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Research article

Phenotypic correlates of potential range size and range filling in European trees



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ABSTRACT

Understanding the biological correlates of range sizes in plant species is important to predict the response of species to climate change. We used climate envelope models to estimate species' potential range size and range filling for 48 European tree species. We hypothesized that potential range size relates to the climatic tolerances of plant species, and that the degree of range filling is influenced by species dispersal. We tested these hypotheses using, for each species, estimates for tolerance to cold and drought, type of dispersal, fruit size and seed size. Consistent with previous observations, we found that both the size of potential ranges and range filling increase from south to north. Species tolerance to temperature and water stress, as well as their dispersal-related traits also showed marked spatial patterns. There was, moreover, a significant positive partial correlation between cold tolerance and potential range size, when drought tolerance was partialled out, and a non-significant partial correlation between drought tolerance and potential range size, with cold tolerance partialled out. Range filling was not significantly larger in species dispersed by wind than in those dispersed by animals. There was a negative correlation between seed mass and range filling, but its statistical significance varied across different subsets of species and climate envelope algorithms; the correlation between fruit length and range filling was not significant. We conclude that climatic tolerances and dispersal traits influence species range size and range filling, and thus affect the range dynamics of species in response to global change. Using traits will therefore help to predict future distribution of species under climate change.

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Introduction

The idea that climate limits the distributions of plants was formalized through the 'law of tolerance' formulated by Shelford (1913). The hypothesis states that the tolerance of plant species to both deficiency and excess of factors that affect organisms determines the range of values along an environmental axis in which it can survive, that is the tolerance range. More recent theoretical studies propose that birth and death rates are, at least in part, controlled by the interplay between the abiotic variables

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and the tolerances of species to these variables (Osmond et al., 1987), with populations declining as conditions depart from the species-specific optima (Hengeveld and Haeck, 1982). It follows from this reasoning that a positive relationship between the climatic tolerances of species and their range sizes should exist, since greater tolerances would necessarily imply that greater amounts of environmental suitability would be available for species (Williams et al., 2007). Also, range size might be controlled by the dispersal ability of species (Baselga et al., 2012). The 'site colonization hypothesis' (Lester et al., 2007) is likely to operate when species had relatively little time to expand their ranges from glacial refugia (Svenning et al., 2008). In this case, a relationship between dispersal-related traits and the occupied fraction of the potential range ('range filling') would be expected. Range size may also be time-limited over macroevolutionary scales, increasing with species age (Paul et al., 2009) as originally proposed by Willis (1922) in his 'age-and-area hypothesis', although the predictions arising from this hypothesis have not been confirmed in a number of studies (e.g. Jablonski, 1987). In conclusion, the size of geographical ranges should at least partly be explained by species-specific tolerances and dispersal capacities.

Many studies have correlated the range of species with extrinsic factors such as climate, topography or distances to Pleistocene refugia (Svenning and Skov, 2004; Angert et al., 2011), but very few have integrated at large scales the role of phenotypic traits and other intrinsic factors to understand why some species inhabit and colonize different regions. Here, we focus on phenotypic correlates of potential range size and range filling as provided by climate envelope models (CEMs). We analyze trait-based drivers of variation in range size using information about the distribution of 48 European tree species, their species-specific tolerances to climate, and their dispersal capacities, while taking into account potential phylogenetic effects on range heritability (Diniz-Filho et al., 2012a,b). We only use climatic variables to model the potential distribution of species for making our findings most relevant to understand the future distribution of species under climate change.

Specifically, we determine the spatial patterns (1) in potential range size, and range filling of European tree species; (2) of tree species tolerance to cold and drought; and (3) of traits related to species dispersal such as vector of dispersal, fruit size and seed size. We hypothesize also that the potential range sizes of species are related to their climatic tolerances, i.e. tolerance to cold and drought. We specifically test (4) whether the potential range size of tree species correlates with cold and drought tolerance. Finally, we investigate (5) whether range filling is affected by the type of dispersal and diaspore (fruit or seed) size. We hypothesize that range filling will increase with increasing dispersal ability. Therefore, range filling should increase with decreasing seed size, because small-seeded species tend to be dispersed by wind over greater distances than large-seeded, zoochorous tree species (Guo et al., 2000; Morin and Chuine, 2006; Cousens et al., 2008). All analyses were carried out after accounting for phylogenetic signals.

Material and methods

Source data on species distribution and climatic conditions

The study area encompasses Europe between latitudes 34–72° N and longitudes 11° W to 32° E. Species records east of this geographical window were excluded, because of uneven quality of the original species distributions data in these areas (Williams et al., 2000). Within this constrained geographical window, we measured range size of all major European tree species for which trait data, and consistently mapped distributions, were

Table 1

List of study species, their potential and realized range size, and range filling. Nomenclature follows Atlas Flora Europaea.

