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# ECOGRAPHY

## Research

### Of niches and distributions: range size increases with niche breadth both globally and regionally but regional estimates poorly relate to global estimates

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The relationship between species' niche breadth (i.e. the range of environmental conditions under which a species can persist) and range size (i.e. the extent of its spatial distribution) has mostly been tested within geographically restricted areas but rarely at the global extent. Here, we not only tested the relationship between range size (derived from species' distribution data) and niche breadth (derived from species' distribution and co-occurrence data) of 1255 plant species at the regional extent of the European Alps, but also at the global extent and across both spatial scales for a subset of 180 species. Using correlation analyses, linear models and variation partitioning, we found that species' realized niche breadth estimated at the regional level is a weak predictor of species' global niche breadth and range size. Against our expectations, distribution-derived niche breadth was a better predictor for species' range size than the co-occurrence-based estimate, which should, theoretically, account for more than the climatically determined niche dimensions. Our findings highlight that studies focusing on the niche breadth vs range size relationship must explicitly consider spatial mismatches that might have confounded and diminished previously reported relationships.

Keywords: global distribution, niche breadth, vegetation database.



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## Introduction

The niche is a keystone concept in ecology to quantify and to ultimately predict a species' occurrence in space and time (Pulliam 2000, Guisan and Thuiller 2005, Soberón 2007, Colwell and Rangel 2009). There are several different definitions of the niche (Chase and Leibold 2003). Hutchinson, in particular, defined the niche by means of the sum of all environmental factors (resources and regulators) that constrain a species' performance and survival, conceived in an  $n$ -dimensional hypervolume (Hutchinson 1957). Based on this concept, the species' tolerance or niche breadth is the range of environmental conditions under which populations can persist indefinitely. Since a species' fundamental niche is almost impossible to capture (as it may comprise unpopulated, but suitable environmental conditions, that are beyond dispersal reach, or from which the species is excluded due to biotic interactions, or which do not exist on Earth at the surveyed time; Colwell and Rangel 2009), we hereafter refer to the niche as the realized niche, i.e. the range of abiotic and biotic conditions under which a species actually occurs (Soberón 2007).

One of the early hypotheses in macroecology is that generalist species with larger tolerances along abiotic gradients – comprising, for instance, temperature, water supply, nutrient availability and disturbance regime – are more abundant and geographically more widespread than more specialized species, resulting in positive relationships between niche breadth and range size (Brown 1984). However, plant species' distributions can also be limited by negative interactions with competitors, herbivores and pathogens (Bruehlheide and Scheidel 1999, Bütof and Bruehlheide 2011, Gaston 2003). Other factors, such as the geographic configuration of specialized habitats and climate stability (Morueta-Holme et al. 2013) or the genetic structure and colonization ability of species (Lowry and Lester 2006), were also shown to influence plant range sizes. Many of these factors differently affect species' range boundaries and operate in interaction (Soberón 2007, Gaston 2009), thereby masking potentially significant relationships between niche breadth and range size in individual species. Alternatively, the relationship between niche breadth and range size was also shown to possibly result from artifactual effects, at least in some geographic instances (e.g. Mediterranean islands; Lambdon 2008).

Yet, a positive relationship between species' niche breadth and range size has been confirmed by Slatyer et al. (2013) in a meta-analysis across 64 studies which covered animal and plant species and niche breadth estimates from environmental gradients (environmental niche breadth), the number of habitats (habitat niche breadth) and the variety of food resources utilized (dietary niche breadth). However, only few of the studies included in this comprehensive meta-analysis actually compiled data on species' global range sizes and, in the case of plant species, none compared relationships between niche breadth and range size at different spatial scales. Only Köckemann et al. (2009) and Luna and Moreno (2010) actually assessed global range sizes for 25 tree and 53 herbaceous species, respectively (Table 1). While Köckemann et al. (2009)

demonstrated that global range size was strongly and positively related to niche breadth for temperature but not for soil properties, Luna and Moreno (2010) found no such correlation with niche breadth estimates derived from germination requirements (see also Thompson and Ceriani 2003). Thus, Brown's hypothesis (Brown 1984) on the positive relationship between niche breadth and range size still lacks scrutinized testing at the global extent for plant species. Besides, it has rarely been assessed whether range size and niche breadth also co-vary positively across spatial scales (but see Thuiller et al. (2012) for some aspects of nestedness), and especially whether regionally derived niche breadth estimates can predict species' global range sizes. This might be particularly useful in the case of biological invasions since regional niche breadth estimates derived from species' native ranges can inform on potential species' range sizes at the global extent, including the invasive ranges (Thuiller et al. 2005, Pyšek et al. 2015).

For species analysed across large spatial extents (e.g. continents), only coarse-resolution ( $\geq 1 \text{ km}^2$ ) climate data are available to assess species' niche breadth. Additionally, as outlined by Gaston (2003), climate data only capture some of the factors that affect population fitness and thus distribution boundaries. To circumvent the need to conduct numerous environmental and biological measurements at fine spatial resolution and across large spatial extents, Fridley et al. (2007) proposed an approach that allows for conjointly estimating the relative niche breadth for a large set of species, a measure that is calculated solely from species co-occurrence data. Based on the assumption that different environmental conditions result in different community compositions, the dissimilarity (i.e. the taxonomic beta diversity) among a set of plant communities (vegetation plots) in which a focal plant species occurs is used as a proxy for its realized niche breadth. This relative metric thus explicitly accounts for biotic interactions and implicitly for the abiotic components of the realized niche as well as for the impact of dispersal limitations due to either species' intrinsic dispersal abilities or physical barriers on the realized niche. Furthermore, it can be argued that Fridley's metric becomes independent of species' local abundances, which are often related to species range sizes (Thompson et al. 1998, Gaston 2003), because it is repeatedly calculated across random subsets of all records in which a focal species is present (Fridley et al. 2007). Previous studies focusing on plants already demonstrated the utility of this approach to test, for instance, niche assembly hypotheses (Manthey et al. 2011), niche differentiation along latitudinal gradients (Wasof et al. 2013), trade-offs between species' tolerance and dominance (Boulangéat et al. 2012) as well as the relationship between niche breadth and range size within the French Alps (Boulangéat et al. 2012) and Eurasia (divided in  $10^\circ$  cells; Pannek et al. 2013, 2016).

