



## RESEARCH PAPER

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# Testing macroecological abundance patterns: The relationship between local abundance and range size, range position and climatic suitability among European vascular plants

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**Abstract**

**Aim:** A fundamental question in macroecology centres around understanding the relationship between species' local abundance and their distribution in geographical and climatic space (i.e. the multi-dimensional climatic space or climatic niche). Here, we tested three macroecological hypotheses that link local abundance to the following range properties: (a) the abundance–range size relationship, (b) the abundance–range centre relationship and (c) the abundance–suitability relationship.

**Location:** Europe.

**Taxon:** Vascular plants.

**Methods:** Distribution range maps were extracted from the Chorological Database Halle to derive information on the range and niche sizes of 517 European vascular plant species. To estimate local abundance, we assessed samples from 744,513 vegetation plots in the European Vegetation Archive, where local species' abundance is available as plant cover per plot. We then calculated the 'centrality', that is, the distance between the location of the abundance observation and each species' range centre in geographical and climatic space. The climatic suitability of plot locations was estimated using coarse-grain species distribution models (SDMs). The relationships between centrality or climatic suitability with abundance was tested using linear models and quantile regression. We summarized the overall trend across species' regression slopes from linear models and quantile regression using a meta-analytical approach.

**Results:** We did not detect any positive relationships between a species' mean local abundance and the size of its geographical range or climatic niche. Contrasting yet significant correlations were detected between abundance and centrality or climatic suitability among species.

**Main conclusions:** Our results do not provide unequivocal support for any of the relationships tested, demonstrating that determining properties of species' distributions at large grains and extents might be of limited use for predicting local abundance, including current SDM approaches. We conclude that environmental factors influencing individual performance and local abundance are likely to differ from those factors driving plant species' distribution at coarse resolution and broad geographical extents.

**KEYWORDS**

abundance, climatic suitability, commonness and rarity, range size, realized climatic niche, resolution, species distribution models, vegetation-plot data

**1 | INTRODUCTION**

A fundamental question in macroecology centres around what drives spatial variation in species' abundance, with species' abundance across the geographical range having recently been proposed as one of the so-called essential biodiversity variables (Jetz et al., 2019). Much effort has gone into identifying the drivers of local abundance, and there is a substantial body of literature establishing that it depends on local factors such as environmental suitability and local

biotic interactions (e.g. Andrewartha & Birch, 1954; MacArthur, Diamond, & Karr, 1972; Peterson et al., 2011; Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017). Similarly, it has been established that the limit of species' distribution is a function of the interplay between environmental conditions and barriers affecting dispersal and evolution (Baselga, Lobo, Svenning, & Araújo, 2012). Based on metapopulation and metacommunity concepts, local and regional processes are hypothesized to be mechanistically linked (Leibold et al., 2004), and relationships between species'

**TABLE 1** Description and references to the three tested relationships that link species' local abundance to distribution in coarse-grain geographical or climatic space