Species	Potential range (Mio km ²)	Realized range (Mio km ²)	Range filling (%)
<i>Abies alba</i>	3.1	1.1	34.7
<i>Abies cephalonica</i>	0.5	0.1	10.7
<i>Alnus cordata</i>	0.1	0.0	35.0
<i>Alnus glutinosa</i>	3.8	4.0	104.2
<i>Alnus incana</i>	3.1	2.6	85.5
<i>Betula pendula</i>	3.4	3.6	106.7
<i>Betula pubescens</i>	3.3	3.3	99.1
<i>Carpinus betulus</i>	2.8	2.4	83.0
<i>Castanea sativa</i>	3.2	0.6	18.9
<i>Celtis australis</i>	3.2	0.6	19.0
<i>Corylus colurna</i>	1.8	0.2	11.9
<i>Cupressus sempervirens</i>	1.2	0.0	2.5
<i>Fagus orientalis</i>	0.3	0.1	28.3
<i>Fagus sylvatica</i>	3.0	2.6	85.4
<i>Juglans regia</i>	2.1	0.3	13.4
<i>Juniperus excelsa</i>	0.6	0.0	8.6
<i>Juniperus thurifera</i>	2.6	0.1	4.8
<i>Larix decidua</i>	1.9	0.4	20.4
<i>Laurus nobilis</i>	1.3	0.4	27.5
<i>Ostrya carpinifolia</i>	2.9	0.6	20.9
<i>Picea abies</i>	2.4	2.1	87.3
<i>Pinus brutia</i>	0.4	0.0	5.9
<i>Pinus cembra</i>	1.7	0.2	10.7
<i>Pinus halepensis</i>	1.3	0.3	26.2
<i>Pinus heldreichii</i>	1.7	0.1	4.8
<i>Pinus mugo</i>	2.6	0.5	21.1
<i>Pinus nigra</i>	2.8	0.5	17.0
<i>Pinus peuce</i>	0.8	0.1	8.0
<i>Pinus pinaster</i>	1.2	0.4	29.8
<i>Pinus pinea</i>	0.9	0.2	27.3
<i>Pinus sylvestris</i>	3.6	2.8	78.3
<i>Platanus orientalis</i>	1.3	0.2	16.5
<i>Populus alba</i>	3.3	1.7	51.9
<i>Populus nigra</i>	3.1	2.2	72.3
<i>Populus tremula</i>	3.9	4.1	105.7
<i>Quercus cerris</i>	2.5	0.9	36.1
<i>Quercus faginea</i>	1.3	0.4	28.7
<i>Quercus frainetto</i>	2.1	0.5	26.0
<i>Quercus ilex</i>	1.9	1.0	54.7
<i>Quercus petraea</i>	3.0	2.9	96.2
<i>Quercus pubescens</i>	2.9	0.5	15.8
<i>Quercus pyrenaica</i>	1.1	1.6	140.5
<i>Quercus suber</i>	1.0	0.4	41.7
<i>Salix alba</i>	3.5	3.0	85.9
<i>Salix caprea</i>	3.8	4.0	104.6
<i>Salix fragilis</i>	3.3	2.5	74.9
<i>Taxus baccata</i>	3.4	1.6	47.3
<i>Ulmus glabra</i>	3.3	2.8	85.4
<i>Ulmus laevis</i>	2.4	1.3	56.0

available. We defined trees as self-supporting woody species reaching ≥ 20 m in height, or species falling just under this limit (More and White, 2003). Species selection was constrained by data availability on geographical distribution, climatic tolerances and dispersal capacities. The final list contained 48 tree species with complete information (Table 1). Nomenclature and information about the distributions of the selected species were taken from Atlas Flora Europaea, AFE (Jalas and Suominen, 1972–1996; www.fmnh.helsinki.fi/english/botany/afe). The records in AFE were mostly from native origin, though populations with unknown status were also considered if they had been present for a long time. We restricted modeling to species occurring in at least ten AFE cells to avoid problems of fitting models with extremely small sample sizes (Stockwell and Peterson, 2002; Munguía et al., 2012). The AFE used near-equal area mapping units of 50 km \times 50 km (Williams et al., 2000; Nogués-Bravo and Araújo, 2006), based on the Universal Transverse Mercator projection and the Military Grid Reference System, hereafter referred to as AFE cells.

Data for climate envelope modeling included three variables developed for Europe in the context of the EU-funded ATEAM project (www.pikpotsdam.de/ateam; Schroter et al., 2005), covering the period 1961–1990 with a spatial resolution of 0.5 °C: (1) growing degree days (GDD), calculated following Prentice et al. (1992) as the number of days with more than 5 °C; (2) minimum temperature (T_{\min}), the mean temperature of the coldest month; and (3) a moisture index (MI), calculated as the ratio of mean annual actual evapotranspiration to the mean annual potential evapotranspiration. These variables are often seen as controlling factors of the environmental processes limiting the spatial distribution of plant species (Sakai and Weiser, 1973; Prentice et al., 1992; Huntley et al., 1995; Sykes et al., 1996). Although climatic extreme events such as heat waves or severe droughts can constrain the distributions of species, it has been shown that they do not markedly improve the ability of climate envelope models for predicting the distribution of species (see Zimmermann et al., 2009).

Indicators of cold and drought tolerances and dispersal ability

We used hardiness, a horticultural expert assessment ranging from zero tolerance of frost (0%) to effectively total resistance at –40 °C (100%), as an estimate of cold tolerance (More and White, 2003). Homogenized drought tolerance rank values were taken from Niinemets and Valladares (2006), ranging from 1 ('very intolerant') to 5 ('very tolerant'). These values were obtained from field records of presence and abundance of each tree species in contrasting environmental conditions. Niinemets and Valladares (2006) combined hundreds of sources from forester records to scientific publications, and from PhD studies to questionnaires sent to scientists that have published work in less accessible journals in countries like China or Russia. Common trees in all rankings were used to cross calibrate the relative order of the species according to their tolerance to drought conditions.

