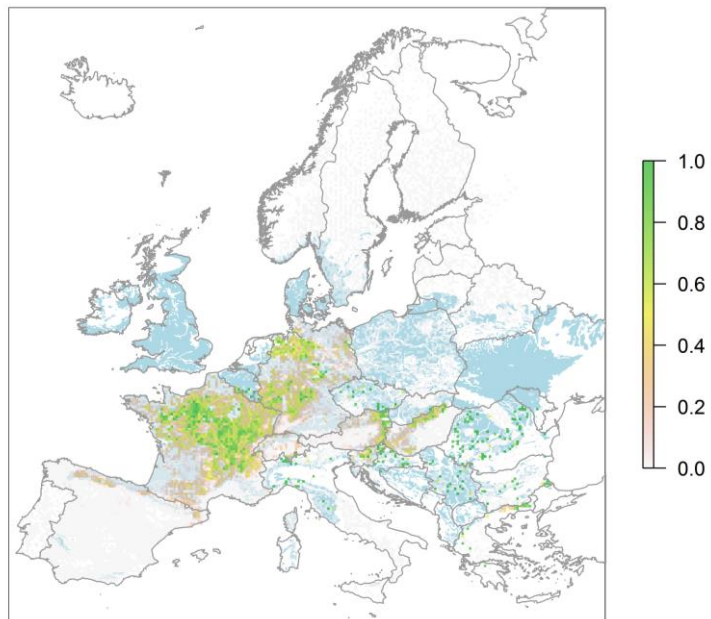
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832 **Fig. S4** Probability of occurrence of *Pinus sylvestris* observed within a 16 km raster of  
833 Europe (see legend). Distribution area of the species according to Bohn et al. (2003) is  
834 displayed in bluish background colors.

835

836



837

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

841

842 **Soil data**

843 **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  
844 types from FAO (1974).

845

<b>Order</b>	<b>Trophic status</b>	<b>Soil types</b>
1	Oligotrophic	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

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847