To date, however, no study has tested whether co-occurrence-based niche breadth estimates are better predictors of species' range size than niche breadth estimates that are derived from abiotic or biotic conditions. Since the majority of the studies included in the meta-analysis of Slatyer et al. (2013) did not assess species' range sizes at the global extent,

Table 1. Studies on the relationship between the niche breadth and range size of plants, compiled in the meta-analyses of Slatyer et al. (2013). Niche breadth estimates were derived from either species' environmental tolerances or the number of occupied habitats.

Study	NB estimate	Are species RSs comprehensive?
Baltzer et al. (2007)	Habitat	No – species are classified as widespread or southern based upon their distribution with respect to the Kangar–Pattani line
Boulangeat et al. (2012)	Habitat	No – the authors measured only regional area occupancy within the French Alps
Callaghan and Ashton (2008)	Habitat	No – the authors measured rarity within a region of north-west England and the British Isles
Essl et al. (2009)	Tolerance/Habitat	<b>Yes</b> – but the authors restricted their work to species endemic to Australia
Kessler (2002)	Tolerance	No – the author interpolated the species' distribution on the basis of the species' ecological requirements and the distribution of main vegetation types
Köckemann et al. (2009)	Habitat	<b>Yes</b> – the authors used the entire distribution range of several central European tree species
Kolb et al. (2006)	Habitat	No – the authors measured regional area occupancy restricted to Germany
Luna and Moreno (2010)	Tolerance	<b>Yes</b> - Latitudinal range compiled in the Flora del Paisos Catalans
Luna et al. (2011)	Tolerance	No – the authors classified species distributions into three categories (endemic, Mediterranean, widely distributed)
Pither (2003)	Tolerance	<b>Yes</b> – the author measured area occupancy of species endemic to continental United States of America and Canada
Williams et al. (2010)	Tolerance	No – the authors excluded occurrence records outside the Western Hemisphere

it still remains to be tested whether regionally derived niche breadth estimates are sufficient predictors for species' global range sizes. Here, we provide niche breadth and range size estimates for a large number of terrestrial vascular plant species at both the regional ( $n = 1255$ ) and the global extent ( $n = 180$ ) by using a regional vegetation database of co-occurrence data at the plot level (Lenoir et al. 2012) as well as a unique dataset of global species range maps (Chorology Database Halle, CDH) overlaid on global and regional climatic grids ranging from 5 km to 250 m in spatial resolution, respectively.

Based on these data, we perform a cross-scale analysis of the relationship between species' niche breadth and range size. We hypothesize that (H1) species' regional range size is positively correlated with species' regional niche breadth, regardless of whether the latter is derived from relatively coarse-grained climatic conditions or plot-level species co-occurrences. More specifically, we predict that (H2) niche breadth derived from co-occurrence data at the plot level explains more variation in regional range size than niche breadth derived from climatic conditions at relatively coarser spatial resolution because the former implicitly considers all relevant ecological gradients. We further hypothesize that (H3) species' global range size is positively correlated with species' global niche breadth derived from coarse-grained climatic conditions observed across the species range. Finally, we expect (H4) that species' global range size is positively correlated with the regionally derived niche breadth although the correlation is likely to be weaker than with globally derived niche breadth estimates.

## Material and methods

### Vegetation records at the regional extent

To provide reliable estimates of vascular plant species' niche breadth at the regional extent, we used a comprehensive, high-resolution regional vegetation database of

species co-occurrence data (community data) spanning a wide range of environmental conditions from forest habitats in the lowlands to alpine grasslands in the highlands, namely the Alps Vegetation Database (AVD, GIVD ID EU-00-014; Lenoir et al. 2012). Totalling 35 731 georeferenced vegetation plots that are distributed throughout the French, Swiss and Austrian Alps, the database comprises 5023 plant taxa from the temperate and Mediterranean terrestrial biomes. Species nomenclature follows The Plant List (<[www.theplantlist.org](http://www.theplantlist.org)>). Because it was impossible to disentangle natural from planted forest stands in the database, we discarded all macro-phanerophytes (i.e. tree species), based on the species' growth form classification of the Ecological Flora of the British Isles (<[www.ecoflora.co.uk](http://www.ecoflora.co.uk)>, Fitter and Peat 1994).

In order to reduce the statistical noise in the data when linking vegetation records to climatic data, we removed all plots with imprecise location coordinates ( $> 500$  m). For plots with identical geographical coordinates (e.g. in case of time series) we only retained the most recent or the largest one. After these filtering and data cleaning steps, a total of 23 319 vegetation plots harbouring 3112 vascular plant species were retained for the analyses at the regional extent.

### Range maps at the global extent

Species' presence-absence records at the global extent were derived from global range maps curated by the Chorology working group at the Univ. of Halle-Wittenberg (Chorology Database Halle, CDH). There, range maps of plant distributions are continuously digitized and compiled from: published range maps (Meusel et al. 1965, 1978, 1992); occurrence data from the Global Biodiversity Information Facility (GBIF, <[www.gbif.org](http://www.gbif.org)>); national and regional floristic datasets; and further maps from the floristic literature (Lundqvist and Jäger 1995–2007, Tralau 1969–1981, Lundqvist and Nordenstam 1988, Lundqvist 1992).