To evaluate the predictive power of dispersal-related traits on range variation, we compiled information on the type of dispersal, and fruit and seed size. Each plant species was classified as wind- or animal-dispersed. Both the effects of fruit and seed size were tested, since for some species the whole fruit (including accessory tissue and more than one seed) is the dispersal unit. The length of the major axis of the fruit was used, since it is more readily measured and was available for almost all species. With respect to seed size, hereon called seed mass, we used the fresh mass of single seeds, as this has been recorded for many more taxa than dry mass. Fruit length and seed mass were significantly correlated ($r^2 = 0.88$, $P < 0.001$). Data on both dispersal traits were systematically compiled by searching through the British Ecological Flora (Fitter & Peat, 1994), FRUBASE (Jordano, 1995), TREE database (www.fem.wur.nl; University of Wageningen), B&T World Seeds (<http://b-and-t-world-seeds.com>), and BROT (Paul et al., 2009). Two additional sources, i.e. Herrera (1987) and García-Fayos (2001), were used for some Mediterranean species.

Measuring ranges, potential ranges and range filling of species

We used climate envelope models, CEMs, to estimate the potential range size (P_{clim}) of each species. Range size was the sum of the terrestrial surface area of climatically suitable AFE cells for each species across Europe. The area of every cell was measured as a function of three factors: (1) cell position within the AFE reticule, (2) marine area within every AFE cell, and (3) the area added by topographic variation (Nogués-Bravo and Araújo, 2006). The surface area for the European AFE grid system is freely available at www.ibiochange.mncn.csic.es/projects/former-projects/alarm/outputs/data. We measured range filling as the ratio

between realized and potential range ($R/P_{\text{clim}} * 100$), following Svenning and Skov (2004).

Climate Envelope Models statistically describe the geographical distribution of a given species (Peterson et al., 2011). CEMs face several challenges in the enduring task of modeling abiotic range limitations in terms both of theoretical assumptions, such as species–climate equilibrium or the stability of climatic niches through time (Nogués-Bravo, 2009; Araújo and Peterson, 2012). Furthermore, there are several methodological issues that can affect the estimates of potential ranges of species such as the choice of the model algorithm (e.g. Pearson et al., 2006), the choice of the pseudo-absences or background used for calibration of the models (Peterson et al., 2011; Barbet-Massin et al., 2012), the choice of the cut-off point to transform probabilities of occurrence or habitat suitability scores into estimates of presence and absence (e.g. Nenzén and Araújo, 2011), and the choice of the consensus methodology for combining model results in an ensemble (e.g. Garcia et al., 2012). However, careful implementations of CEMs have demonstrated the usefulness of the models to infer key properties of species distributions or distribution dynamics, even when independent data are utilized for validation (Araújo et al., 2005; Nogués-Bravo et al., 2008; Dobrowski et al., 2011; Roberts and Hamann, 2012). For example, recent studies showed that CEMs have successfully predicted the temporal trends in population dynamics estimated using ancient DNA and coalescence models (Lorenzen et al., 2011; Metcalf et al., 2014).

We estimated potential climatic ranges of tree species using two model classes that use presence data: Bioclim (Busby, 1986) and Mahalanobis Distance (Farber and Kadmon, 2003), fitted with three bioclimatic parameters (GDD, T_{\min} , MI) as explained above. These two model classes were implemented to account for the variation in the size of the potential ranges that may arise as a consequence of the different modeling procedure (see for a review Araújo and New, 2007). Giving the gradient from potential to observed species distribution, presence-only methods are expected to better reflect the potential range of species compared with more complex model classes such as, for example, neural networks (see Jiménez-Valverde et al., 2008). Furthermore, both Bioclim and Mahalanobis Distance have been used in similar studies of range filling, thus ensuring that results in our study are comparable across a broader literature set (e.g. Svenning and Skov, 2004; Munguía et al., 2008, 2012).

Distribution records were divided randomly into a set for calibration and a set for validation, comprising 80% and 20% of the species ranges, respectively; this procedure was repeated 20 times. For each model class, all 20 cross-validated models were projected and a final consensus map of the potential distributions of the species was generated by unweighted averaging of all projections, i.e. projections overlaying at least 50% of the times were retained (cf. Araújo et al., 2005; Garcia et al., 2012). For each partition a confusion matrix expressing matches and mismatches of observed and predicted occurrences in the cross-validation dataset was also obtained. To minimize the effect of outliers, species records were re-sorted along each variable, and the records that lay within a certain percentile range of the data were used for characterizing the envelopes. Here, we applied a percentile range of 95% for BIOCLIM and 75% for Mahalanobis Distance, which is the default option in most studies using these approaches (e.g. Nogués-Bravo et al., 2008; Munguía et al., 2012). Models were implemented using the BIOENSEMBLES platform for computer-intensive ensemble forecasting (see Rangel et al., 2009).

