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

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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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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 (EQm) 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 (LogEQm) 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 β_0 – β_2 , where β_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

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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		Ecological optimum	
	Shade (STOL)	Drought (DTOL)	in the soil gradient			
			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 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 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

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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				

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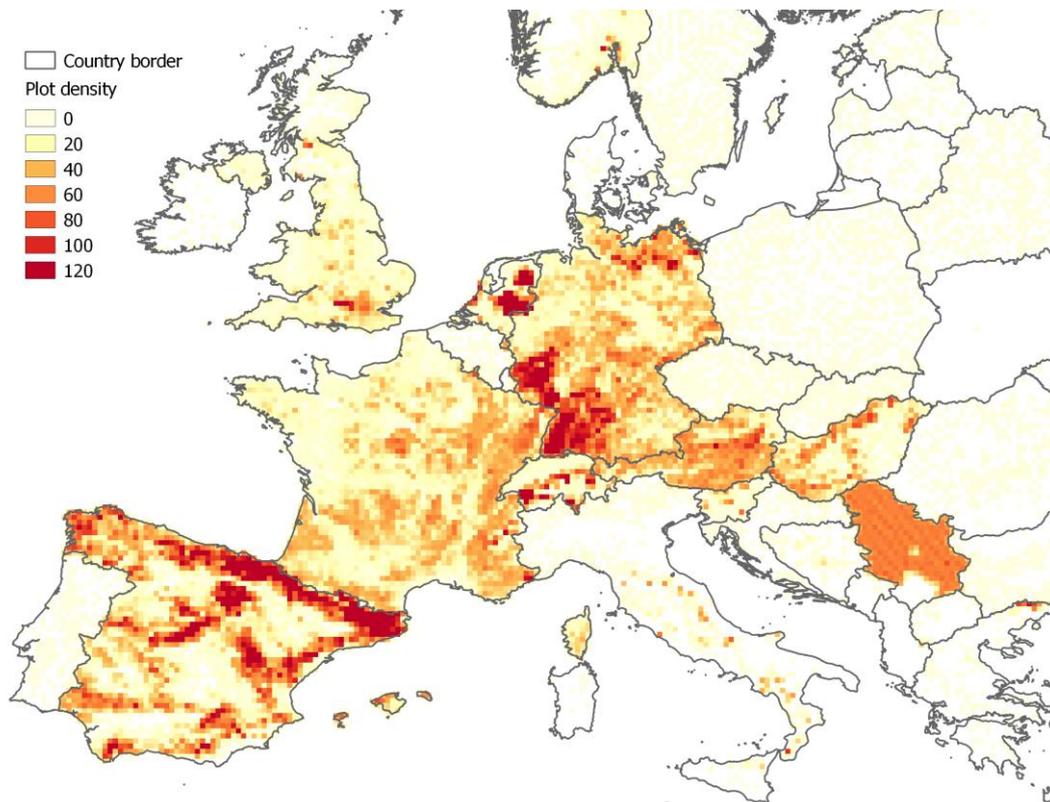
731

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' ($p < 0.05$).