Contiguous areas of plant occurrence were digitized as polygons, whereas spatially isolated occurrences were digitized as single point locations. Polygon borders were statistically corrected by supervised stepwise elimination of marginal 0.05-percentiles. Elimination of outliers was supervised and validated by a species distribution model envelope algorithm that used lower and upper limits of non-interacting climate gradients. During stepwise elimination, species distribution model fit was maximized based on the Jaccard similarity between range polygons and prediction areas. The resulting predicted ranges were rasterized to grid layers of 2.5 arc min (ca  $4.5 \times 4.5$  km at the equator) resolution (WGS 84).

Seventeen species were discarded because their global distribution covered less than 50% of the geographical area covered by the AVD (i.e. the Alps region was at the border of their global distribution). All rasterized global range maps are prone to erroneously include unsuitable habitats. At least in the region of the European Alps, for which more fine-scaled occurrence records were available, we corrected, separately for each species, the erroneous inclusion of global grid cells at implausibly high elevations (i.e. by deletion of all grid cells at higher mean elevation than the species' maximum elevation in the AVD). These corrections only marginally reduced the number of species' global grid cells (median proportion of omitted cells is 0.09% with the highest value of 1.6% for *Phyteuma spicatum* L.).

### Climate data

For every plot record in the AVD and every grid cell from the CDH raster layers, we assigned bioclimatic conditions based on the standard 19 bioclimatic variables (BIO1 to BIO19) described in the WorldClim archive (<www.worldclim.org>, Hijmans et al. 2008). At the global extent, these were extracted from WorldClim at a spatial resolution of 2.5 arc min, which is about  $4.5 \times 4.5$  km at the equator. At the regional extent of the Alps, we extracted all temperature-related variables (BIO1 to BIO11) at a finer spatial resolution of 250 m, using the EuroLST dataset that partly captures topoclimate (Metz et al. 2014, GFOSS Blog 2015). For precipitation-related variables (BIO12 to BIO19), the finest spatial resolution available for the Alps is 30 arc sec, which is about 1 km at the equator (cf. WorldClim).

### Sample sizes

After data filtering and cleaning, regional niche breadth and range size estimates were calculated for 1255 vascular plant species, whereas global estimates were obtained for a subset of 180 species for which global distribution maps were available. In Fig. 1, we illustrated the different datasets and how niche breadth and range size estimates were computed based on the example of *Calluna vulgaris* (L.) Hull. Species' global distribution maps for the 180 species are shown in Supplementary material Appendix 1. All range size and niche breadth estimates are listed in Supplementary material Appendix 2.

### Regional niche breadth estimate derived from co-occurrence data: Reg-NB<sub>Co-oc</sub>

For each species that occurred in at least 40 plots of the AVD, we computed Reg-NB<sub>Co-oc</sub> as proposed by Fridley et al. (2007) using the R script provided by Manthey and Fridley (2008). The best measure to quantify plot dissimilarity is still under debate (Fridley et al. 2007, Manthey and Fridley 2008, Zelený 2008, Manthey et al. 2011, Botta-Dukát 2012). Here, we used the multiple Simpson dissimilarity index (Baselga et al. 2007) because it is independent of species richness and is insensitive to nestedness (i.e. if the species community composition in a given plot is a subset of another plot, the dissimilarity between those two plots is zero). The multiple Simpson dissimilarity index was calculated as:

$$M_{Sim} = \frac{\sum_i S_i - S_T}{\left[ \sum_{i < j} \min(b_{ij}, b_{ji}) \right] + \left[ \sum_i S_i - S_T \right]}$$

where  $S_i$  is the total number of species in site  $i$ ,  $S_T$  is the total number of species in all sites together,  $b_{ij}$  and  $b_{ji}$  is the number of species that occur at site  $i$  and not site  $j$  and that occur at site  $j$  and not at site  $i$ , respectively. We controlled for sample size effects and down-weighted the influence of outlier habitats (i.e. communities in which a focal species was rarely found) following the approach presented in Fridley et al. (2007) by calculating Reg-NB<sub>Co-oc</sub> as the average of 100 dissimilarity indices obtained from 100 random draws of 10 vegetation plots in which the focal species occurred. This number of 10 plots for which the multiple dissimilarity index is calculated had to be determined somewhat arbitrarily. A higher number of records restricts the analyses to only common species whereas a lower number decreases the credibility of the obtained niche breadth estimates. Boulangeat et al. (2012) have demonstrated in the French Alps that the obtained niche breadth estimates for plants were consistent regardless of whether they were calculated from 5, 10 or 15 plots. Hence, we followed their decision and likewise based our results on the dissimilarity of 10 vegetation plots. Based on the information in Flora Indicativa (Landolt et al. 2010), we discarded the resulting niche breadth estimates of all species that were not classified as indigenous or archaeophytes in the European Alps.