Potential range sizes and range filling, estimated with the two presence-only model classes (Bioclim and Mahalanobis Distance) were highly correlated between them ($r = 0.883$, $P < 0.001$, and $r = 0.921$, $P < 0.001$, respectively). Potential range sizes estimated

by Bioclim ($\bar{x} = 2.4$ million km², SD = 1.0 million km²) were larger than potential range sizes estimated by Mahalanobis Distance ($\bar{x} = 1.8$ million km², SD = 0.9 million km²). Consequently, range filling values estimated with Mahalanobis ($\bar{x} = 37.2\%$) were greater than with Bioclim ($\bar{x} = 35.7\%$). With Bioclim there were fewer species with potential ranges projected to be smaller than observed ranges: five species versus ten in Mahalanobis (Table 1). Two factors can cause potential ranges to be smaller than observed ones. First, we forced CEMs to exclude 5% of the projected areas with Bioclim and 25% with Mahalanobis Distance to avoid an overestimation of potential ranges. Second, species whose ranges were underestimated by the models are widespread in Western Europe, occupying 65–80% of the study area. That is, there may often be little leverage to interpolate potential ranges much beyond existing ones.

The main set of analysis was carried out based on the potential range size and range filling provided by Bioclim, due to a lower number of species with smaller potential ranges than the realized ranges.

Data analyses

We calculated full and partial correlations between the proxies for climatic tolerances to temperature and water availability (hardiness and drought, respectively), and potential range size to assess whether the climatic tolerances of the species explain potential range size, P_{clim} . Thus, we tested for partial correlation between hardiness and potential range size, while controlling for drought and vice versa. We also determined the most parsimonious set of environmental predictors using a stepwise regression (Criteria: P -to-enter ≤ 0.05 , P -to-remove ≥ 0.10). Second, we used a General Linear Model, GLM, on ANOVA-type design to test whether range filling (R/P_{clim}) was higher in tree species dispersed by wind than in those dispersed by animals. Third, we calculated the Pearson correlation between fruit length, seed mass and R/P_{clim} to test whether range filling increased with decreasing fruit size or decreasing seed mass. We also calculated the partial correlation between fruit length and R/P_{clim} controlling for seed mass and vice versa. We finally used a GLM on ANCOVA-type design to determine the effect of dispersal (factor), while controlling for the effects of fruit and seed size (covariates). All the analyses were performed taking into account the phylogenetic relatedness among species, using phylogenetic eigenvectors as covariates (Phylogenetic Eigenvector Regression [PVR] method; Diniz-Filho et al., 1998, 2012a,b). We opted for a statistical method such as PVR to take into account species non-independence, rather than a model-based evaluation of phylogenetic components that would require assuming explicit evolutionary models for our traits, because a detailed phylogeny with accurate branch lengths relating all species under study was not available. Previous studies have shown a relatively good statistical performance in these cases (e.g. Martins et al., 2002).

For PVR, we derived a pairwise phylogenetic distance matrix among species from several sources (Supplementary Table 1). We applied a principal coordinate analysis to this matrix and the eigenvectors obtained were used as predictors representing the phylogenetic relatedness among species. PVR then allowed partitioning the variation of a given trait into two components. First, a phylogenetic component (P-component), in which interspecific variation was explained by phylogenetic relationships (the estimated values). Second, another component expressing the deviation from phylogenetic expectations, as expressed in the eigenvectors (i.e. the PVR residuals, or the S-component). We interpreted the r^2 of these models as a measure of phylogenetic signal in traits, whereas the correlations among S-components were biologically interpreted as responses to ecological and environmental

factors driving trait variation among species independent of their phylogenetic history (e.g. Diniz-Filho et al., 2007). The eigenvectors to be used in the models were selected based on the Akaike Information Criterion (see Diniz-Filho et al., 2012b). All our analysis to correlate potential range size and range filling versus proxies for climatic tolerances and dispersal abilities used the S-components.

To ensure that the S-component of PVR expressed variation among species independently of the phylogenetic relatedness, so that effects of common ancestry did not affect Type I errors in further statistical analyses, it was necessary to ensure that no phylogenetic effect remained in this component (i.e. in PVR residuals). This was checked by performing autocorrelation analyses, based on Moran's I coefficient, of model residuals. Finally, we mapped the variation of tolerances to cold, drought and the related dispersal traits within the European study area. Average values for each AFE cell were used across the species occurring in each AFE cell.

Results

Potential range sizes within our study area varied from less than 0.5 million km² (*Alnus cordata*, *Fagus orientalis*, *Pinus brutia*), to larger than 3 million km² (*Alnus glutinosa*, *Populus tremula*, *Salix caprea*). They increased from south to north but not in a strictly linear manner (*deviance explained* = 75%, $P < 0.001$; see Supplementary material for a description of the General Additive models conducted for this correlation), with the largest range sizes in Scandinavia. Average potential range size by cell was above 2 million km² in this region (Figs. 1b, 2). Range filling varied from <10% (*Abies cephalonica*, *Cupressus sempervirens*, *Juniperus excelsa*, *Pinus brutia*, *Pinus heldreichii* and *Pinus peuce*) to >80% (*Alnus incana*, *Betula pubescens*, *Picea abies* and *Populus alba*). Range filling also increased from south to north (*deviance explained* = 75.2%, $P < 0.001$; see Supplementary material for a description of the General Additive models conducted for this correlation), with the lowest range filling values found in the Iberian and Aegean peninsula (<20%; Figs. 1c, 2). We found clear latitudinal patterns of tolerance to cold, i.e. hardiness, and tolerance to drought from southern to northern Europe (Figs. 1 and 2). Low tolerance to cold climatic conditions of tree species was mainly found in southern Europe and it increased northwards. There was also a latitudinal pattern for tolerance to drought conditions. The three Mediterranean peninsulas showed the highest values of tolerance to drought, while the Atlantic regions of Europe had the lowest drought tolerance. Fruit length and seed mass both tended to decrease with latitude but with a rather complex pattern for fruit length (Fig. 1). The Mediterranean Basin and central-eastern Europe showed the highest fruit length values, whereas the lowest ones were located in the western parts of the Iberian Peninsula, western France and England (see Supplementary Fig. 1 for a frequency plot both for fruit and seed size).