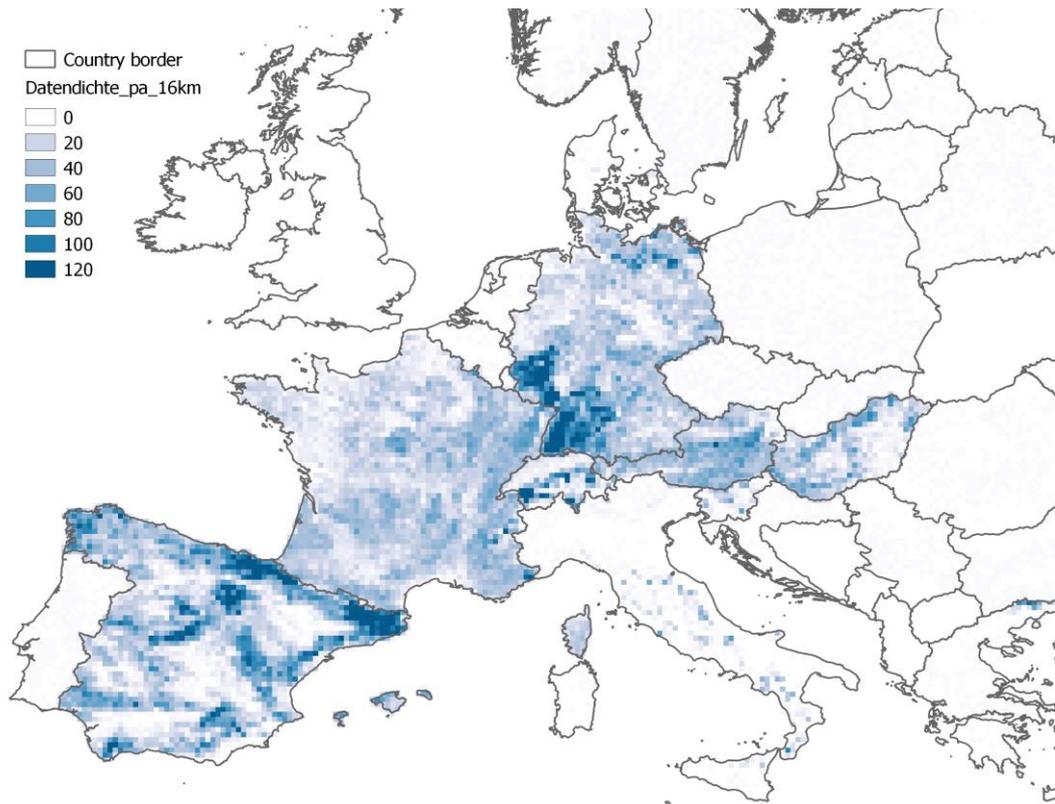
Species	Model	AIC	GCV	TSS	AUC
Aalba	SA only	7829.793 \pm 1.33e+02	73.673 \pm 1.33e+00	0.594 \pm 2.55e-02	0.801 \pm 1.32e-02
	Full	4652.257 \pm 1.26e+02	51.604 \pm 1.35e+00	0.601 \pm 2.13e-02	0.841 \pm 1.16e-02
Fsylv	SA only	14215.162 \pm 2.51e+02	130.175 \pm 2.41e+00	0.473 \pm 1.81e-02	0.741 \pm 9.49e-03
	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

