Perspectives in Plant Ecology, Evolution and Systematics 59 (2023) 125734

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Abiotic stress tolerance can explain range size and filling in temperate woody plants

Giacomo Puglielli[a], Enrico Tordoni[b], Lauri Laanisto[c,*], Jesse M. Kalwij[d,e,f], Michael J. Hutchings[g], Aelys M. Humphreys[h,i]

[a] Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Apartado 1095, 41080 Sevilla, Spain
[b] Institute of Ecology and Earth Sciences, University of Tartu, J. Liivi 2, 50409 Tartu, Estonia
[c] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5a, Tartu 51006, Estonia
[d] Institute of Geography and Geoecology, Karlsruhe Institute of Technology, Karlsruhe, Germany
[e] Centre for Ecological Genomics and Wildlife Conservation, Department of Zoology, University of Johannesburg, Auckland Park 2006, South Africa
[f] Forest and Nature Conservation, Van Hall Larenstein University of Applied Sciences, Larensteinselaan 26-A, 6882 CT Velp, the Netherlands
[g] School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG, United Kingdom
[h] Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden
[i] Bolin Centre for Climate Research, Stockholm University, SE-106 91 Stockholm, Sweden

ARTICLE INFO

Keywords:
Abiotic stress
Cold tolerance
Drought tolerance
Range filling
Range size
Trade-off
Woody plants

ABSTRACT

Efforts to understand the mechanisms explaining the relationship between abiotic stress tolerance and range size and filling have hitherto yielded contradictory results. Unlike previous studies that have focused on single stress factors, we here examine the extent to which range size and filling can be explained by tolerance of multiple abiotic stressors (cold, shade, drought and waterlogging). As range metrics, we used range size and filling (the ratio between actual and potential range) for 331 European and North American temperate woody plant species. Stress tolerance strategies were expressed as a multivariate axis reflecting a cold/waterlogging-drought tolerance trade-off. We used mixed models to evaluate the relationship between range size/filling and this multivariate stress tolerance axis, using latitude as a covariate, and phylogeny and plant functional type as random effects. Range size and stress tolerance were negatively correlated, mostly independently of latitude and continent. Thus, cold/wet-tolerant species had the largest range sizes and cold-sensitive/drought-tolerant species the smallest. In contrast, range filling mostly depended on latitude. Our results show that abiotic stress tolerance can explain interspecific differences in range size, and to a lesser extent range filling, which sets up predictions for range size variation in plants that go beyond latitude.

1. Introduction

Identifying the factors that determine species range size and filling is a major focus of biogeography (Brown, 1984; Gaston et al., 2009). In recent decades, a number of somewhat conflicting theories, have been proposed to explain how species ranges are distributed globally (Colwell and Hurtt, 1994; Sheth et al., 2020; Stevens, 1989). These include a role for extrinsic factors (e.g. the climate variability hypothesis (Stevens, 1989)), intrinsic factors (e.g. species dispersal (Ricklefs and Schluter, 1994)) or niche breadth (Brown, 1984) in explaining differences in range size among species. However, most of the hypotheses formulated to date have emerged from consideration of the causes of range sizes and filling in animals (Fine, 2015). In contrast, the main determinants of range sizes and how they vary at the global scale remain elusive for plants (Sheth et al., 2020).

Different metrics of range size are used in the literature to describe biogeographic patterns for plants. These metrics include latitudinal or longitudinal range, area of occupancy, and the ratio of realized range size (based on known species distributions) to potential range size (usually estimated using species distribution models). This metric is usually referred to as range filling (Paul et al., 2009; Sheth et al., 2020; Svenning and Skov, 2004). Despite the use of different metrics, some consistent biogeographic patterns have been observed. For example, North American regions with higher climate instability have lower species richness and species with larger ranges, while species with smaller ranges inhabit more species-rich regions characterized by more

---

[*] Corresponding author.
E-mail address: laanisto@ut.ee (L. Laanisto).

https://doi.org/10.1016/j.ppees.2023.125734
Received 14 September 2022; Received in revised form 3 May 2023; Accepted 11 May 2023

stable climates (McFadden et al., 2019; Morueta-Holme et al., 2013). For European tree species, potential range size and filling both increase with latitude (Nogués-Bravo et al., 2014; Svenning and Skov, 2004), and both European and North American woody species tend to have larger ranges at higher latitudes (Morin and Chuine, 2006). All these results are consistent with Rapoport's rule (Stevens, 1989), which states that species latitudinal ranges increase with increasing latitude, but mechanistic explanations behind this rule have not yet been found.

Morin and Chuine (2006) proposed that, for woody plants, the proximate driver behind Rapoport's rule is abiotic stress tolerance. This is because a species' ability to persist under a given abiotic stress regime must ultimately explain, at least in part, its distribution. The most common way to link species' abiotic stress tolerances with their range sizes is by analyzing the ability of species to withstand extreme heat and/or cold in relation to the latitudinal limits of their distribution. To date, this has been done mostly for animals (Addo-Bediako et al., 2000; Araújo et al., 2013; Gaston et al., 2009; Sunday et al., 2011), because comprehensive large-scale datasets of thermal tolerances for plants have only appeared recently (Lancaster and Humphreys, 2020). Analyses of these datasets suggest that plant cold and heat tolerances only exhibit clear relationships with latitudinal and climatic gradients under certain conditions. Moreover, cold tolerance seems to be more closely related to climate than to heat tolerance (Araújo et al., 2013; Lancaster and Humphreys, 2020), and these relationships are stronger for northern than southern hemisphere species (Lancaster and Humphreys, 2020). The cold and drought tolerances of tree species do not display straightforward relationships with range filling, however, despite showing a latitudinal pattern across Europe (Nogués-Bravo et al., 2014). Thus, cold, drought and heat tolerances by themselves do not fully explain either species sorting along latitudinal gradients or the relationship between abiotic stress tolerance and species distributions.

Relating species' physiological tolerances to their geographical distribution patterns is complicated by the fact that occupied ranges represent realized niches (e.g. Hutchinson-CSHSymQunBio-1957.pdf, n.d.), whereas physiological tolerances define fundamental niches (Puglielli et al., 2023). Furthermore, adaptations to achieve tolerance of different stressors often show trade-offs, reflecting adaptations to independent axes of the Hutchinsonian hypervolume (Sexton et al., 2017), thus reducing the number and nature of stress tolerance combinations species can evolve. Accounting for trade-offs between multiple stress tolerance responses will therefore more closely reflect species' realized tolerance strategies than considering each stress factor separately (Laanisto and Niinemets, 2015; Niinemets and Valladares, 2006; Puglielli et al., 2021a; Sack, 2004). If abiotic stress tolerance is an important driver of range size variation in plants, this approach should be more likely to reveal consistent relationships with range size. Thus, examination of multivariate trade-off axes between different stress tolerances is expected to shed new light on the relationship between abiotic stress tolerance and range size.