The coefficients of determination (r^2) for PVR were relatively small, ranging from 0.34 (for cold tolerance) to 0.78 (for drought tolerance), using models with 3–8 eigenvectors for the different traits (see Supplementary Table 2). The phylogenetic component of potential range size and range filling was also relatively small, with r^2 equal to 0.345 and 0.358. There was a low phylogenetic signal in the data and all Moran's I in PVR's residuals were smaller than 0.1. This indicates that phylogenetic effects do not remain in the S-components, so that these can safely express interspecific variation independent of phylogenetic common ancestry. Because of the relatively low phylogenetic signal expressed by the PVR's r^2 , especially in the response variables related to range size and range filling, no strong phylogenetic effects on correlations and regressions involving these traits were expected. Even so,

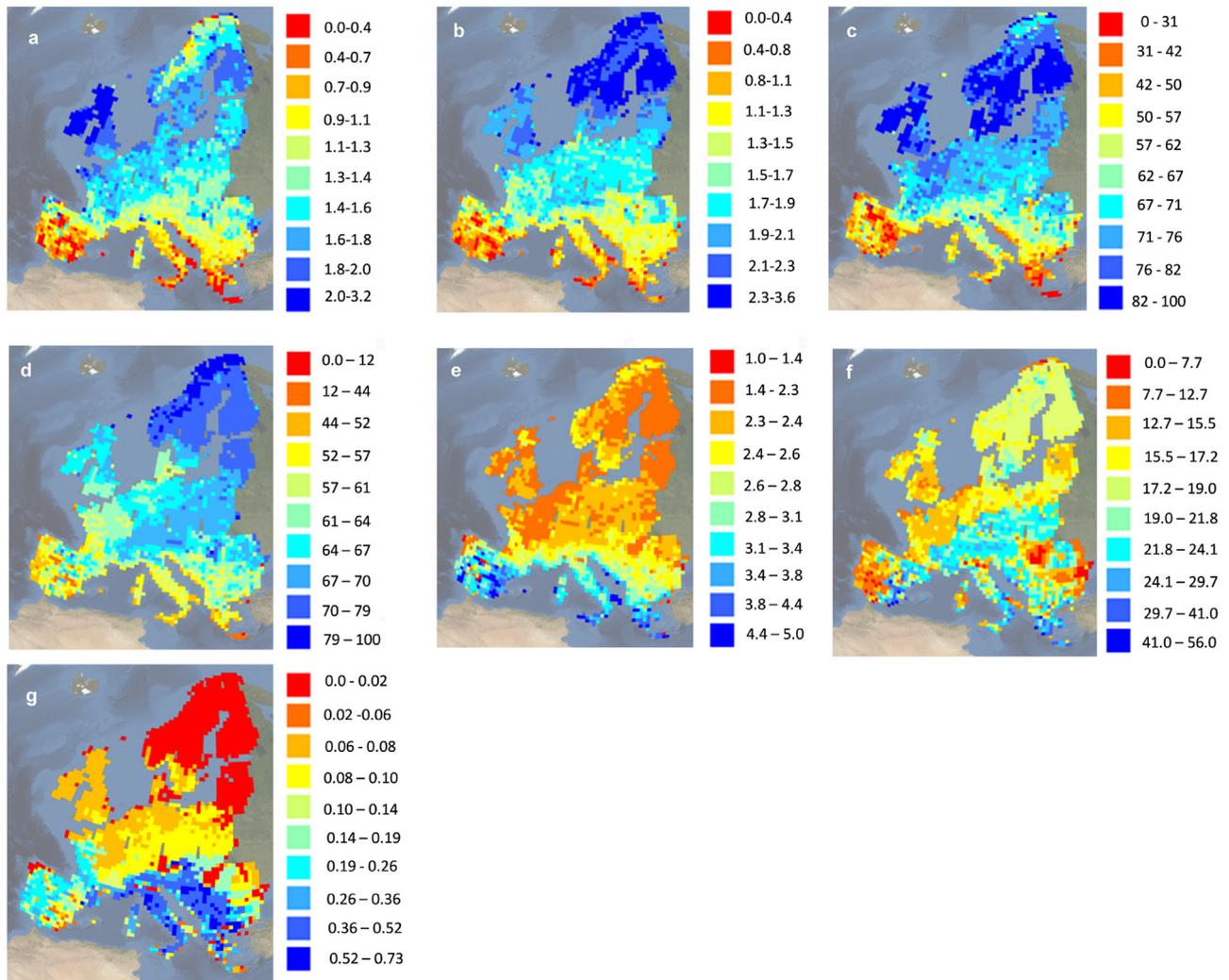


Fig. 1. (a) Mean realized range size of tree species per grid cell (Mio. km²); (b) mean potential range size per grid cell (Mio. km²); (c) mean proportion of the potential range that is filled (%); (d) Mean cold hardness of tree species, ranging from zero frost tolerance (0%) to effectively no sensitivity to frost at -40°C (100%); (e) mean drought tolerance, expressed as homogenized rank values ranging from 1 ('very intolerant') to 5 ('very tolerant'); (f) mean fruit length (mm), and (g) mean seed mass of tree species (g). We use the natural breaks methods to classify the values in the legend. This method seeks to reduce the variance within classes and maximize the variance between classes.

S-components derived from PVR provided a more adequate metric of the intrinsic relationships among species traits without the confounding effects of phylogenetic structure. Also, the S-components were more likely to reflect recent responses at the species level and not associations between traits in the deep phylogenetic history of lineages.