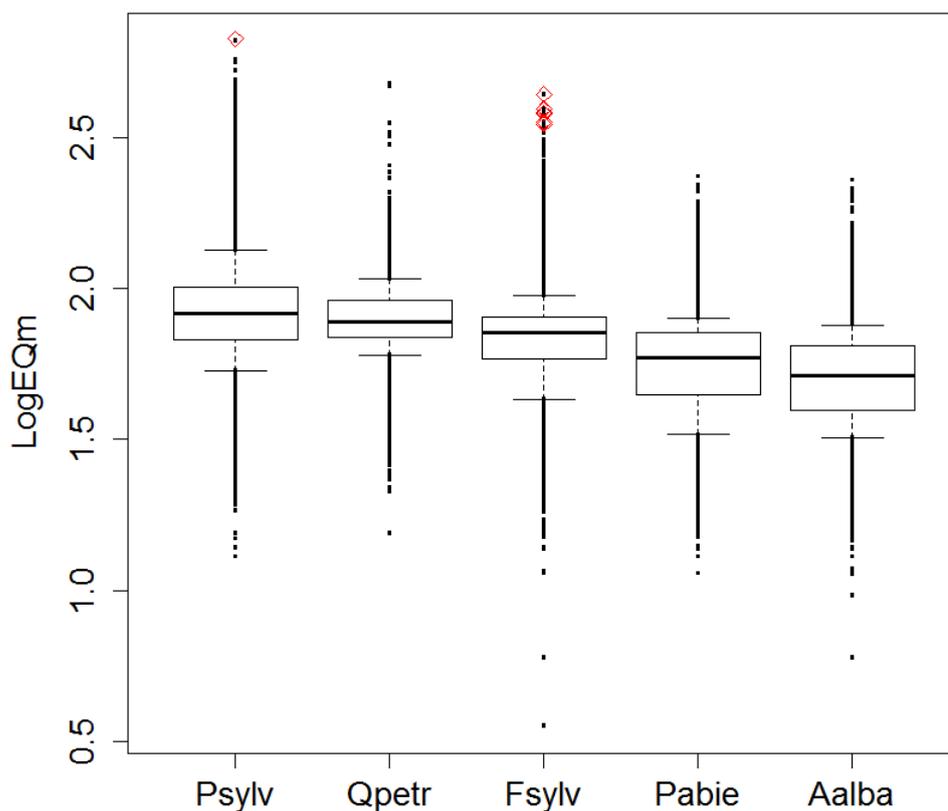


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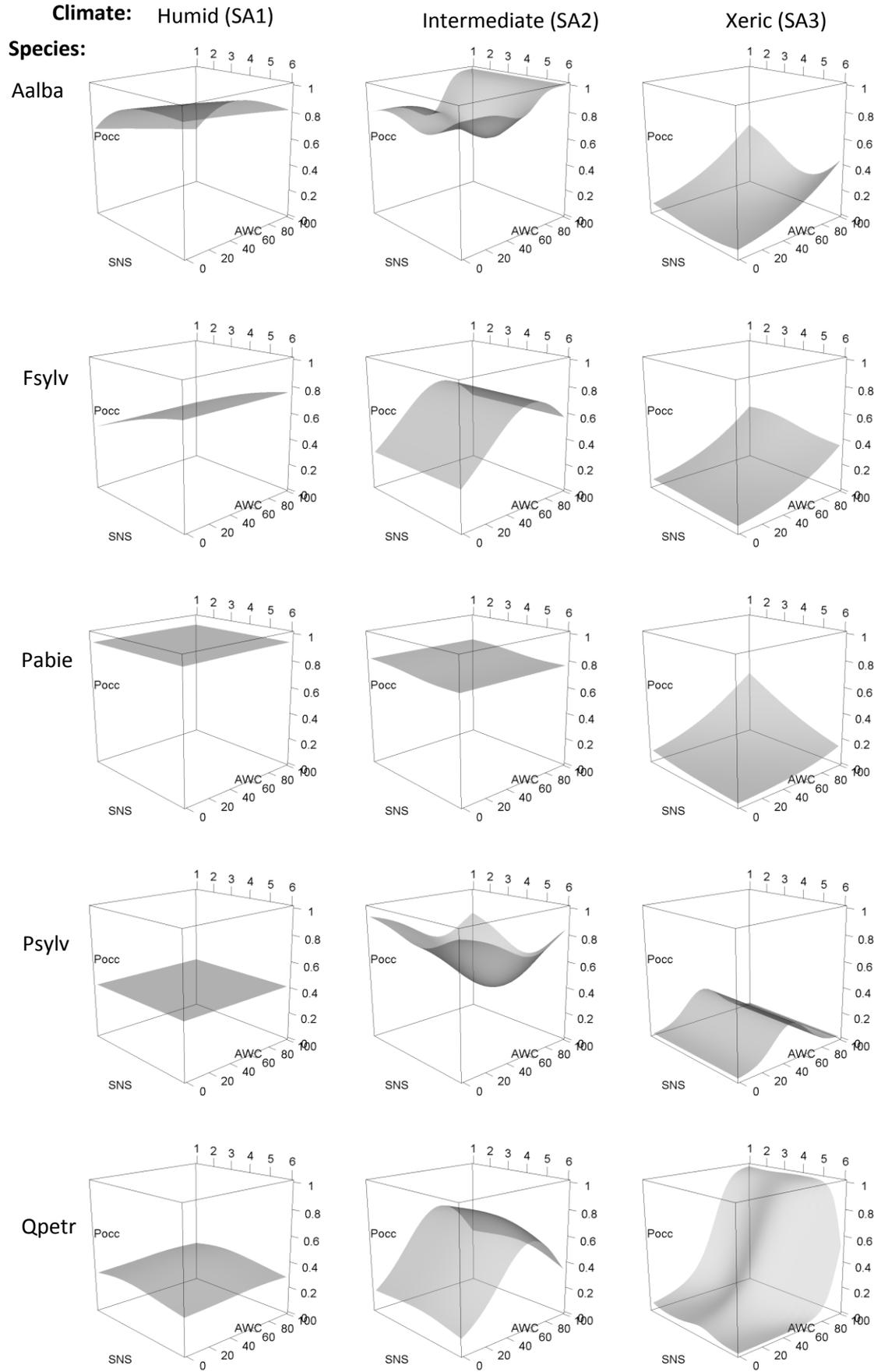
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744

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 9th decile (SA2). Accordingly, points below the lower whisker
 751 represent the 1st decile (SA1, humid climatic conditions) and points above the
 752 upper whisker represent the 10th 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 1st 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 β_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.
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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).