Recently, using published species-specific tolerance data (Laanisto and Niinemets, 2015; Niinemets and Valladares, 2006) for 799 Northern Hemisphere woody plant species, Puglielli et al. (2021a) examined multivariate trade-offs in ecophysiological tolerances of four major abiotic stresses (cold, shade, drought and waterlogging). Ecophysiological tolerance is defined here as the ability of a species to survive long-term extreme shortage or excess of a given abiotic stress (either a resource or a non-resource stress) in its natural environment (Niinemets and Valladares, 2006). In other words, these stress tolerance data reflect species' long-term adaptations to given stress regimes in their natural habitat. Puglielli et al. (2021a) identified two primary stress tolerance dimensions describing different strategies for surviving cold, shade, drought and waterlogging. These are (i) a trade-off between drought and cold/waterlogging tolerance, and (ii) a shade tolerance spectrum that runs from low- to high shade tolerance. These axes are independent of each other and, together, define a triangular *Stress Space* that delineates the realized abiotic stress tolerance strategies of woody plants (for the stressors in question). Each pair of coordinates within the *Stress Space* reflects species-specific multi-stress tolerance strategies shaped by trade-offs between the different responses, and such coordinates can be used to link realized abiotic stress tolerance strategies to other aspects of species' biology, including range size. A framework describing the relationship, and potential trade-offs, between multiple abiotic stress tolerances is a crucial step towards making realistic inferences about the role of abiotic stress tolerance in shaping species distribution patterns (Gaston et al., 2009), including global variation in range sizes.

We studied the relationship between both range size and range filling, and the *Stress Space* axes that were identified by Puglielli et al. (2021a, 2021b), using a dataset of 300 temperate woody plant species from Europe and North America. Building on Morin and Chuine's (2006) proposal that abiotic stress tolerance is a possible explanation of the latitudinal gradient in range size (i.e. Rapoport's rule), we asked whether species' abiotic stress tolerance strategies, reflected by their positioning along the *Stress Space* axes, could explain interspecific differences in range size and range filling, to a greater extent than latitude. We investigated both of these range metrics because they reflect different aspects of species' ranges. Range size reflects historical legacies (e.g. for temperate species it represents the degree to which they have been able to expand since the Last Glacial Maximum, LGM (Estrada et al., 2018; Nogués-Bravo et al., 2014; Normand et al., 2011; Svenning et al., 2008), and ecological constraints (e.g. areas with suitable habitat, Linder et al., 2013)). Traits that are positively correlated with range size are expected to be associated with range expansion in new ecological contexts after LGM (Estrada et al., 2018, 2015). Indeed, identifying a relationship between the tolerance strategies of woody plants and their current range size could provide indirect evidence that contrasting adaptive tolerance syndromes have affected species range expansion to different extents in newly available habitats since the LGM. Range filling, on the other hand, is a measure of the extent to which species' ranges are at a climatic equilibrium (Svenning and Skov, 2004). Traits associated with range filling reflect limits on species' distributions imposed by historical non-climatic factors (e.g. dispersal (Estrada et al., 2018)). Dispersal syndromes have been presumed to play a prominent role in explaining plants' range filling (Nogués-Bravo et al., 2014; Normand et al., 2009; Svenning et al., 2008), although evidence to support this is weak (e.g. Estrada et al., 2018; Nogués-Bravo et al., 2014; Normand et al., 2011; Svenning et al., 2008). The *regeneration niche* theory (Grubb, 1977) also requires that a species can survive the prevailing abiotic (and biotic) conditions in order to establish viable populations (Estrada et al., 2018). Therefore, as for range size, abiotic stress tolerance strategies could, at least in part, also explain interspecific differences in range filling.

With this in mind, and considering that in temperate zones of the Northern Hemisphere cold/waterlogging and drought tolerance strategies typically tend to be more favored at high and low latitudes, respectively (Nogués-Bravo et al., 2014), and given the latitudinal gradient in range size and filling, we had two hypotheses: (1) We expected to observe a negative relationship between range size and the cold/waterlogging-drought trade-off axis. (2) We also expected to observe a similar negative relationship between range filling and the cold/waterlogging-drought trade-off axis, because we expected large-ranged species to have greater range filling as well. Given that the two dimension that define the *Stress Space* are independent of each other, an evaluation of the expected relationship between the cold/waterlogging-drought axis and range size would itself be independent of any influence of species' shade tolerance. This is important, as shade tolerance is assumed to be also independent of latitude (unlike cold/waterlogging and drought stress). Therefore, we included latitude as a separate covariate response in our models. If our analysis demonstrates that the relationship between stress tolerance and range size cannot be significantly explained by latitude, it will provide new evidence for the importance of tolerance of multiple abiotic stressors in shaping range size variation in temperate woody plants.

2. Methods

2.1. Realized range

We carried out an extensive literature search for polygons defining the realized ranges of the 799 woody species in the database assembled by Puglielli et al. (2021a, 2021b). We were able to retrieve polygons defining realized ranges for 331 species. These polygons were used to calculate range size, expressed in km^2.

Spatial distributions of North American species (n = 201) were obtained from the "*Digital representations of tree species range maps from Atlas of United States Trees*" (the digitalized expert-drawn range maps by E.L. Little, Volumes 1–5, available at https://github.com/wpetry/USTreeAtlas). Little's maps are the most reliable approximation of