### Regional niche breadth estimate derived from regional climate data: Reg-NB<sub>Clim</sub>

For all vegetation plots in the AVD, we reduced the dimensionality of the 19 bioclimatic variables by means of a principal component analysis (PCA). As the first two PCA axes jointly explained 84.5% of the overall climatic variation among vegetation plots, we used the position of each vegetation plot along the first two PCA axes to derive its position in the available climatic space. Reg-NB<sub>Clim</sub> was calculated as the area of the minimum convex polygon (MCP) encapsulating all vegetation plots in which the focal species occurred across the available climatic space. Similar to Reg-NB<sub>Co-oc</sub>, we down-weighted the influence of outlier plots and controlled for

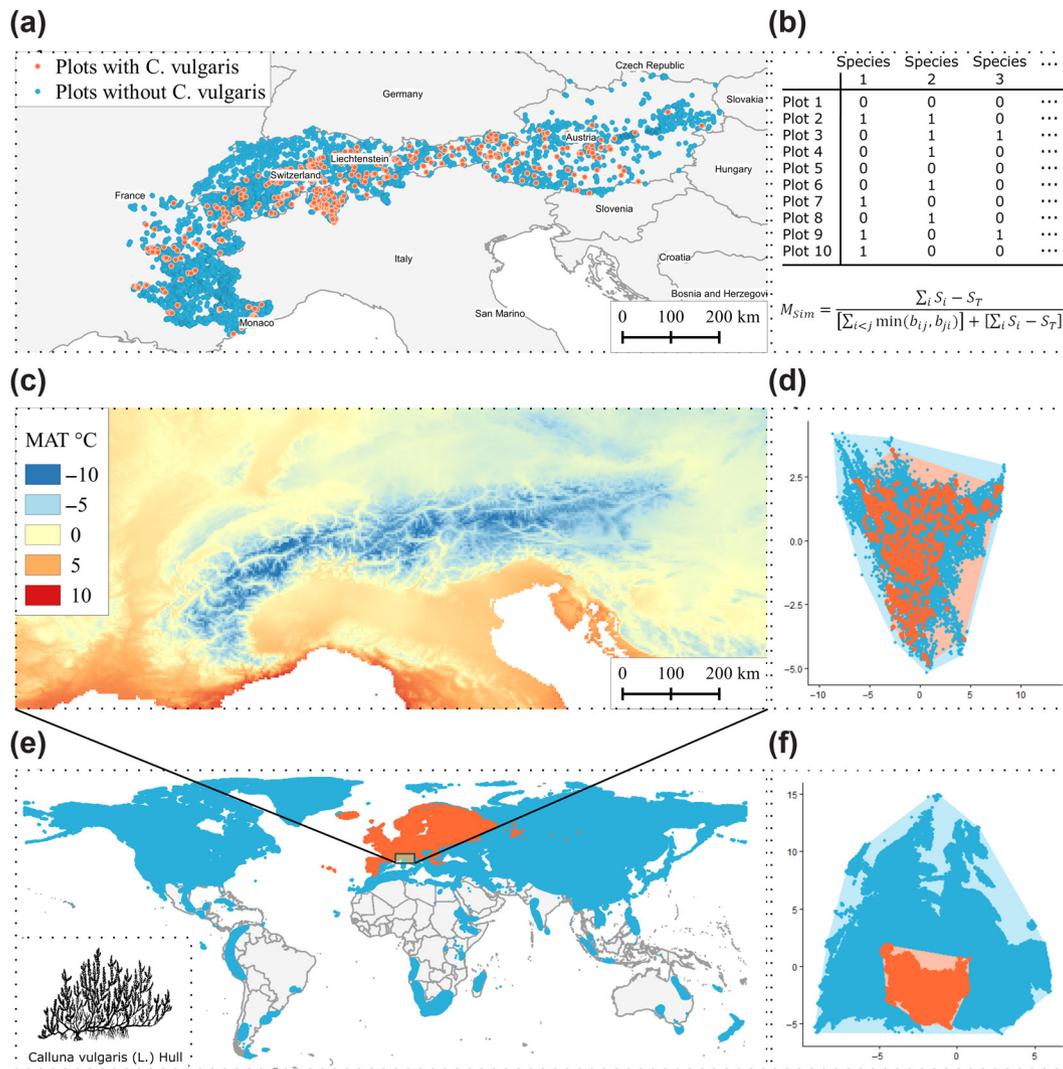


Figure 1. Illustration of the datasets and methods applied to calculate species' range size and niche breadth estimates. Vegetation surveys and grid cells that are covered by all studied species (1255 at the regional extent and a subset of 180 at the global extent) are shown in blue. Exemplary vegetation plots and grid cells in which *Calluna vulgaris* (L.) Hull occurred are shown in orange. a) 23 319 plots from the Alps Vegetation Database (AVD, Lenoir et al. 2012) with *C. vulgaris* occurring in 968 plots. b) Reg-NB<sub>Co-oc</sub> estimates derived from species co-occurrence in the AVD based on the multiple Simpson index. c) Exemplary distribution of a climate variable (here, mean annual temperature) across the regional extent of the AVD. d) Reg-NB<sub>Clim</sub> estimates derived from species presence across the climatic space of the AVD. Depicted are the minimum convex hulls encapsulating all the records (presences in orange and absences in blue) along the first two axes of a principal component analysis based on all 19 bioclimatic variables. e) 5 813 739 global grid cells in which at least one of the 180 plant species with global range maps occurred (blue). The orange area represents the 495 334 cells in which *C. vulgaris* occurred. f) Glob-NB<sub>Clim</sub> estimates derived from species' presences in the global climatic space. Depicted are the minimum convex hulls encapsulating all the grid cells (presences of *C. vulgaris* in orange and absences in blue) along the first two axes of a principal component analysis based on all the 19 bioclimatic variables.

sample size effects by calculating Reg-NB<sub>Clim</sub> as the average of 100 MCP area values obtained from 100 random draws of 10 vegetation plots in which the focal species occurred.