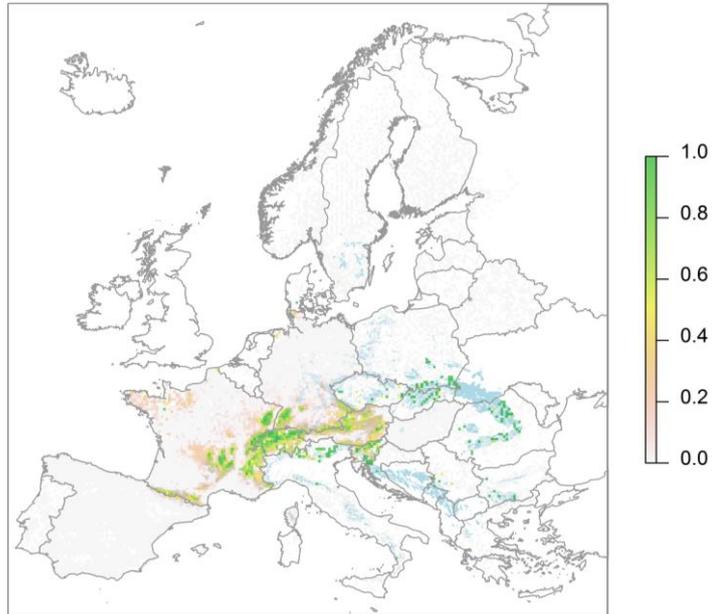
797 *P. sylvestris* is widely distributed throughout Eurasia. *P. sylvestris* is a light-
798 demanding weak competitor (Niinemets and Valladares ,2006). Although the species
799 tolerates all kinds of site conditions it grows best on fertile soils (intermediate SNS,
800 Ellenberg, 1988; Leibundgut, 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