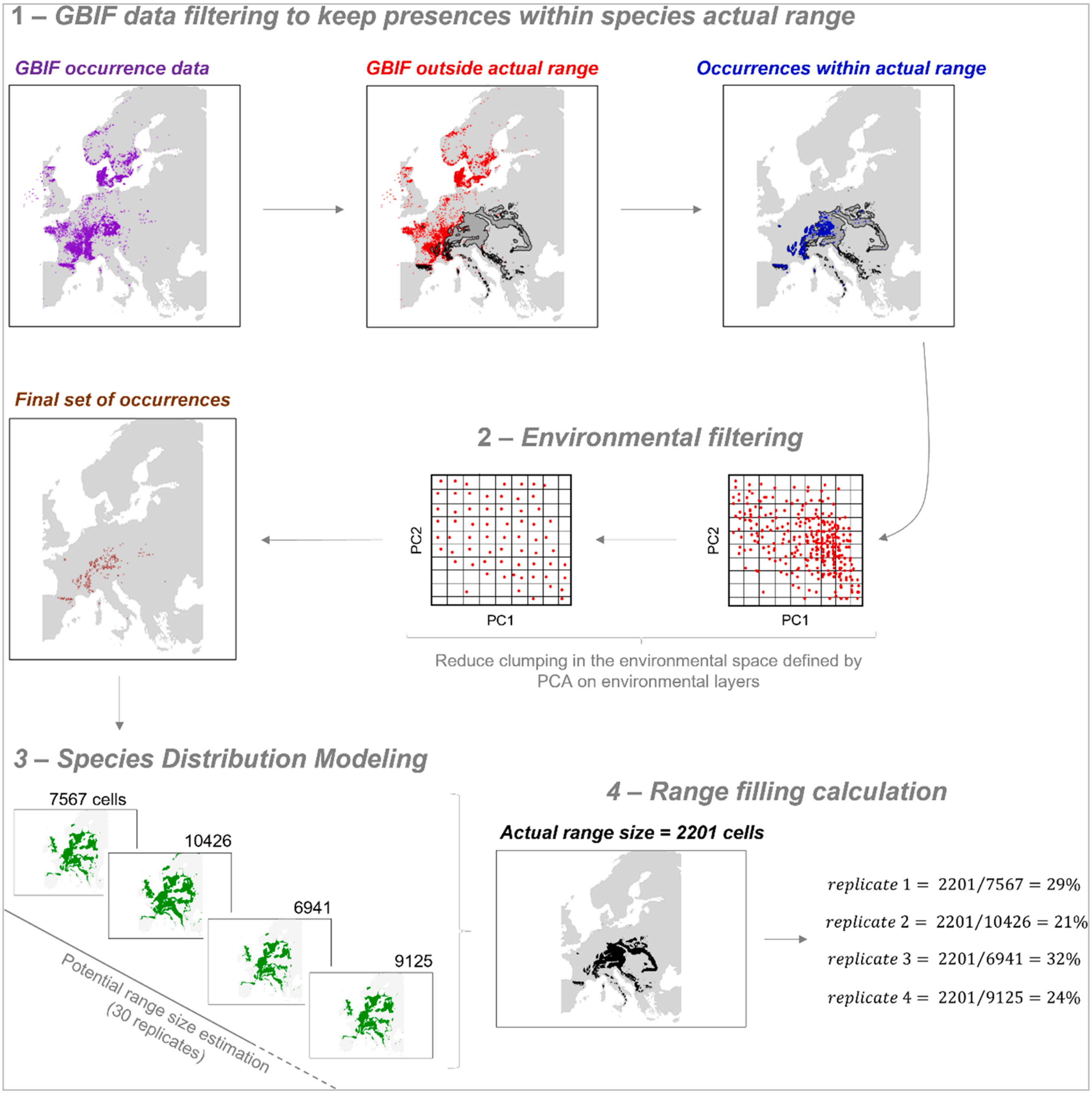

Fig. 1. Representation of the filtering process applied to obtain the most reliable presence data for fitting species distribution models and an example of range filling calculation: 1. Filtering of species presence data obtained from the Global Biodiversity Information Facility (GBIF) to keep only data points falling within a species' realized range (in this example, for *Abies alba,* the polygon describing the realized range was obtained from the European forest genetic resources program (EUFORGEN, http://www.euforgen.org/species.) 2. Subsequent environmental filtering. Note that the grids used for displaying the environmental filtering step have only demonstrative purposes and are not based on real data. 3. The final set of occurrences was used to fit Species Distribution Models for estimating potential range size (number in the top right portion of the panels displaying a green area). 4. The realized range size of a species (in this case 2201 cells) was then divided by each value of potential range size obtained across replications. For demonstrative purposes, calculations are reported here only for four replicates but a total of 30 replicates per species were used to estimate a single mean range filling value. All the stages in this example include only information for *Abies alba*, but the same procedure was applied to each species included in the study.

historical realized ranges of North American trees and shrubs currently available, because Little intentionally excluded range alterations following Euro-American settlement (Seliger et al., 2021). Furthermore, more recent plant occurrence databases are often limited to continental United States (Seliger et al., 2021), while many of the species we analyzed extend into Canada and Northern Mexico. Distributions of European species ($n = 130$) were gathered from the International Union for Conservation of Nature (IUCN, www.iucnredlist.org), the European forest genetic resources program (EUFORGEN, http://www.euforgen.org/species), and published papers (Caudullo et al., 2017; Kalwij et al., 2014; Wazen et al., 2020).

2.2. Potential range size and range filling calculation

To quantify range filling, we estimated species' potential range sizes using presence-only Species Distribution Models (SDMs) – i.e. BIOCLIM (Busby, 1986), and Maxent (Phillips et al., 2006). We used two different model types in order to account for differences in potential range size that may arise from algorithmic differences (Nogués-Bravo et al., 2014). Species occurrence records for modeling potential range size were obtained from the Global Biodiversity Information Facility (GBIF, www.gbif.org/, accessed 21/12/2018; full list of data sources in Appendix S1). GBIF data were carefully cleaned using both standardized and customized procedures (Appendix S1, Fig. 1). Following Nogués-Bravo et al. (Nogués-Bravo et al., 2014), giving a possible mismatch between species' realized and modeled species distributions, presence-only methods are expected to return more reliable and parsimonious potential range estimates than more complex model classes in broad comparative studies. Each model was fitted with three environmental parameters: (i) growing degree days at 5 °C (GDD, unitless); (ii) climatic moisture index (the ratio of annual precipitation to annual potential evapotranspiration, CMI, unitless), (iii) mean minimum temperature of the coldest month (T_{min}, °C). The GDD and CMI data were obtained from the ENVIREM dataset (Title and Bemmels, 2018) and T_{min} (i.e. Bio6) from WorldClim (Hijmans et al., 2005), each at 10′ resolution. We decided to use only these three environmental predictors because they are considered key environmental factors summarizing the processes that limit the spatial distribution of plant species at a coarse scale, and they have been extensively used in previous studies (Nogués-Bravo et al., 2014; Seliger et al., 2021; Svenning and Skov, 2004), ensuring comparability of our results with previous findings.

Before computing SDMs, occurrence data were filtered using the "environmental filtering process" proposed by Varela et al. (2014) (Appendix S1, Fig. 1). All the 331 species we included in SDMs analysis had > 20 occurrence records, which has been considered a reasonable threshold (minimum sample size) for fitting SDMs (Guisan et al., 2017). The SDMs were fitted using the *sdm* R package (Naimi and Araújo, 2016). For each run, 80 % of species data were used for training, and the remaining 20 % for evaluating the model. Thirty replicates per species were generated through bootstrapping and 20,000 background points were generated at each run. The Area under the ROC Curve (AUC, Fielding and Bell, 1997) and the True Skill Statistic (TSS, Allouche et al., 2006) were used to evaluate model performance. The SDMs predictions were converted into presence/absence maps by using the threshold that maximized both sensitivity and specificity of the model, which is considered the best option for presence-only methods (Liu et al., 2013). The total number of 10′ cells suitable for occupation in the binary maps corresponded to potential range size. To calculate range filling (%) as (Range size/Potential range) × 100, we re-expressed range size as the number of 10′ cells occupied by the polygons defining species' realized ranges (Fig. 1, Appendix S2). As using either realized ranges expressed in km^2 or as the number of 10′ cells did not alter the results obtained (Table S1), we chose to always show the results with range size expressed as the number of 10′ cells, in order to be consistent with range filling estimates. Following Nogués-Bravo et al. (2014), only BIOCLIM-derived estimates of potential range were used in subsequent analyses, because they produced fewer species with range filling estimates greater than 100 % (see Appendix S2, Figs. S2–4, Table S2 for considerations on model performance and range filling estimates).

Finally, to account for broad differences in species' adaptive syndromes (Puglielli et al., 2021b), species were classified according to three major functional types: deciduous angiosperms, evergreen angiosperms and evergreen gymnosperms. The complete list of species, range sizes (log_{10}-transformed number of 10′ cells), range fillings, centroid latitudes (obtained from the polygons defining species' realized ranges), continental origins (N. America, Europe) and functional types, see Table S3.

2.3. Abiotic stress tolerance data

The species-specific estimates of tolerance of shade, drought, cold and waterlogging used to define the *Stress Space* were obtained from the datasets of Niinemets and Valladares (2006) and Laanisto and Niinemets (2015). In the original data compilation (Niinemets and Valladares, 2006), shade, drought and waterlogging tolerance were independently estimated by cross-calibrating multiple tolerance scales reported in the literature, where multiple survival measurements for one species were available across tolerance scales. Cold tolerance data were extracted from USDA plant hardiness data and represent species-specific averages gathered from multiple sources (Laanisto and Niinemets, 2015). All the stress tolerance scores vary continuously between 1 (very sensitive) and 5 (very tolerant) (Laanisto and Niinemets, 2015; Niinemets and Valladares, 2006).