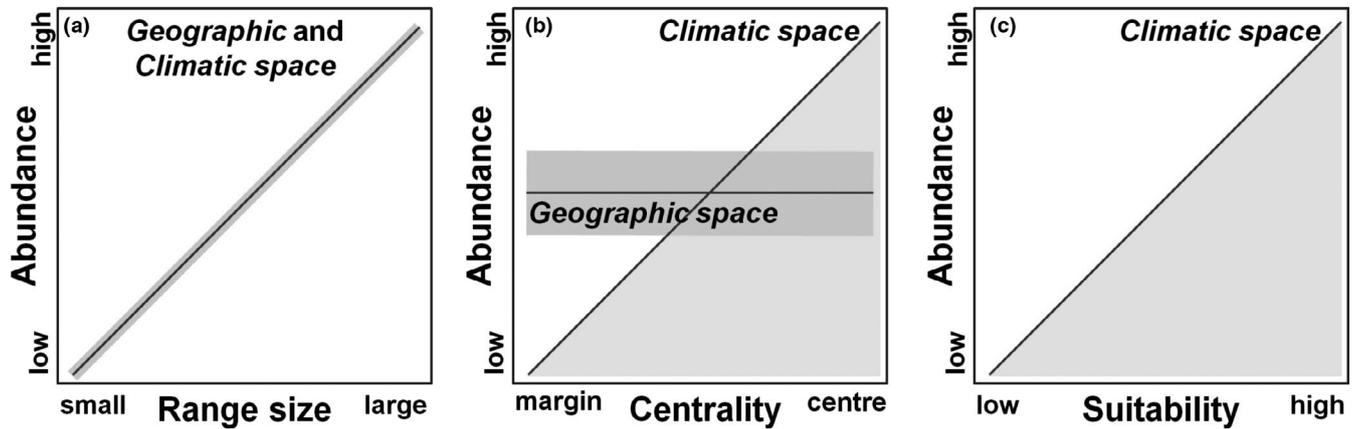
Relationship	Description	References
(Interspecific) abundance–range size relationship	Locally rare species tend to be narrowly distributed, whereas locally abundant species tend to be more widespread in geographical or climatic space	Brown, 1984; Gaston & Blackburn, 2008; Gaston et al., 1997; Hanski, 1982; Reif et al., 2006; Thompson et al., 1998
(Intraspecific) abundance–range centre relationship	Sites with low abundance are located towards range or niche margins, whereas sites with high abundance are clustered at the centre of a species' range or niche	Brown, 1984; Hengeveld & Haeck, 1982; Osorio-Olvera et al., 2020; Pironon et al., 2017; Sagarin & Gaines, 2002; Sagarin et al., 2006; Santini et al., 2019,
(Intraspecific) abundance–suitability relationship	Species show lower local abundance in climatically less suitable areas but achieve higher local abundance in climatically more suitable areas	Dallas & Hastings, 2018; Gomes et al., 2018; Santini et al., 2019; VanDerWal et al., 2009; Weber et al., 2017;

local abundance and geographical distribution may be expected. However, supporting empirical data, especially for herbaceous plants, is lacking. In this paper, we explore whether local abundance is associated with geographical distribution in 517 European vascular plant species at broad geographical extents. Specifically, we focus on three macroecological relationships: (a) the abundance–range size relationship, (b) the abundance–range centre relationship and (c) the abundance–suitability relationship (Table 1). To test the relationships, we interrogated existing data on the species' geographical range characteristics and local abundances, deriving range information from the Chorological Database Halle (CDH; E. Welk et al., unpublished data) and local abundance data from the European Vegetation Archive (EVA; Chytrý et al., 2016). The EVA data are recorded as percentage cover per plot, which we extrapolated to determine local abundance following Preston (1948).

For the first relationship, we checked for associations between species' local abundance and the size of the respective geographical range or climatic niche and ask whether locally abundant species are generally more widely distributed, that is, whether they have larger geographical ranges than species with relatively lower local abundance values (Table 1). Such a relationship has been widely and empirically documented (Brown, 1984; Gaston & Blackburn, 2008; Gaston, Blackburn, & Lawton, 1997; Hanski, 1982; Reif et al., 2006), and several mechanisms have been proposed as drivers (Gaston et al., 1997). For instance, when a species can tolerate a large variability of climatic conditions across its range, it should be able to cope with local temporal climatic variability and thus perform better than local competitors with narrower climatic niches and limited plasticity, resulting in it showing higher local abundance. This mechanism relies on the assertion that a species' geographical distribution is driven by the same climatic tolerances that influence its local abundance, which may not be the case (Guisan & Thuiller, 2005; Mertes & Jetz, 2018). Gaston et al. (1997) reviewed eight other mechanisms that could lead to this relationship, two of which were artefactual, while the others considered niche breadth, resource availability, habitat selection, dispersal limitation, metapopulation dynamics or position within the distributional range. In conclusion, the authors noted that none of the proposed mechanisms has received unequivocal support. As such, the abundance–range size

relationship has seen mixed empirical support (Gaston et al., 1997; Köckemann, Buschmann, & Leuschner, 2009), and there have been concerns that species' abundance and range size were mostly analysed at completely different, or inappropriate, scales (Conlisk, Conlisk, Kassim, Billick, & Harte, 2012; Kambach et al., 2019; Thompson, Hodgson, & Gaston, 1998). For our study, on a large group of herbaceous plant and shrub species predominantly over their full distributional ranges, we expected locally less abundant species to be more narrowly distributed, and locally abundant species to be more widespread in geographical and climatic space (Figure 1a).