### Regional range size estimate derived from co-occurrence data: Reg-RS

For each species that occurred in at least 40 plots of the AVD, we calculated the geographic area of the minimum convex polygon (MCP) encapsulating all vegetation plots in which the focal species occurred across the geographical space

(based on the equal area Mollweide projection). Analogous to Reg-NB<sub>Co-oc</sub> and Reg-NB<sub>Clim</sub> we down-weighted the influence of outlier plots by calculating Reg-RS as the average of 100 MCP area values obtained from 100 random draws of 10 vegetation plots in which the focal species occurred.

### Global niche breadth estimate derived from global climate data: Glob-NB<sub>Clim</sub>

Analogous to the calculation of Reg-NB<sub>Clim</sub>, we reduced the dimensionality of the 19 bioclimatic variables at the

global extent by means of a PCA. We used the position on the first two PCA axes (which, together, explained 67.6% of the climatic variation) to determine a grid cell's position in the climatic space.  $\text{Glob-NB}_{\text{Clim}}$  was calculated as the climatic area of the minimum convex polygon (MCP) encapsulating all grid cells within which the focal species occurred across the climatic space. Again, we down-weighted the influence of outlier grid cells by calculating  $\text{Glob-NB}_{\text{Clim}}$  as the average of 100 MCP area values obtained from 100 random draws of 10 grid cells in which the focal species occurred.

### Global range size estimate derived from global range maps: Glob-RS

We determined species' Glob-RSs as the summed number of grid cells in which the focal species occurred.

### Statistical analyses

Prior to statistical analyses, the values of Reg-RS,  $\text{Reg-NB}_{\text{Clim}}$  and  $\text{Glob-NB}_{\text{Clim}}$  were square-root transformed to achieve approximate normality and all values (Reg-RS,  $\text{Reg-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Co-oc}}$ , Glob-RS,  $\text{Glob-NB}_{\text{Clim}}$ ) were, then, standardized (i.e. subtracting their means and then dividing by their standard deviations) to allow direct comparisons. For  $\text{Reg-NB}_{\text{Co-oc}}$  we did not have to use any transformation to achieve approximate normality but we also standardized it. The associations between all pairs of niche breadth and range size estimates were assessed by means of Pearson's product-moment correlation.

To test hypotheses H1 and H2, we calculated three separate linear models with Reg-RS as the response variable and either  $\text{Reg-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Co-oc}}$  or both as predictor variables. Model significance was determined via analyses of variance. We used a variation partitioning approach, based on adjusted  $R^2$  values (Borcard et al. 1992), to calculate the proportion of variation in Reg-RS values that is explained by the unique and shared effects of  $\text{Reg-NB}_{\text{Clim}}$  and  $\text{Reg-NB}_{\text{Co-oc}}$ .

Hypothesis H3 was tested using a linear model linking Glob-RS as the response and  $\text{Glob-NB}_{\text{Clim}}$  as the predictor variable for which we determined the model significance via analysis of variance. To test hypothesis H4 we calculated separate linear models with Glob-RS as the response variable and all possible combinations of predictor variables (i.e.  $\text{Glob-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Clim}}$  and  $\text{Reg-NB}_{\text{Co-oc}}$ ). Analogous to hypothesis H2, we then partitioned the variation in Glob-RS values that is explained by the unique and shared effects of  $\text{Glob-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Clim}}$  and  $\text{Reg-NB}_{\text{Co-oc}}$ .

To ascertain that model estimates did not suffer from phylogenetic autocorrelation, we tested for phylogenetic signals in all niche breadth and range size estimates and in the residuals from the regional and global models that incorporated all predictor variables. Based on a pruned *Daphne* phylogenetic tree (Durka and Michalski 2012), we calculated Blomberg's K values for 1,003 species at the regional extent and 180 species at the global extent for which phylogenetic information

was available. The significance of the obtained K values was tested against 999 permutations.

All calculations were performed in R (R Core Team) and by using the following packages: 'ade4' for principal component analyses (Dray and Dufour 2007); 'ggplot2', 'corrplot' and 'venneuler' for graphical representations (Wickham 2009, Wilkinson 2011, Wei 2013); 'picante' and 'ape' for phylogenetic analyses (Paradis et al. 2004, Kembel et al. 2010); 'Taxonstand' for species names standardization (Cayuela et al. 2012); and 'raster' and 'sp' for spatial data processing (Pebesma and Bivand 2005, Hijmans 2013).

## Results

Species' niche breadth derived from local climate ( $\text{Reg-NB}_{\text{Clim}}$ ) was positively correlated to the niche breadth that was derived from species' regional co-occurrence data ( $\text{Reg-NB}_{\text{Co-oc}}$ ; Pearson's correlation coefficient = 0.75,  $p < 0.001$ ). Species' regional range size was positively related to both regionally derived niche breadth estimates ( $F = 3059$ ,  $p < 0.001$ ,  $R_{\text{adj}}^2 = 0.71$  for  $\text{Reg-NB}_{\text{Clim}}$  and  $F = 1175$ ,  $p < 0.001$ ,  $R_{\text{adj}}^2 = 0.48$  for  $\text{Reg-NB}_{\text{Co-oc}}$ ; Fig. 2, see also Supplementary material Appendix 3 Table A1) albeit the variation uniquely explained by  $\text{Reg-NB}_{\text{Clim}}$  was higher than the variation uniquely attributable to  $\text{Reg-NB}_{\text{Co-oc}}$  (Fig. 3a).