The formalization of the *Stress Space* by Puglielli et al. (2021a) revealed that two dimensions (principal components) capture ~ 80 % of the variance in species-specific combinations of shade, drought, cold and waterlogging. Each pair of coordinates in the *Stress Space* corresponds to a species-specific stress tolerance strategy. PC1 is positively correlated with drought tolerance and negatively correlated with both waterlogging and cold tolerance. It is interpreted as a cold-drought tolerance trade-off axis (CD_{to}), where the term cold indicates a short growing season. This interpretation stems from the positive covariance between cold and waterlogging tolerance in our dataset: the highest cold tolerance is expected where snowpacks are greater, resulting in later snowmelt, followed by waterlogging, and consequently a shorter growing season (Chuine, 2010). PC2 is positively correlated with shade tolerance and represents a shade tolerance spectrum that is independent of PC1. For each of the 331 species included in this study, we extracted its position along the cold-drought tolerance axis from Puglielli et al. (2021a). Note that the second axis was not used in further analyzes.

2.4. Data analysis

Range size data were log_{10}-transformed before analysis, as data distributed along a relative scale (in this case range filling) has a different effect depending on the correlative value (in this case range size) – e.g. 50 % change in range filling represents a different area depending on the absolute size of the distribution range. Range filling was strongly correlated with log_{10}-transformed range size ($R^2 = 0.46$, $p < 0.001$, $n = 331$), but not with log_{10}-transformed potential range size ($R^2 = 0.02$, $p < 0.001$, $n = 331$). Thus, we used the residual variance of the relationship between range size and range filling as a metric for range filling (Seliger et al., 2021).

The relationships between the stress axes and both range metrics (size and filling) were tested at different levels. First, we used Ordinary Least Square (OLS) regressions. Then, we used quantile regressions to further explore how the studied relationship varied in different portions of the range size distribution (i.e., to understand if the observed relationship differed for different range classes, for instance between large- vs. small-ranged species). In this way, we could robustly test the target relationship even in the presence of possible outliers by taking the range size distribution tails into account (Ricotta et al., 2010). Quantile regressions were computed using the R (R Core Team, 2021) package *quantreg* (Koenker and Bassett, 1978), using the following quantiles of the range metrics distributions (0.1, 0.25, 0.50, 0.75 and 0.90 quantile).

Fitting models for between-species variances while ignoring phylogenetic relationships might lead to inflated type I errors (Freckleton et al., 2002). Therefore, as a third step, we computed Phylogenetic Generalized Linear Mixed Models (PGLMMs (Ives and Helmus, 2011)) using the *phyr* R package (Li et al., 2020). Specifically, we used either range size or range filling as the response variable, cold-drought tolerance, centroid latitude, plus the first-order interaction between them as independent variables, and species' phylogenetic relatedness and functional type (3 levels: deciduous angiosperms, evergreen angiosperms, and evergreen gymnosperms) as random effects. When there was no significant interaction between explanatory variables, only the main effects were considered.

Phylogenetic data were retrieved for 325 of the 331 species using the mega-tree available via the *V.PhyloMaker* R package (Jin and Qian, 2019). The mega-tree combines the phylogenies developed by Zanne et al. (2018) and Smith and Brown (2018). Species nomenclature followed The Plant List v.1.1 (2013). We also tested for potential signals of spatial autocorrelation in the model residuals, using spline correlograms from the *ncf* R package (Bjornstad and Cai, 2022) and with 95 % pointwise bootstrap confidence intervals computed from 5000 bootstrap samples of Pearson residuals.

All the data analysis procedures were conducted separately for European and North American species to allow for the possibility of different patterns between these geographic regions. Furthermore, even though there were no species that were present in both the European and North American species sets, we explored whether differences between the two species sets could be driven by genera present on only one continent. Out of the 106 genera in the whole dataset, 29 had representatives in both the species sets, and these common genera contributed 70 % of the total species pool in our sample. Therefore, we repeated the modeling procedure described above without the genera that were unique to either Europe or North America.

3. Results

3.1. Range size

Range size scaled negatively with species positioning along the cold-drought tolerance trade-off axis for species from both continents (Europe: slope = − 0.10, $R^2 = 0.06$, $p = 0.01$, $n = 130$; North America: slope = − 0.18, $R^2 = 0.14$, $p < 0.01$, $n = 201$) (Fig. 2 **a,c**). A negative relationship was also observed across the considered quantiles of the response variable, but with differences between the two continents. For European species, the quantile regressions were mostly significant at average to high quantiles of range size (Fig. 2 **a**). For North American species, quantile regressions were all significant, except for the lowest quantile (Fig. 2 **c**).