The second intraspecific abundance–range centre relationship tested here links local abundance values to the distance of the locality from the centre of the species' geographical range or climatic niche (Table 1). The hypothesis stems from the assumption that the environment tends to be more suitable at the centre of the range than near its edges (Brown, 1984; Grinnell, 1922; Hengeveld & Haeck, 1982). However, it has become clear that species' geographical ranges can be shaped by barriers such as mountains or coastlines (Hargreaves, Samis, & Eckert, 2013), and ecological conditions do not systematically follow geographical gradients (Pironon et al., 2017). Thus, the geographical distribution of suitable environment can be unrelated to the geometry of a species' range (Manthey et al., 2015). Empirical support for the positive form of this relationship in geographical space is weak (e.g. Dallas, Decker, & Hastings, 2017; Gaston et al., 1997; Pironon et al., 2017; Sagarin, Gaines, & Gaylord, 2006). While supported in theory, empirical support for the hypothesis in climatic space is mixed, with some studies finding stronger support for this relationship in climatic than in geographical space (Martínez-Meyer, Díaz-Porras, Peterson, & Yáñez-Arenas, 2013; Osorio-Olvera, Yáñez-Arenas, Martínez-Meyer, & Peterson, 2020; Van Couwenberghe, Collet, Pierrat, Verheyen, & Gégout, 2013), while others finding weak or no support (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Dallas, Pironon, & Santini, 2020; Pironon, Villellas, Morris, Doak, & García, 2015). For our study, we therefore expected the relationship between local abundance and distance from the range centre to be weak or absent in geographical space, while to be positive in climatic space (Figure 1b).



**FIGURE 1** Hypothesized relationships between local abundance and (a) the size of the geographical range or climatic niche derived at the coarse grain; (b) the vegetation-plot position (i.e. distance to centre) within the species' range in either geographical or climatic space and (c) the climatic suitability of a grid cell within which a local plot is situated in the species' range in climatic space

The third abundance–suitability relationship assumes that the more suitable the climate for a species within a larger area, the higher the abundance of the species should be within local plots in that area (Table 1). By equating occurrence probability with climatic suitability, it is expected that favourable climatic conditions support higher species' abundance as a result of improved population and/or individual performance (Araújo, Williams, & Fuller, 2002). While some previous studies have found strong support for this relationship (VanDerWal, Shoo, Johnson, & Williams, 2009; Weber, Stevens, Diniz-Filho, & Grelle, 2017), others failed to detect any effects (Gomes et al., 2018; Santini, Pironon, Maiorano, & Thuiller, 2019). As statistically significant relationships have only been recorded for a few species, a low generality of climatic suitability as a predictor of spatial patterns of abundance may be assumed (VanDerWal et al., 2009). In addition, species' responses to differing climatic conditions can be non-Gaussian (i.e. skewed, bi-modal or truncated) (Austin, 1987). Therefore, species' climatic niche may not show highest climatic suitability in the very centre, but somewhere closer to the edges. For this study, we expected local abundance to be positively related to the coarse-grain climatic suitability predicted for the 15 km<sup>2</sup> grid cells containing the respective vegetation plots (Figure 1c).

It is noted that there is a suite of mechanisms that can weaken or limit the above-described relationships by affecting species' local abundance but without affecting their overall geographical distribution. Examples include environmental and demographic stochasticity (Lande, Engen, & Saether, 2003), particularly when they are temporally synchronous over large geographical extents; biotic interactions (Dallas et al., 2017); soil and disturbance parameters (VanDerWal et al., 2009), or isolation by dispersal barriers (Reif et al., 2006).

Since correlative models of climatic suitability do not integrate these factors, species might be absent or show low abundance at sites with predicted high climatic suitability (VanDerWal et al., 2009). Consequently, relationships could be absent or triangular (Figure 1b and c), which are common forms of relationship between macroecological variables (Brown & Maurer, 1987), indicating more limiting factors at play than just a linear response of central tendency (as in Figure 1a).