For the subset of 180 species for which global range maps were available, species' global range size (Glob-RS) was positively related to species' niche breadth derived from global climate ( $\text{Glob-NB}_{\text{Clim}}$ ;  $F = 608.6$ ,  $p < 0.001$ ,  $R_{\text{adj}}^2 = 0.77$ , Fig. 4). Glob-RS was not related to the two regionally derived niche breadth estimates ( $F = 1.28$ ,  $p = 0.26$ ,  $R_{\text{adj}}^2 = 0$  for  $\text{Reg-NB}_{\text{Clim}}$  and  $F = 0.03$ ,  $p = 0.86$ ,  $R_{\text{adj}}^2 = 0$  for  $\text{Reg-NB}_{\text{Co-oc}}$ ; Fig. 5, see also Supplementary material Appendix 3 Table A2). Accordingly, only  $\text{Glob-NB}_{\text{Clim}}$  explained a significant amount of variation in Glob-RS values (Fig. 3b).

We found the phylogenetic signal in all niche breadth and range size estimates to be negligible with Blomberg's K values being below 0.03 for the values of Reg-RS,  $\text{Reg-NB}_{\text{Clim}}$  and  $\text{Reg-NB}_{\text{Co-oc}}$  as well as the residuals from the model that incorporated both regionally derived niche breadth estimates. In the subset of species for which global distribution maps were available, Blomberg's K values were below 0.1 for Glob-RS,  $\text{Glob-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Clim}}$ ,  $\text{Reg-NB}_{\text{Co-oc}}$  and the residuals of the model that incorporated all three niche breadth estimates. Correlations between Glob-RS and Reg-RS as well as  $\text{Glob-NB}_{\text{Clim}}$  and  $\text{Reg-NB}_{\text{Clim}}$  were both weak, albeit significant ( $r = 0.16$  and  $p = 0.03$  for Glob-RS vs Reg-RS;  $r = 0.15$  and  $p = 0.04$  for  $\text{Glob-NB}_{\text{Clim}}$  vs  $\text{Reg-NB}_{\text{Clim}}$ ; see also Supplementary material Appendix 3 Fig. A1–A2).

## Discussion

Using a combination of datasets that covered both the regional and global distribution of 1255 and 180 vascular plant species, respectively, we found positive relationships between

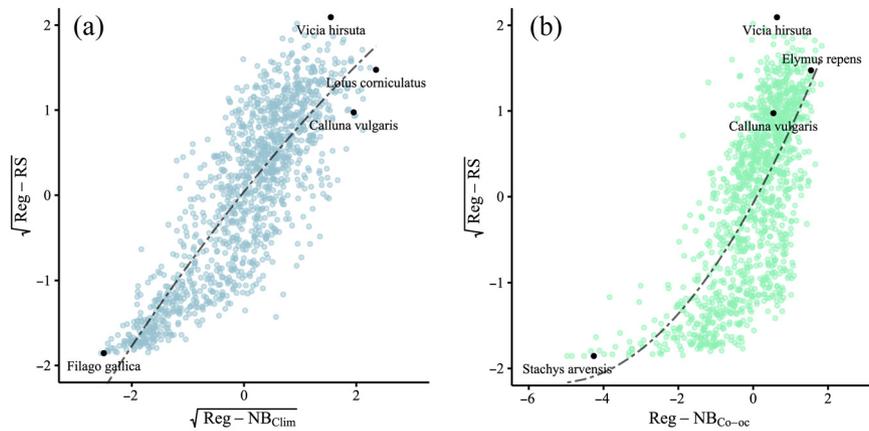


Figure 2. Relationships between species' regional range size (Reg-RS) and regional niche breadth estimates derived from either a) regional climate (Reg-NB<sub>Clim</sub>) or b) species' co-occurrence (Reg-NB<sub>Co-oc</sub>). Reg-RS and Reg-NB<sub>Clim</sub> values were square-root transformed and all values were standardized. Dotted lines indicate significant regression slopes from separate linear models ( $R_{adj}^2 = 0.71$  and  $0.48$  for Reg-NB<sub>Clim</sub> and Reg-NB<sub>Co-oc</sub>, respectively). Species names highlight the position of exemplary outlier species and *C. vulgaris*.

species' niche breadth and range size both at the regional (cf. H1) and the global (cf. H3) extents. This supports our hypotheses and former findings for other taxonomic groups (Slatyer et al. 2013).

At the regional extent, species' regional specialization (i.e. niche breadth) explained a higher amount of variation in species' regional range sizes ( $R_{adj}^2 = 0.72$ ) than previously reported (the highest  $R^2$  being 0.43 in Thompson et al. 1999, but see also Kolb et al. 2006, Essl et al. 2009, Pannek et al. 2013, Early and Sax 2014). At the global extent, species' globally derived niche breadth likewise explained a higher amount of variation in species' global range sizes ( $R_{adj}^2 = 0.56$ ) than reported in previous publications (e.g.  $R^2 = 0.45$  in Köckemann et al. 2009 and  $R^2 = 0.06$  in Luna and Moreno 2010), most likely because we calculated species' niche breadth and range size at the same, global extent and alleviated the effects of outlier grid cells.

In contrast to our hypothesis H2, niche breadth derived from species co-occurrences, although theoretically accounting for more niche dimensions (biotic interactions, dispersal limitations and disturbance tolerances) and recorded at a finer spatial resolution, was a much weaker predictor of species' regional range size than the purely climate-derived niche breadth estimate. Unfortunately, we cannot compare these findings of a weaker predictive power of niche breadth estimates that are derived from species co-occurrences than estimates that are derived from coarser-grained climatic conditions because this study is, to our knowledge, the first one to compare the ability of both approaches to predict species' range size. However, we suppose that this unexpected finding might result from a combination of the following factors: a) unaccounted local edaphic conditions; b) species' interactions; c) stochastic events; and d) the spatial resolution of the available data.