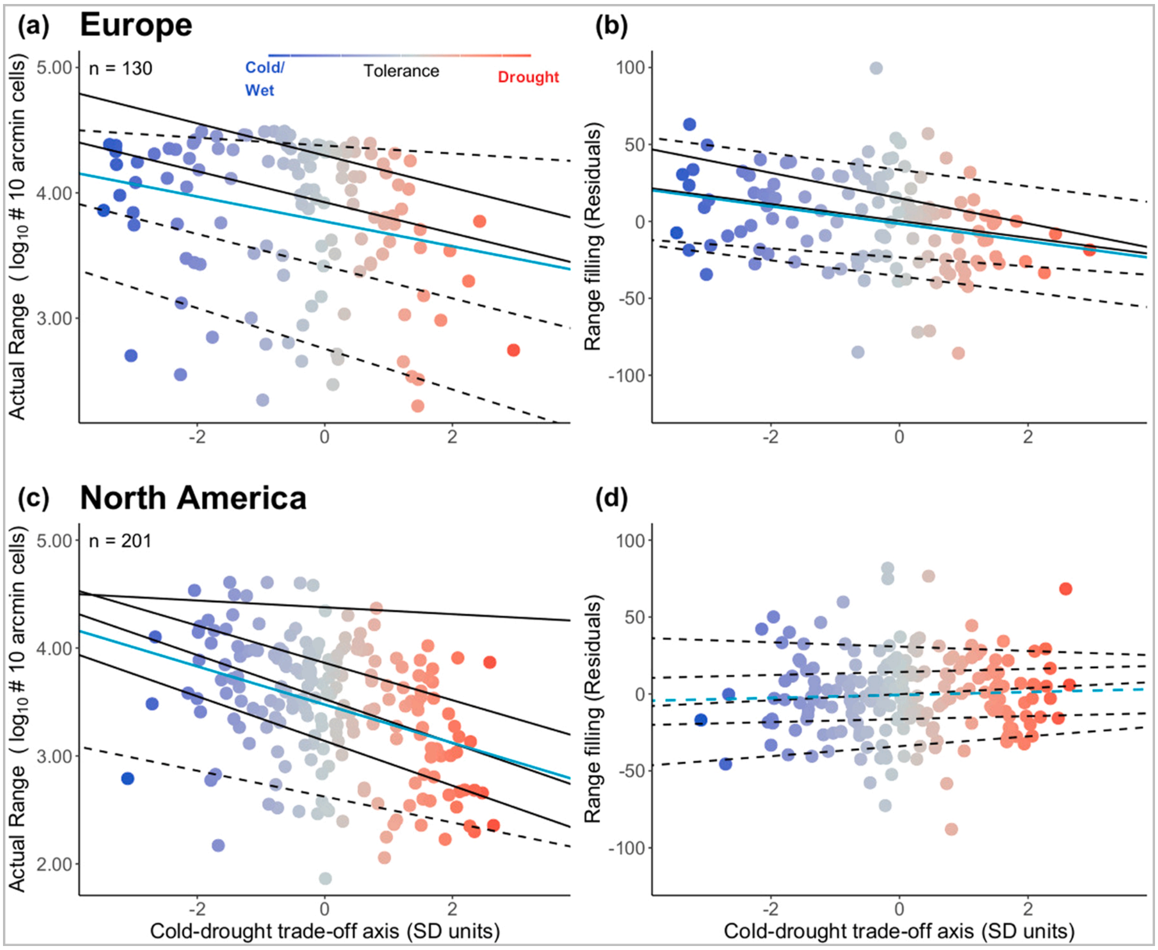

Fig. 2. Relationships between the cold-drought trade-off axis (Standard Deviation units) and (**a, c**) range size ($\log_{10}$-transformed number of 10′ cells) and (**b, d**) range filling (residuals, see Methods) for: **(a, b)** European, and **(c, d)** North American woody plant species. Pale blue line represents the Ordinary Least Square fit. Black lines show the quantile regressions fitted at the 0.1, 0.25, 0.50, 0.75 and 0.90 quantile of the response variable distribution. Solid lines depict significant relationships ($p \leq 0.05$); dashed lines represent non-significant relationships. The color gradient reflects the progression from cold/wet-tolerant to cold-sensitive/drought-tolerant species along the cold-drought trade-off axis.

The negative relationship between range size and cold-drought tolerance was not affected by including latitude as an additional main effect, and the CD$_{\mathrm{to}}$ effect was always greater than that of latitude for each continent (Table 1). However, some differences were found between continents. For European species, the CD$_{\mathrm{to}}$ effect was only marginally significant ($p = 0.06$); there was no effect of latitude, and the model explained only 7 % of the variance in range size. In contrast, for North American species, the effects of both CD$_{\mathrm{to}}$ and latitude were significant, but with opposite sign: the CD$_{\mathrm{to}}$ remained negatively correlated with range size, whereas the correlation with latitude was positive ($p < 0.01$ and $p < 0.05$, respectively). This model explained 23 % of the variation in range size, and indicates that range sizes are larger for species with higher levels of cold/wet tolerance as well as at higher latitudes. There was no significant interaction between CD$_{\mathrm{to}}$ and latitude in any model involving range size as the response variable, for either the European or North American species. Thus, species positioning along CD$_{\mathrm{to}}$ was the main driver of interspecific differences in range size on both continents (Fig. S6 a,c for range size variation in relation to the CD$_{\mathrm{to}}$ and latitude).

When the analyzes were repeated excluding genera that were unique to one or the other continent, the relationship remained significant for North American species, but changed from marginally to highly significant for European species ($R^2 = 0.12$, Table S4). This indicates that differences in results between continents are partly caused by differences in the generic composition of their constituent species.

3.2. *Range filling*

Range filling scaled negatively with species positioning along the CD$_{\mathrm{to}}$ axis for European species (slope $= -5.66$, $R^2 = 0.07$, $p < 0.01$, $n = 130$) and, as for range size, the quantile regressions were mostly significant at intermediate to high range filling quantiles (Fig. 2 **b**). No significant relationship was found between range filling residuals and the CD$_{\mathrm{to}}$ axis for North American species, and the relationship was not significant at any considered quantile (Fig. 2 **d**).

The differences in results between continents were more pronounced for range filling than for range size (Table 1). A significant positive interaction between CD$_{\mathrm{to}}$ and latitude was found for European species, in a model that explained approximately 19 % of the variance. For North American species, range filling showed a negative relationship with latitude and there was no significant relationship with CD$_{\mathrm{to}}$. This model suggests greater range filling at lower latitudes, but it explained only 4 % of the variance, leaving range filling largely unexplained for North American species (Fig. S6 b, d for range filling data in relation to the CD$_{\mathrm{to}}$ and latitude).

3.3. *Effects of phylogenetic relatedness, functional type, and spatial autocorrelation*

Regardless of the model used, the effect of phylogenetic relatedness among species was negligible (Table 1). Plant functional type did not affect the strength or the sign of the relationship between CD$_{\mathrm{to}}$ and either range size or range filling. However, as a random effect in PGLMMs, plant functional type had a greater effect overall than phylogenetic relatedness in terms of variance explained (Table 1). Finally, the spline correlograms (Fig. S7) did not reveal any evidence of spatial autocorrelation in the PGLMMs residuals; spatial autocorrelation therefore appears not to influence model parameter estimates.

4. Discussion

Our results show that a trade-off between cold and drought tolerance (CD$_{\mathrm{to}}$) (as defined by Puglielli et al. (2021a) partly explains interspecific differences in range size between temperate woody plant species (Fig. 2). Species that are most tolerant of colder and wetter conditions tend to have larger ranges than those that are cold sensitive but tolerant of dryer conditions. Despite some nuanced variation discussed below, this result was largely independent of continent, latitude, plant functional type and phylogeny, indicating its generality. In contrast, range filling showed different patterns in Europe and North America: an interaction between cold-drought tolerance and latitude provided the strongest explanation for range filling differences among European species, whereas only latitude had a significant effect on range filling for North American species.

4.1. *Towards understanding range size variation in temperate woody plants*

For North American species, we found that cold/wet tolerant species occurring at high latitudes (e.g. *Salix* spp., *Larix laricina* (Du Roi) K. Koch) generally have the largest ranges (Table 1). Consistent with this, large-ranged, cold-tolerant North American tree species are known to be generally absent from regions that are consistently warm and moist, such as the southeastern region of the continent (Pither, 2003). Paleoecological records also provide evidence for rapid northward range shifts in North American large-ranged tree species after the most recent ice age (Seliger et al., 2021). Conversely, some species have maintained relatively small realized ranges following deglaciation, perhaps due to

Table 1
Results of the phylogenetic generalized linear mixed models.