There was a positive correlation between cold tolerance and potential range size ($r=0.607$, $P<0.001$; Fig. 3), and a weak and non-significant correlation between drought and potential range size ($r=-0.164$, $P=0.395$). Similarly, there was a positive partial correlation between cold tolerance and potential range size ($r=0.581$, $P<0.001$), but no correlation between drought and potential range size ($r=-0.222$, $P=0.257$). We ran again the correlation test but leaving out one species each time to assess the robustness of the correlation between cold tolerance and potential range size. Results were significant in all cases ($P<0.05$), and the r values were ranging from 0.519 to 0.620 with a median of 0.557. We also conducted a stepwise regression including tolerance to cold and drought as predictor variables, which only retained cold tolerance as a significant climatic variable accounting for potential range inter-specific size variation ($r=0.551$, $P=0.002$). The results remained constant when

using Mahalanobis Distance (see "Sensitivity of results to model algorithm" section in Supplementary material).

Range filling was not significantly larger among species dispersed by wind than those dispersed by animals, and this was true before (ANOVA; $F=1.91$, $P=0.154$) and after accounting for the phylogenetic signal ($r=0.097$, $P=0.526$). The analysis showed a significant negative correlation between seed mass and range filling ($r=-0.459$, $P=0.008$) and a non-significant correlation between fruit length and range filling ($r=-0.187$, $P=0.235$). For the partial correlation analysis, we found a non-significant negative partial correlation ($P>0.05$) between seed mass and range filling ($r=-0.328$, $P=0.067$; Fig. 3), with the correlation between fruit length and range filling being also not significant ($r=0.087$; $P=0.585$). To assess the robustness of the correlation between seed mass and potential range size, we run the correlation test leaving one species out at the time. Results were non-significant in 92% of the cases ($P>0.05$), with a median P value across species of 0.072, and the r value ranging from -0.272 to -0.423 . However, we found a negative correlation between seed mass and range filling after removing *Juglans regia* (or *Ostrya carpinifolia* or *Taxus baccata*). We also found that neither seed mass or fruit length were retained in