Co-occurrence based niche breadth measures might be distorted in places where a complex topography (Graae et al. 2018) or disturbance events (e.g. windfall,

flooding, trampling and human activities, Lembrechts et al. 2018) created small patches of favourable conditions in generally unfavourable habitats. If species are able to colonize these sanctuary patches from nearby suitable habitats, they might be recorded within a vastly different community, whereas the climate conditions match those of nearby favourable habitats. If such spots of favourable edaphic conditions (regarding water and nutrient status) allow whole plant communities to persist in otherwise unsuitable climatic conditions these spots might furthermore increase species' range sizes and climate-based niche breadth estimates but not those estimates that are based on species co-occurrence.

If certain species can alter the composition of their co-occurring neighbours, either via facilitating the establishment of other species (e.g. in harsh environments, D'Amen et al. 2017) or via replacing competitors (e.g. in nutrient rich environments) these 'community engineers' could also lead to

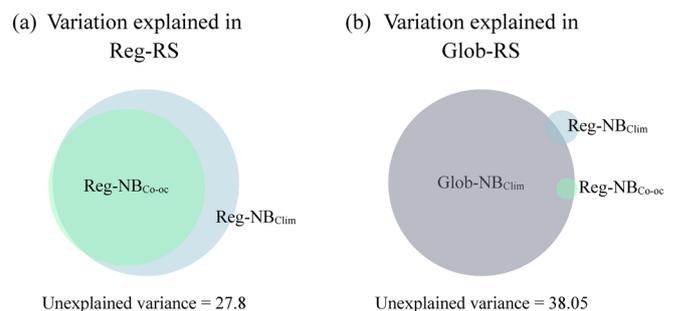


Figure 3. Variation partitioning for each combination of niche breadth estimates. The area of the circles relates to the amount of explained variation in a) species' range sizes across the European Alps region (Reg-RS) or b) species' global range sizes (Glob-RS). Overlapping areas show the amount of explained variation that is shared between variables. Niche breadth estimates were derived from regional climate data (Reg-NB<sub>Clim</sub>), regional co-occurrence (Reg-NB<sub>Co-oc</sub>) and global climate data (Glob-NB<sub>Clim</sub>).

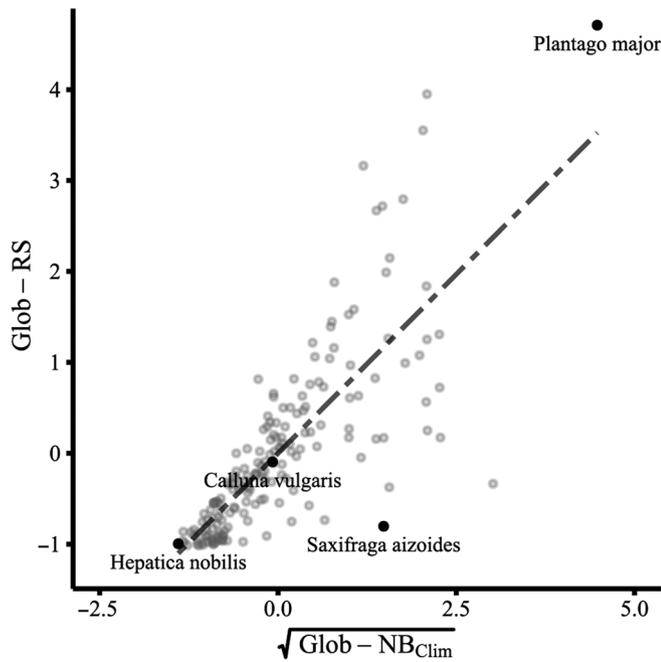


Figure 4. Relationship between species' global range size (Glob-RS) and niche breadth estimates derived from species' global distribution (Glob-NB<sub>Clim</sub>). Glob-NB<sub>Clim</sub> values were square-root transformed and all values were standardized. The dotted line indicates the significant regression slope from a linear model ( $R_{adj}^2=0.77$ ). Species names highlight the position of exemplary outlier species and *C. vulgaris*.

divergences between co-occurrence and abiotic niche breadth measurements.

Regarding the spatial resolution of our data, the plant range size estimates, which we calculated from minimum convex polygons, should only be considered crude estimates of species' heterogeneous, patchy and fine-scaled distributions. These coarse estimates likely match niche breadth measures obtained from similarly coarse data but not the

finer, plot-based, resolution of co-occurrence based niche breadth estimates. Especially in the case of specialist species that might exhibit rather punctual and scattered distributions, the minimum convex polygons that did not account for species' absences might yield overly large range size estimates. A very typical example of this scale effect on species distribution is the case of *Clematis fremontii* in the Ozark glades of Missouri (Erickson 1945) which looks like a continuously distributed species at the continental scale but has strongly clustered populations at the landscape scale. A more accurate estimate of species' range size at the regional extent might even result in a stronger predictive power of similarly fine-scaled co-occurrence based niche breadth estimates. We thus argue that the strength of the relationship between niche breadth and range size strongly depends on the spatial match between the investigated response variable and the set of explanatory variables.

The correlation we found between species' co-occurrence-based niche breadth and regional range size ( $R_{adj}^2=0.48$ ) was similarly reported from the Western Carpathians (Mráz et al. 2016) and higher than the correlations reported from Slovenia (Marinšek et al. 2015), the French Alps (Boulangeat et al. 2012) and southern France (Vimal and Devictor 2015). Likewise, the correlation we found between both regionally derived niche breadth estimates ( $r=0.75$ ) ranks on the upper limit of previously published relationships (Fridley et al. 2007, Carboni et al. 2016, Pannek et al. 2016).