Response	Continent	Main effects	Estimate	SE	p	R^2	n	Random effects	Variance
Range size	**Europe**	*Intercept*	3.39	0.34	< 0.001	0.07	128	*PFT*	0.007
		CD$_{to}$	-0.07	0.04	0.06			*Phylogeny*	≈ 0
		Latitude	0.01	0.01	n.s.				
	North America	*Intercept*	2.9	0.22	< 0.001	0.23	197	*PFT*	0.05
		CD$_{to}$	-0.11	0.03	< 0.01			*Phylogeny*	≈ 0
		Latitude	0.01	0.01	< 0.05				
Range filling	**Europe**	*Intercept*	27.08	17.37	n.s.	0.19	128	*PFT*	33.12
		CD$_{to}$	-43.18	11.77	< 0.001			*Phylogeny*	0.003
		Latitude	-0.56	0.34	n.s.				
		*CD$_{to}$ * Latitude*	0.69	0.22	< 0.01				
	North America	*Intercept*	22.96	9.25	< 0.05	0.04	197	*PFT*	3.97
		CD$_{to}$	0.01	1.56	n.s.			*Phylogeny*	0.001
		Latitude	-0.6	0.22	< 0.01				

Models were run separately for each continent (Europe and North America) using range size ($\log_{10}$-transformed number of 10′ cells) and range filling (Residuals, see Methods) as response variables, the cold-drought tolerance trade-off (Standard Deviation units) and latitude (centroid latitude, °) as main effects, and Plant Functional Type (*PFT*) and species phylogenetic relatedness (*Phylogeny*) as random effects. Estimates of the main effects and their standard errors (SE), together with the variance explained by the model (Model R^2) and sample size (n), are shown. The variance explained by the random effects is also shown. Significance level was set at $p \leq 0.05$. n. s. = not significant.

trait syndromes guaranteeing competitive advantages only in specific ice age refugia (Seliger et al., 2021). For example species with drought tolerance strategies that have prevented northward range expansions after glacial retreat, such as *Juniperus deppeana* Steud., *Pinus monophylla* Torr. & Frém., *Quercus douglasii* Hook. & Arn., and other species with relatively small ranges, that are confined to southwestern North America. Long-term drought, and adaptations to tolerate such conditions, are an important constraint on plant species distributions (Normand et al., 2009), possibly due to different trait adaptations associated with drought and cold tolerance strategies. Similarly, Pither (2003) hypothesized that latitudinal patterns in the range sizes of North American woody species reflect a potential trade-off between species' cold tolerance strategies and their competitiveness in warmer environments. In support of this, our results showed that CD_{to}, which largely reflects species biogeographical history, is one determinant. However, the relatively low explained variance of the models suggests that other factors not tested here are important too.

Cold-tolerant European species also have large ranges (Fig. 2 **a**), but the signal was weaker than for North American species (Table 1). This difference between the continental species sets is partly caused by some unique European genera – as demonstrated by the fact that removing them from the analysis improved overall model performance (see Results) – and by a cluster of European species with intermediate positions along the cold-drought axis having large ranges (Fig. 2 **a**). These large-ranged species include *Picea abies* (L.) H. Karst, *Pinus sylvestris* L. and *Betula pendula* Roth. These species survived the LGM in central and/or eastern Europe, and were able to migrate rapidly northwards into Northern Europe after the ice retreated (Normand et al., 2011). While these species are all cold tolerant, their tolerance syndromes include at least some drought tolerance and waterlogging sensitivity as well, shifting them towards the center of the cold-drought trade-off axis. This effectively decouples these species from the negative relationship between the cold-drought trade-off and range size, emphasizing the importance of considering multivariate stress tolerance syndromes rather than single-factor tolerances when analyzing the reasons for range size variation. Other European species that are potentially decoupled from this relationship also belong to genera that do not occur in the North American species set. Other studies have indicated how these continental differences could be due to selective survival of species with particular functional traits in discrepant Quaternary geological history (Dynesius and Jansson, 2000). The differences in species pool might thus be the cause of the lower R^2 of the models for European species compared to those for North American species (Table 1). For European and North American species alike drought-tolerant species have relatively small distribution ranges (e.g. Normand et al., 2009).

The negative scaling of range size with stress tolerance is also consistent with macrophysiological evidence suggesting that pre-adaptation to low temperature, or species-specific ability to adapt to freezing temperatures, may have favored species' northward migration after glacial retreat (Araújo et al., 2013; Lancaster and Humphreys, 2020). In contrast, the cold-drought tolerance tradeoff might limit expansion into cooler environments for woody species in warmer environments already adapted to drought. Even though drought and heat stress can co-vary in warm-temperate ecosystems, we argue that the effect of drought tolerance on range size should be considered separately from that of heat tolerance. The most heat tolerant plant species occur in both dry and moist environments (Lancaster and Humphreys, 2020), and although transpirational cooling generally costs water, plants have also evolved adaptations to reduce the detrimental effects of heat stress under drought (Flexas et al., 2014). For example, among a plethora of other adaptations, increased water-use efficiency, or leaf movements as stress avoidance mechanisms, can decouple leaf physiological responses to high temperatures from responses to drought in Mediterranean woody plants (Flexas et al., 2014; Puglielli et al., 2017).

We have shown that abiotic stress tolerance, in particular the cold-drought tradeoff axis, can explain some of the interspecific differences in range size among woody species, and that it contributes to shaping their realized niches across continents. Species positioning in the *Stress Space*, which is determined by trade-offs between multiple stress tolerances (Puglielli et al., 2021a), can be interpreted as a measure of a species' realized tolerance niche more than as a measure of its fundamental niche (Puglielli et al., 2023). In support of this interpretation, the trade-offs between different abiotic stress tolerances act to reduce the size of the fundamental niche towards that of the realized niche (Sack, 2004). Therefore, by representing the typical multiple abiotic stress levels to which a plant species has adapted, its position in the *Stress Space* inherently corresponds to a set of energy and allocation constraints underlying its tolerance strategy. Such strategies are thought to directly control species' geographic distributions (Morin and Chuine, 2006). Species position along defined niche-axes is a strong predictor of range size and occupancy in many animal groups (Seliger et al., 2021), and our results show that this is also true for temperate woody plants.

4.2. *The relationship between range filling and the cold-drought tolerance trade-off*

All species are constrained in the extent to which they fill their potential range because of specific physiological and ecological limits (Paul et al., 2009), and trade-offs between them. Importantly, in contrast to our results for range size, we identified different range filling determinants between the Europe and North America. These differences were not caused by differences in generic composition between the species pools of the two continents (Table S4).

Range filling in European species was driven by a positive interaction between latitude and CD_{to}. Despite a significant main effect of the CD_{to} axis on range filling (Table 1), we did not interpret this effect as a significant interaction. Instead, we regard the interaction between CD_{to} and latitude as the main driver of interspecific differences in range filling across European species. We interpreted this interaction as the signal of the effect of other factors co-varying with latitude, which were not considered in this study, such as climatic factors or dispersal syndromes (Estrada et al., 2015). These might be important for explaining range filling patterns in European species. Such non-climatic and climatic limitations across latitudes might also co-vary with species' abiotic stress tolerance strategies, possibly explaining why we observed a positive interaction between CD_{to} and latitude as a driver of range filling differences in European species. Similarly, Nogués-Bravo et al. (2014) proposed that the negative correlation between seed mass and range filling found across 38 European tree species could be caused by covariation between seed mass and other factors, including species' drought tolerances, supporting our interpretation. In contrast, North American species' range filling was influenced only by a negative effect of latitude. A negative relationship between range filling and latitude has also been found previously for North American species (Seliger et al., 2021); this study also reported a positive range filling-longitude relationship, suggesting that longitude can alter the expected range filling-latitude relationship.