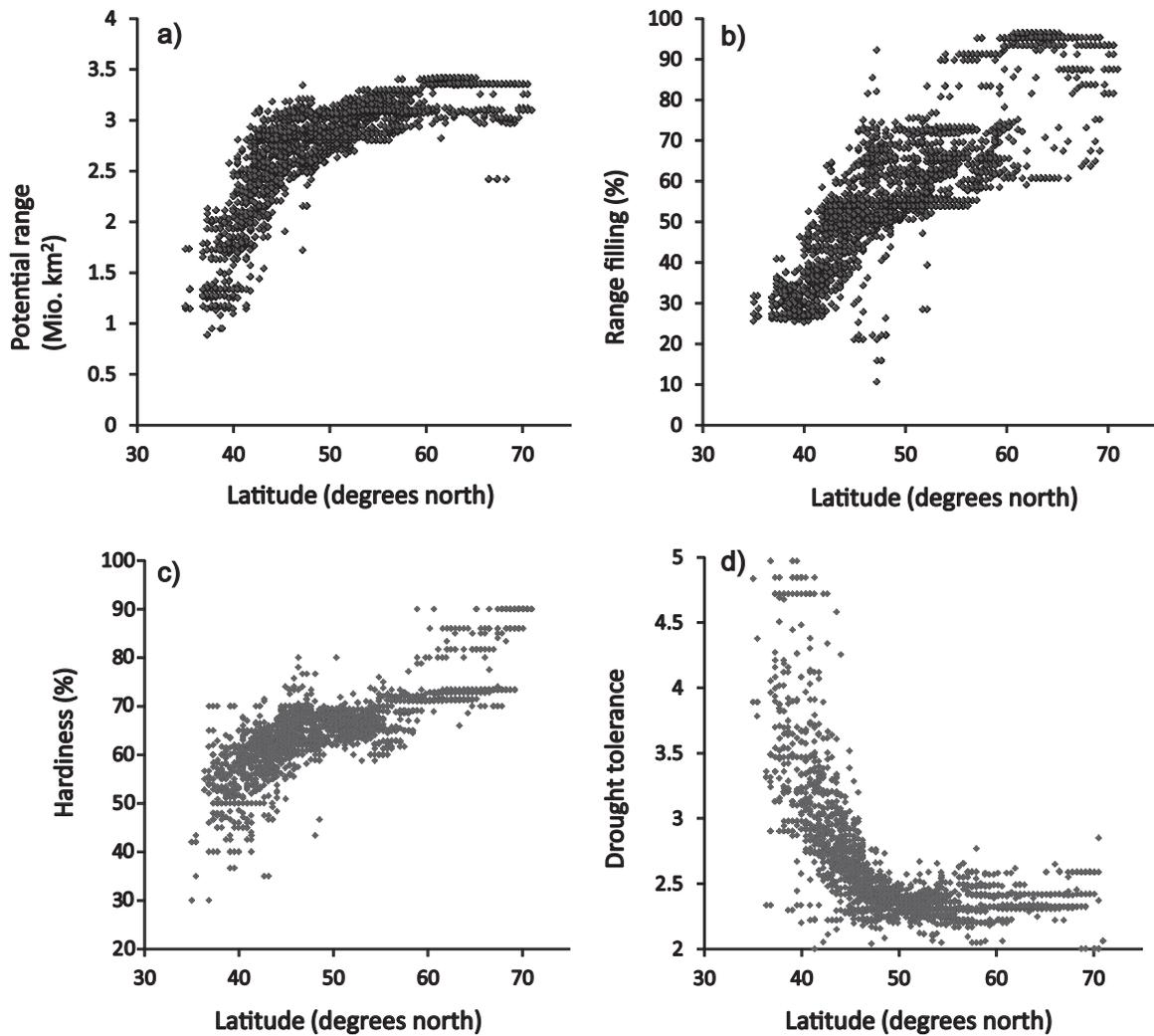


Fig. 2. Latitudinal patterns of (a) mean potential range size; (b) mean range filling; (c) mean frost tolerance, and (d) mean drought tolerance per grid cell for 48 European tree species. Each dot denotes the mean value within each 50 km × 50 km grid cell.

the stepwise regression model ($r = -0.32$, $P = 0.067$). Finally, both the correlation test r and the stepwise regression showed a significant negative partial correlation between seed mass and range filling (see “Sensitivity of results to model algorithm” section in Supplementary material), when the estimates of range filling were based on Mahalanobis Distance.

Discussion

We studied the large-scale variation of the geographical ranges of tree species with respect to their climatic tolerances and dispersal ability as phenotypic correlates of potential range size and range filling. The results show that species with lower cold

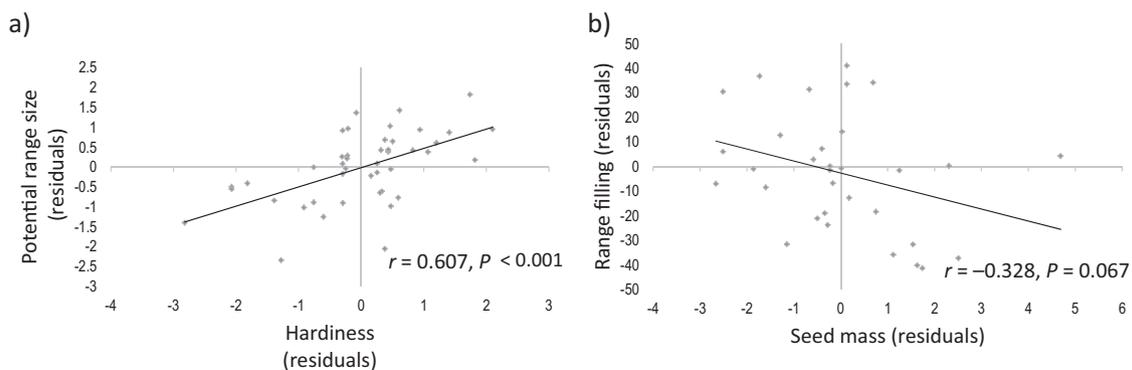


Fig. 3. The relationship between (a) potential range size and hardiness, and between (b) the proportion of the potential range filled and tree seed mass. Each dot represents a tree species. Variables were adjusted based on expectations from the phylogeny.

tolerance have smaller potential ranges than those with greater tolerance to cold. We also found that small-seeded species tend to fill a larger portion of their potential ranges than large-seeded species, although this second finding was contingent on the method used to model species potential distributions and on the subset of species used in the analysis. In contrast, we found no consistent support for the prediction that the dispersal vector affected range filling. Earlier studies have analyzed the effect of tolerance to cold conditions (Svenning and Skov, 2004) or dispersal abilities (Morin and Chuine, 2006; Normand et al., 2011; Hof et al., 2012) on the range of European trees and freshwater insects, while we integrated for the first time species-specific climatic tolerances and dispersal abilities to explain potential range size and range filling.

