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► To cite this version:

Karl H. Mellert, Jonathan Roger Michel Henri Lenoir, Susanne Winter, Christian Kölling, Isabel Dorado-Liñán, et al.. Soil water storage appears to compensate for climatic aridity at the xeric margin of European tree species distribution. *European Journal of Forest Research*, 2018, 137 (1), pp.79-92. 10.1007/s10342-017-1092-x . hal-02357326

HAL Id: hal-02357326

<https://hal.science/hal-02357326>

Submitted on 24 Nov 2019

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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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Keywords: climatic aridity, edaphic conditions, European Soil Database, forest ecosystems, macroecology, soil nutrient status

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

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Acknowledgements

This study was funded by the Federal Ministry of Food and Agriculture as well as the Federal Environment Ministry of Germany (project number 28WB4058) and the Bavarian State Forest Administration (project number W42), an authority of the Ministry for Nutrition, Agriculture and Forestry. We acknowledge ICP Forests and the involved country representatives for providing Level-I data. Our thanks also go to Nikolaos Grigoriadis from Greece, Aleksander Marinšek, Alexey Zharov from Germany and Doganay Tolunay from Turkey for data provision. However, the Turkish data could not be used in this analysis, as the ESDB do not contain

76 soil data from this country. Additionally we are deeply indebted to our
77 colleagues, Solti György, Markus Neumann and Heino Polley for providing us
78 access to the national forest inventories of Hungary, Austria, and Germany,
79 respectively, as well as Monika Konnert (Bavarian Institution for Forest Seeding
80 and Planting) for providing data from provenance plots. Furthermore, we thank
81 all other contributors of vegetation databases and other data sources as well as
82 two anonymous reviewers whose comments helped to clarify important issues.
83

Abstract

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

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, Beauregard 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 (Beauregard 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**

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

Target species

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

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

Table 1: Species traits

Tree distribution data

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

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

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Figure 1: Plot density in Central and Southern Europe

Table 2: Data overview – Number of plots by countries

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Climate data

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

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

Figure 2: Boxplot for LogEQm

Soil data

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

Soil nutrient status (SNS) variable was defined as an ordinal variable with 6 levels characterizing the availability of macro- and micro nutrients in the entire soil profile (Table 3) along a gradient from strongly acidic to calcareous or alkaline soils. Due to acidification and/or substrate stratification chemical properties exhibit characteristic vertical gradients in soil profiles (Kölling et al.,

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

Table 3: *Classification of soil nutrient status*

Data aggregation

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

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

302

303 Statistical modelling

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

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

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

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)

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

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

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

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

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

Results

Modeling results

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

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

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

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

Table 4: Model evaluation

Discussion

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

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

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

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

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

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

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

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

503

504 **Conclusions**

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

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

518

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

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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

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

Index number	Soil nutrient status (SNS)	Short characteristic determining the nutrition status	Soil reaction	Base saturation and ionic strenght	Typical nutrient deficiencies for not adapted plants
1	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				

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).
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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 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

1. Species description

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

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

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

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

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

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

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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.

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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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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.

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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).

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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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