Differences in the relationships observed between the two continents might ultimately depend on their geographical extent, since Europe has a much smaller latitudinal and longitudinal range, and less gradual geographical clines than North America (Morin and Chuine, 2006). Difference between continents in geographical extent can also affect extinction patterns, creating conditions that promote the survival of species with particular functional traits and range sizes (Dynesius and Jansson, 2000). The Quaternary glacial events, including the last glacial maximum ∼ 10,000 years ago, and previous glaciations that have occurred periodically every ∼ 100,000 years, had negative effects on tree diversity in Asia and North America. Local extinctions during these events were much more severe in Europe than in North America, because of its more limited geographical extent (Dynesius and Jansson, 2000). In addition, some European species have Eurasian ranges. Constraining our model's range size projections to Europe instead of across

Eurasia might have caused overestimations of range sizes for these species. Overestimation of potential range size causes underestimation of range filling (see Appendix S2 for further discussion). While further research is needed to clarify these issues, our findings suggest that continent-specific interactions between the cold-drought tolerance tradeoff, specific continental features and other species-specific adaptations such as dispersal syndromes, are likely to co-determine continent-specific levels of range filling.

5. Limitations of the study

Comparable data on range size and abiotic stress tolerances were available for only a fraction of the temperate woody species that occur in Europe and North America. This may have implications for the generality of our findings, especially in a biogeographical context – range filling patterns are probably determined by the evolutionary and geological history of the regions concerned, and the way in which species pools have changed throughout the history of massive disturbances, such as ice ages. Further studies are needed to assess the relationships between abiotic stress trade-offs and range filling in other continents and regions, and for other plants, but data for such comprehensive analyses are simply not yet available. We expect our results to be upheld outside the temperate zone, although studies including tropical and/or herbaceous plants will be needed to verify this. The effects of abiotic stress tolerance on species ranges are probably smaller in the tropics and in low-disturbance areas with climates that are close to optimal for growth. There are likely to be interesting stress tolerance patterns to be discovered in regions where milder climates meet space limitations and extreme conditions for dispersal, such as on certain islands, and particular combinations of abiotic stress, such as in polar and alpine deserts.

6. Conclusions

Abiotic stress tolerance, in particular the cold-drought tolerance trade-off, explains some interspecific differences in range size across temperate woody plant species. Importantly, this relationship is largely independent of latitude, and consistent with species biogeographical histories in Europe and North America. Notably, our findings also suggest that accounting for species' abiotic stress tolerance strategies can reconcile macroecological and macrophysiological theories explaining range size differences among woody plants, supporting the hypothesis (Morin and Chuine, 2006) that abiotic stress tolerances and trade-offs between them play a crucial role in shaping species ́distributions.

Our results reveal a prominent role of species abiotic stress tolerance strategies in determining plant distribution patterns, in particular with respect to range size variation. At the same time, our models leave some interspecific differences in range size and range filling unexplained. It is clear that some other factors that were not considered here, possibly co-varying with latitude and/or abiotic stress tolerance syndromes, play important roles in shaping range sizes, and range filling patterns in particular. All in all, species position along defined niche axes is a strong predictor of range size and occupancy in temperate woody plants.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

GP was supported by MCIN/AEI/10.13039/501100011033 [Grant no. IJC2020-043331-I] and by the grant PID2021-122214NA-I00 funded by MCIN/AEI/10.13039/501100011033 and by FEDER "ESF Investing in your future". ET was supported by the Estonian Research Council [Grant no. MOBJD1030]. LL was supported by the Estonian Academy of Sciences [Research Professorship for Arctic Studies].

Author contributions

GP, LL and AMH conceived the idea. GP and AMH planned the data analysis. GP and ET analysed the data. GP and JK collected the data. MJH contributed conceptualization and critical revision of the manuscript. GP and AMH led the writing. All the authors critically revised the manuscript to reach the final version.

Data accessibility statement

The data used in this study are available in Supporting Information Table S3.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2023.125734.

References

Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 267, 739–745. https://doi.org/10.1098/rspb.2000.1065.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L., 2013. Heat freezes niche evolution. Ecol. Lett. 16, 1206–1219. https://doi.org/10.1111/ele.12155.

Bjornstad, O.N., Cai, J., 2022. ncf: Spatial Covariance Functions.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279. https://doi.org/10.1086/284267.

Busby, J.R., 1986. A biogeoclimatic analysis of Nothofagus cunninghamii (Hook.) Oerst. in southeastern Australia. Aust. J. Ecol. 11, 1–7. https://doi.org/10.1111/j.1442-9993.1986.tb00912.x.

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Brief. 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007.

Chuine, I., 2010. Why does phenology drive species distribution. Philos. Trans. R. Soc. B: Biol. Sci. 365, 3149–3160. https://doi.org/10.1098/rstb.2010.0142.

Colwell, R.K., Hurtt, G.C., 1994. Nonbiological gradients in species richness and a spurious rapoport effect. Am. Nat. 144, 570–595.

Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Natl. Acad. Sci. 97, 9115–9120. https://doi.org/10.1073/pnas.97.16.9115.

Estrada, A., Morales-Castilla, I., Meireles, C., Caplat, P., Early, R., 2018. Equipped to cope with climate change: traits associated with range filling across European taxa. Ecography 41, 770–781. https://doi.org/10.1111/ecog.02968.

Estrada, A., Meireles, C., Morales-Castilla, I., Poschlod, P., Vieites, D., Araújo, M.B., Early, R., 2015. Species' intrinsic traits inform their range limitations and vulnerability under environmental change. Glob. Ecol. Biogeogr. 24, 849–858. https://doi.org/10.1111/geb.12306.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49. https://doi.org/10.1017/S0376892997000088.

Fine, P.V.A., 2015. Ecological and evolutionary drivers of geographic variation in species diversity. Annu. Rev. Ecol. Evol. Syst. 46, 369–392. https://doi.org/10.1146/annurev-ecolsys-112414-054102.

Flexas, J., Diaz-Espejo, A., Gago, J., Gallé, A., Galmés, J., Gulías, J., Medrano, H., 2014. Photosynthetic limitations in Mediterranean plants: a review. Environ. Exp. Bot. 103, 12–23. https://doi.org/10.1016/j.envexpbot.2013.09.002 (Response to abiotic stresses of plants of Mediterranean-type ecosystems).

Freckleton, R.P., Harvey, P.H., Pagel, M., Losos, A.E.J.B., 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat. 160, 712–726. https://doi.org/10.1086/343873.

Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S., Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L., Schulte, P.M., Spicer, J.I., Stillman, J.H., Terblanche, J.S., van

Kleunen, M., 2009. Macrophysiology: a conceptual reunification. Am. Nat. 174, 595–612. https://doi.org/10.1086/605982.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: With Applications in R [WWW Document]. Cambridge Core. 〈https://doi.org/10.1017/9781139028271〉.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Hutchinson-CSHSymQunBio-1957.pdf, n.d.

Ives, A.R., Helmus, M.R., 2011. Generalized linear mixed models for phylogenetic analyses of community structure. Ecol. Monogr. 81, 511–525. https://doi.org/10.1890/10-1264.1.

Jin, Y., Qian, H., 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42, 1353–1359. https://doi.org/10.1111/ecog.04434.

Kalwij, J.M., Robertson, M.P., Ronk, A., Zobel, M., Pärtel, M., 2014. Spatially-explicit estimation of geographical representation in large-scale species distribution datasets. PLoS One 9, e85306. https://doi.org/10.1371/journal.pone.0085306.

Koenker, R., Bassett, G., 1978. Regression quantiles. Econometrica 46, 33–50. https://doi.org/10.2307/1913643.