The match between climatic tolerances and potential range size of European tree species suggests that climate is one of the major drivers of geographical ranges at large scales (Thomas, 2010). This is consistent with the finding that cold tolerance, being physiologically more labile than tolerance to heat, is more likely to contribute to turnover in species ranges (Araújo et al., 2013). Our results also confirm the few empirical tests that have examined the effects of species' environmental limits on range sizes at large scales (butterflies, Brandle et al., 2002; butterflies and plants, Ohlemüller et al., 2008; molluscs, Lee et al., 2009; amphibians, Van Bocxlaer et al., 2010). In terms of colonization and local extinctions, ecological bottom-up dynamics in local population trends and biogeographic factors across large spatial scales, like migration routes from refugia, are some of the main factors determining the location and size of geographical ranges. As recruitment is a prerequisite for the maintenance of viable populations, local performance can ultimately shape range boundaries (Gaston, 2003). Within the context of European trees, recruitment rates in yew populations (*T. baccata*), for example, are strongly affected by water availability at the local scale, which in turn results in a predictable pattern of regeneration at regional and continental scales (Sanz et al., 2009). Therefore, local population performance may drive global geographical ranges.

Dispersal ability of European trees, as related to seed mass, correlates with range filling. However, the statistical significance of such correlation varies with the method used to model species potential range and with the subset of species included in the analysis. Seed mass might affect range filling through greater effective dispersal capacity, and small-seeded species produce far more propagules than large-seeded ones (Guo et al., 2000). Furthermore, there is also a negative relationship between seed mass and realized range size for trees in North America and Europe, with seed mass explaining 14% of the variation in range size (Morin and Chuine, 2006). Similar results were reported in a global analysis of *Pinus* species (Procheş et al., 2012). Indigenous range size of *Pinus* species decreased with increasing seed mass, explaining 13% of the total variability of range size across species. Differences in range filling and seed mass across latitude indicate that tree species with smaller seeds inhabiting southern and central European refugia during the Last Glacial Maximum had a better capacity to colonize in the postglacial higher latitudes, eventually occupying a larger part of their potential geographical ranges (Svenning and Skov, 2004). These results are consistent with earlier ideas on the role of seed size for tracking climatic changes during the Pleistocene (notably Campbell, 1982). The low range filling of southern European trees is likely exacerbated by the many sea and mountain barriers in the region, limiting postglacial and long-term dispersal within the region (Baselga and Araújo, 2010; Svenning et al., 2010). For example, *Aesculus hippocastanum*, *O. carpinifolia* and *Carpinus orientalis* were present on the Iberian Peninsula in the Early and Middle Pleistocene, but subsequently

became extinct and failed to recolonize the area (Postigo-Mijarra et al., 2010) despite suitable climatic conditions. The association between seed mass and range filling could also arise due to covariation of seed mass with climatic tolerances, but in our case seed mass was neither correlated to cold nor to drought tolerance ($r = -0.246$, $P = 0.182$; $r = -0.039$, $P = 0.863$). Finally, there was a noticeable correlation between cold tolerance and range filling ($r = 0.607$, $P < 0.001$), and cold tolerance having the largest independent effect. These findings suggest that cold-tolerant species have more northerly LGM refugia (Svenning et al., 2008), and thus were in a better position to be the first trees to colonize much of northern Europe with low competition allowing them to spread faster. Later arrivals would have to spread through established forests and thus likely have had much lower spread rates (Svenning and Skov, 2004).

Note that all above explanations involve contemporary and Late Quaternary factors, and are not driven by deep-time evolutionary signals throughout plant phylogeny, since these relationships were established using an explicit phylogenetic comparative analysis that takes these historical factors into account.

Concluding remarks

More than a decade ago, Brown (1999) argued that “*The challenge for the future is to build and evaluate mechanistic models which can explain macroecological patterns*”. Macroecology has been intensively describing large-scale biological patterns under the promise that they could be explained by a mechanistic evaluation of processes operating at different spatial and temporal scales (Brown, 1999). However, much macroecological research has focused only on correlative tests between climate and species distribution (or richness or beta-diversity) with little consideration on how species traits shape large-scale biodiversity patterns. Studies such as ours, showing how interacting traits have effects on different aspects of range size such as potential range size and range filling are a necessary step to gain more mechanistic insights into species range dynamics at large scales.

Species traits and the way they interplay with the environment resulting in certain distribution patterns are also relevant for conservation. In fact, the International Union for Conservation of Nature, IUCN, has recognized the necessity for including in conservation guidelines such as IUCN Red List Species those species traits that make them more vulnerable to global climate change (Foden and Collen, 2007). For example, species with disappearing suitable climatic conditions within their environmental tolerance ranges and with poor dispersal abilities might be more vulnerable to climate change. Indeed, large seed size would likely limit dispersal opportunities, thus reducing the chances for range expansion of large seed size species under climate. Therefore, those populations of temperate species located in the rear edge of their geographical ranges and with large seed size (such as some species of *Corylus*, *Fagus*, *Juglans* and *Quercus*) might be more prone to become locally extinct due to their inability to track the projected future climate change during this century (Hampe and Petit, 2005). Anthropogenic effects may strongly affect such dynamics, though, via direct plantation beyond the native range on sometimes massive scales as well as via land-use effects and effects on dispersers, as illustrated by the recently strongly enhanced spread of *J. regia* into semi-natural habitats in Central and Eastern Europe (Lenda et al., 2012).

In summary, we consider that understanding the effects of species traits and other aspects not included in this study such as population dynamics (Keith et al., 2008; Brook et al., 2009) on the drivers of the geographical range of species will lead to a more mechanistic understanding of macroecological patterns.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2014.05.005>.

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