However, neither of the regionally derived niche breadth estimates significantly predicted species' global range sizes, thus leading us to reject hypothesis H4. The weak correlations between regional and global range sizes as well as regionally and globally derived niche breadth estimates all highlighted the limited transferability of species' regional specialization and distribution patterns to the global extent. Similarly, for Amazonian palms, Kristiansen et al. (2009) found regionally derived niche breadth estimates to be unrelated to species' continental range sizes. In case of invasive species,

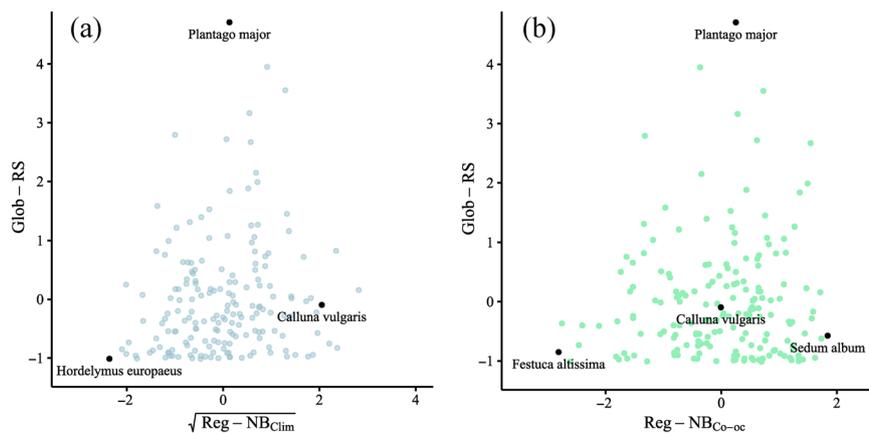


Figure 5. Relationships between species' global range size (Glob-RS) and regional niche breadth estimates derived from either a) species' distribution (Reg-NB<sub>Clim</sub>) or b) co-occurrence (Reg-NB<sub>Co-oc</sub>). NB<sub>Clim</sub> values were square-root transformed and all values were standardized. Both relationships were non-significant in separate linear models ( $R_{adj}^2=0$  for both relationships). Species names highlight the position of exemplary outlier species and *C. vulgaris*.

however, there appears to be a strong link between species' niche breadth and invasiveness and the range of the naturalized area (Lambdon 2008, Thuiller et al. 2012, Higgins and Richardson 2014). Since we discarded all marginally distributed and introduced plant species (i.e. those not classified as indigenous or archaeophyte species) we might thereby have minimized the impact of these ongoing colonization processes on our analyses.

For most of the species investigated, the Alps region represents only a limited fraction of the global distribution covered by these species (Supplementary material Appendix 1). However, because of the very wide environmental gradients covered in the Alps, ranging from sub-Mediterranean to alpine habitats, we expected the Alps dataset, albeit restricted to a relatively small spatial extent, to yield niche breadth estimates that could be reflective of species' niche breadth attributes at the global scale. If forces that drive natural selection vary in space and species' local populations are able to locally adapt to the prevailing conditions (Williams 1966), this could lead to distinct populations that occupy different and even non-overlapping niches, all being narrower than the species' realized niche (Valladares et al. 2014). Wasof et al. (2015), however, found a large overlap of realized climatic niches for disjunct populations of vascular plant species between the Alps and Fennoscandia, particularly in the case of specialist species such as arctic-alpine plants. For widespread generalist species, any mismatch between the spatial extent at which species' niches and range sizes are assessed can distort the observed relationships, especially in the case of species having a patchy distribution at the local scale. This conclusion holds for spatially heterogeneous abiotic conditions as well as biotic interactions that can either increase (mutualism, facilitation) or decrease (competition, parasitism or predation) species' realized niche breadth (Chase and Leibold 2003).

It must be noted that our results are purely correlative and that we therefore cannot readily differentiate whether species' range sizes are determined by their niche breadth or vice versa or if both depend on a third, unobserved, factor. For instance, Lambdon (2008) provides an extensive list of potential drivers (biogeographical, ecological and other dependencies as well as artefactual explanations) that could all lead to positive relationships between niche breadth and range size. In case of alien and native plants on Mediterranean islands, the author furthermore found that widespread species had a higher chance of spreading into less favourable habitats. He thus concluded that plant species' observed niche breadths on Mediterranean islands were determined by species' range sizes and not the other way round. However, one could also argue that widespread species spreading into less favourable habitats reflects source-sink dynamics such as a spillover effect of source populations providing propagules for sink populations. In that particular case, we can assume that species' range size is determined by species' niche breadth through source-sink dynamics and not the other way round. Moreover, to

a high degree we can rule out artificial relationships (*sensu* Lambdon 2008) because we carefully filtered our dataset to limit such artefacts, and because we furthermore down-weighted the impact of outlier records (with regard to climate, community composition and regional geographic distribution).

In summary, our results corroborate the close relationship between range size and niche breadth, when scales are equivalent. Going beyond previous studies, however, we also demonstrate the key role of matching scales when analysing the relationship between niche breadth and range size. In particular, regional niche breadth was found to be a weak predictor of global range size, most likely because of a mismatch in the spatial resolutions used among the response variable and the predictors. While an inference on causation between niche breadth and range size certainly requires further investigation, our results nevertheless highlight that an explicit consideration of scale issues is mandatory and likely revealing, in studies relating niche breadth to range size. A mismatch in scales between measurements of range size and niche breadth can confound any relationship, and may explain some of the previously found low correlations.

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Supplementary material (Appendix ECOG-03495 at <[www.ecography.org/appendix/ecog-03495](http://www.ecography.org/appendix/ecog-03495)>). Appendix 1–3.