Laanisto, L., Niinemets, Ü., 2015. Polytolerance to abiotic stresses: how universal is the shade–drought tolerance trade-off in woody species? Glob. Ecol. Biogeogr. 24, 571–580. https://doi.org/10.1111/geb.12288.

Lancaster, L.T., Humphreys, A.M., 2020. Global variation in the thermal tolerances of plants. PNAS 117, 13580–13587. https://doi.org/10.1073/pnas.1918162117.

Li, D., Dinnage, R., Nell, L.A., Helmus, M.R., Ives, A.R., 2020. phyr: an r package for phylogenetic species-distribution modelling in ecological communities. Methods Ecol. Evol. 11, 1455–1463. https://doi.org/10.1111/2041-210X.13471.

Linder, H.P., Antonelli, A., Humphreys, A.M., Pirie, M.D., Wüest, R.O., 2013. What determines biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid grasses. J. Biogeogr. 40, 821–834. https://doi.org/10.1111/jbi.12070.

Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40, 778–789. https://doi.org/10.1111/jbi.12058.

McFadden, I.R., Sandel, B., Tsirogiannis, C., Morueta-Holme, N., Svenning, J.-C., Enquist, B.J., Kraft, N.J.B., 2019. Temperature shapes opposing latitudinal gradients of plant taxonomic and phylogenetic β diversity. Ecol. Lett. 22, 1126–1135. https://doi.org/10.1111/ele.13269.

Morin, X., Chuine, I., 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. Ecol. Lett. 9, 185–195. https://doi.org/10.1111/j.1461-0248.2005.00864.x.

Morueta-Holme, N., Enquist, B.J., McGill, B.J., Boyle, B., Jørgensen, P.M., Ott, J.E., Peet, R.K., Šímová, I., Sloat, L.L., Thiers, B., Violle, C., Wiser, S.K., Dolins, S., Donoghue, J.C., Kraft, N.J.B., Regetz, J., Schildhauer, M., Spencer, N., Svenning, J.-C., 2013. Habitat area and climate stability determine geographical variation in plant species range sizes. Ecol. Lett. 16, 1446–1454. https://doi.org/10.1111/ele.12184.

Naimi, B., Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39, 368–375. https://doi.org/10.1111/ecog.01881.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.

Nogués-Bravo, D., Pulido, F., Araújo, M.B., Diniz-Filho, J.A.F., García-Valdés, R., Kollmann, J., Svenning, J.-C., Valladares, F., Zavala, M.A., 2014. Phenotypic correlates of potential range size and range filling in European trees. Perspect. Plant Ecol. Evol. Syst. 16, 219–227. https://doi.org/10.1016/j.ppees.2014.05.005.

Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A., Svenning, J.-C., 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. Glob. Ecol. Biogeogr. 18, 437–449. https://doi.org/10.1111/j.1466-8238.2009.00451.x.

Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O., Svenning, J.-C., 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. Proc. R. Soc. B: Biol. Sci., vol. 278, pp. 3644–53. 〈https://doi.org/10.1098/rspb.2010.2769〉.

Paul, J.R., Morton, C., Taylor, C.M., Tonsor, S.J., 2009. Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant Genus Psychotria (Rubiaceae). Am. Nat. 173, 188–199. https://doi.org/10.1086/595762.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Pither, J., 2003. Climate tolerance and interspecific variation in geographic range size. Proc. R. Soc. Lond. Ser. B: Biol. Sci., vol. 270, pp. 475–81. 〈https://doi.org/10.1098/rspb.2002.2275〉.

Puglielli, G., Hutchings, M.J., Laanisto, L., 2021a. The triangular space of abiotic stress tolerance in woody species: a unified trade-off model. New Phytol. 229, 1354–1362. https://doi.org/10.1111/nph.16952.

Puglielli, G., Redondo-Gómez, S., Gratani, L., Mateos-Naranjo, E., 2017. Highlighting the differential role of leaf paraheliotropism in two Mediterranean Cistus species under drought stress and well-watered conditions. J. Plant Physiol. 213, 199–208. https://doi.org/10.1016/j.jplph.2017.02.015.

Puglielli, G., Laanisto, L., Poorter, H., Niinemets, Ü., 2021b. Global patterns of biomass allocation in woody species with different tolerances of shade and drought: evidence for multiple strategies. New Phytol. 229, 308–322. https://doi.org/10.1111/nph.16879.

Puglielli, G., Laanisto, L., Gori, A., Cardoso, A.A., 2023. Woody plant adaptations to multiple abiotic stressors: where are we. Flora 299, 152221. https://doi.org/10.1016/j.flora.2023.152221.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ricklefs, R.E., Schluter, D. (Eds.), 1994. Species Diversity in Ecological Communities. University of Chicago Press, Chicago, IL.

Ricotta, C., Godefroid, S., Rocchini, D., 2010. Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. Biol. Invasions 12, 233–240. https://doi.org/10.1007/s10530-009-9445-0.

Sack, L., 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation. Oikos 107, 110–127. https://doi.org/10.1111/j.0030-1299.2004.13184.x.

Seliger, B.J., McGill, B.J., Svenning, J.-C., Gill, J.L., 2021. Widespread underfilling of the potential ranges of North American trees. J. Biogeogr. 48, 359–371. https://doi.org/10.1111/jbi.14001.

Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R., Slatyer, R.A., 2017. Evolution of ecological niche breadth. Annu. Rev. Ecol. Evol. Syst. 48, 183–206. https://doi.org/10.1146/annurev-ecolsys-110316-023003.

Sheth, S.N., Morueta-Holme, N., Angert, A.L., 2020. Determinants of geographic range size in plants. New Phytol. 226, 650–665. https://doi.org/10.1111/nph.16406.

Smith, S.A., Brown, J.W., 2018. Constructing a broadly inclusive seed plant phylogeny. Am. J. Bot. 105, 302–314. https://doi.org/10.1002/ajb2.1019.

Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am. Nat. 133, 240–256.

Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proc. R. Soc. B: Biol. Sci. 278, 1823–1830. https://doi.org/10.1098/rspb.2010.1295.

Svenning, J.-C., Skov, F., 2004. Limited filling of the potential range in European tree species. Ecol. Lett. 7, 565–573. https://doi.org/10.1111/j.1461-0248.2004.00614.x.

Svenning, J.-C., Normand, S., Kageyama, M., 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. J. Ecol. 96, 1117–1127. https://doi.org/10.1111/j.1365-2745.2008.01422.x.

Title, P.O., Bemmels, J.B., 2018. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography 41, 291–307. https://doi.org/10.1111/ecog.02880.

Varela, S., Anderson, R.P., García-Valdés, R., Fernández-González, F., 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37, 1084–1091. https://doi.org/10.1111/j.1600-0587.2013.00441.x.

Wazen, N., Garavaglia, V., Picard, N., Besacier, C., Fady, B., 2020. Distribution maps of twenty-four Mediterranean and European ecologically and economically important forest tree species compiled from historical data collections. Ann. Silvic. Res. 44, 95–101. https://doi.org/10.12899/asr-1933.

Zanne, A.E., Pearse, W.D., Cornwell, W.K., McGlinn, D.J., Wright, I.J., Uyeda, J.C., 2018. Functional biogeography of angiosperms: life at the extremes. New Phytol. 218, 1697–1709. https://doi.org/10.1111/nph.15114.