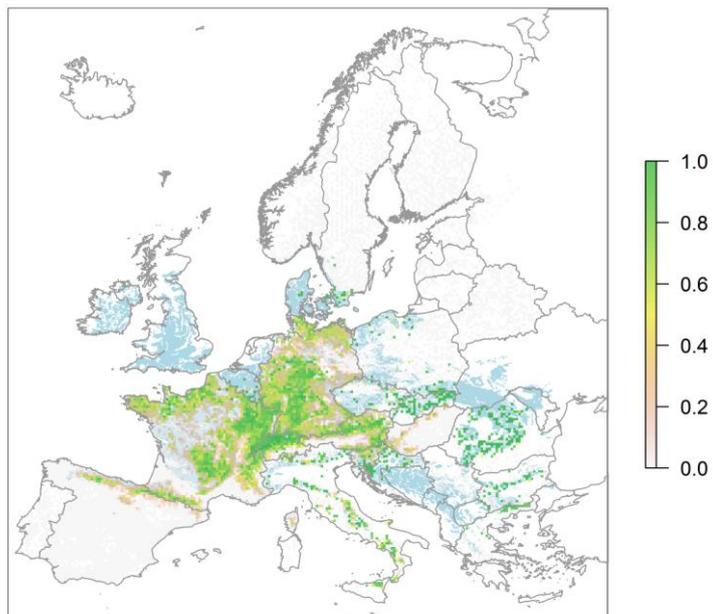


814

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

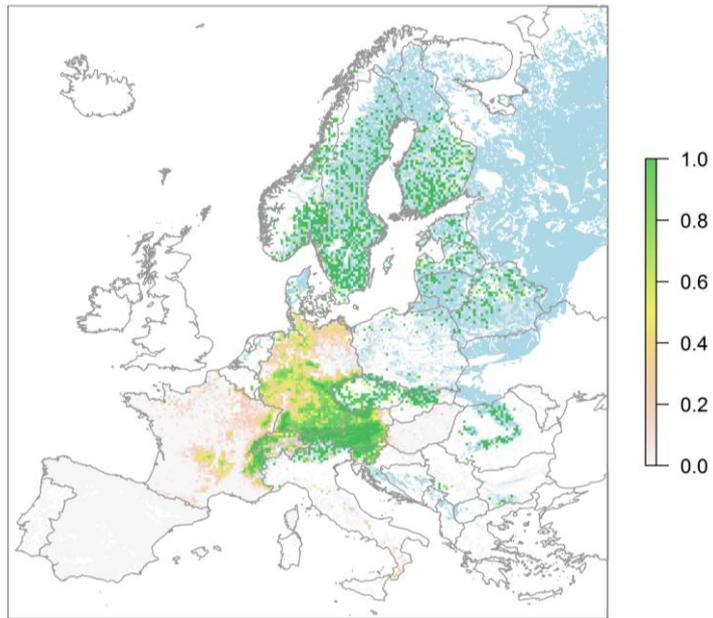
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820

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

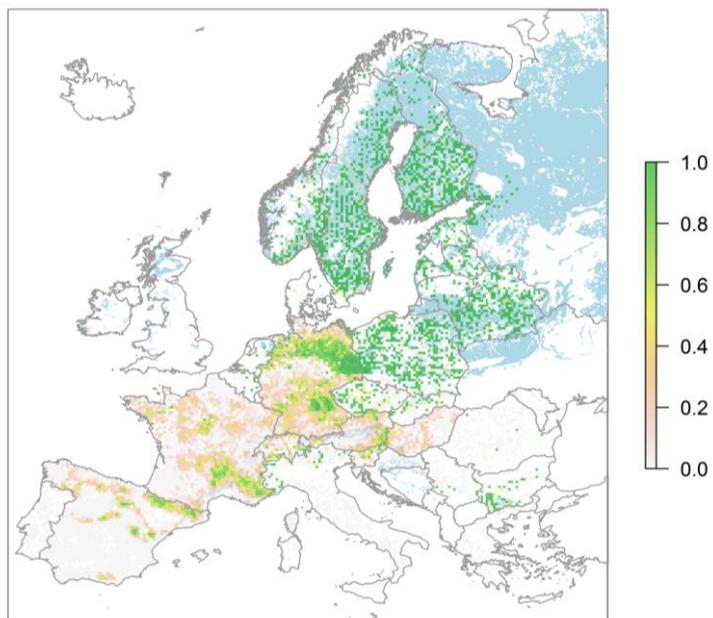


825

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.

829

830

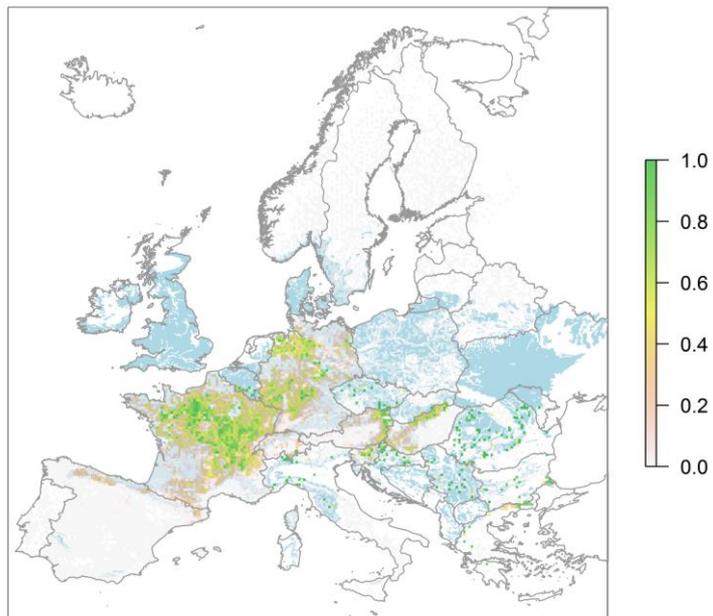


831

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

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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

Order	Trophic status	Soil types
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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