## 2 | MATERIALS AND METHODS

### 2.1 | Geographical ranges

For this study, we used existing data on the geographical ranges of European vascular plant species from the CDH (E. Welk et al., unpublished data). The study area comprised all geographical European countries as well as Turkey, Georgia, Armenia and Azerbaijan (see Appendix S1.1 and 1.2). We only included species for which digitized GIS-data were available (i.e. range polygons and point occurrences). We excluded trees, bryophytes, lichens, fungi and algae from the vegetation-plot records to obtain a more homogeneous dataset of herbaceous species, dwarf shrubs and shrubs. Data on a total of 517 species were consequently amassed for the study, which represents approximately 10% of all Central European vascular plant species (Meusel & Jäger, 1992). Species' range information was processed to coarse-grain raster layers of 2.5-min resolution, which corresponded to grid cells covering approximately 15 km<sup>2</sup> each across Central Europe (see e.g. the range of *Inula conyzae* in Figure 2a). The measure of range size for each species then corresponded to the number of grid cells it occupied (Area of Occupancy) (IUCN, 2019).

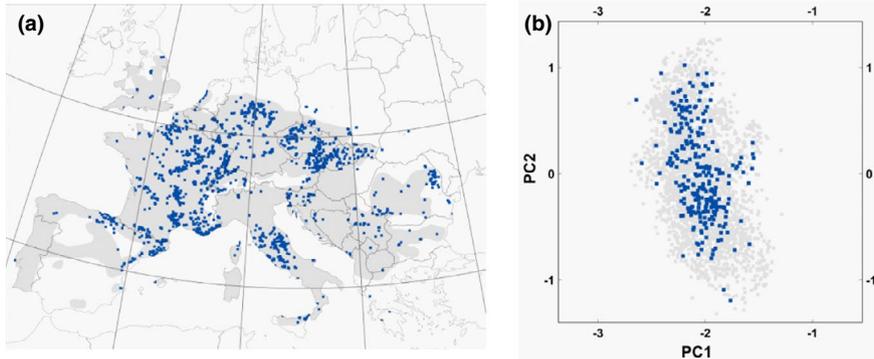
**FIGURE 2** Range of *Inula conyzae* (grey) and locations of vegetation plots (blue dots) from EVA in (a) geographical and (b) climatic space. Centrality and predicted climatic suitability for *Inula conyzae* illustrated in blue (low centrality/suitability) to red (high centrality/suitability). The distance to range centroid in (c) geographical and (d) climatic space refers to the abundance–range centre relationship. The distance to niche centroid in (e) geographical and (f) climatic space refers to the abundance–range centre relationship. The predicted climatic suitability from the model 'random forest' (rf) in (g) geographical and (h) climatic space refers to the abundance–suitability relationship



Geographic space

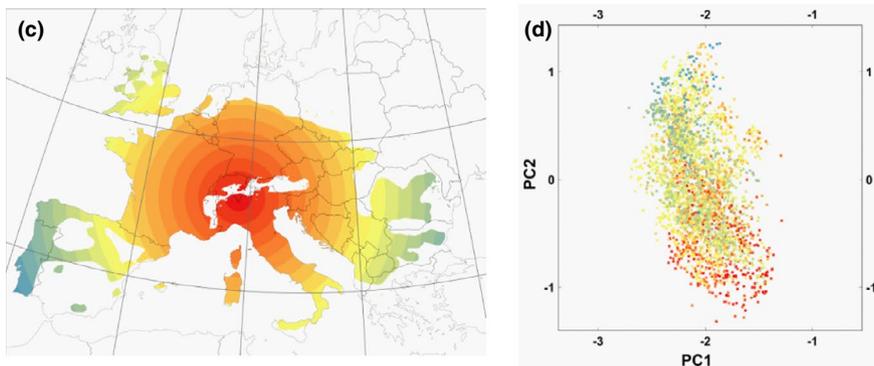
Climatic space

**Geographic range and climatic niche**

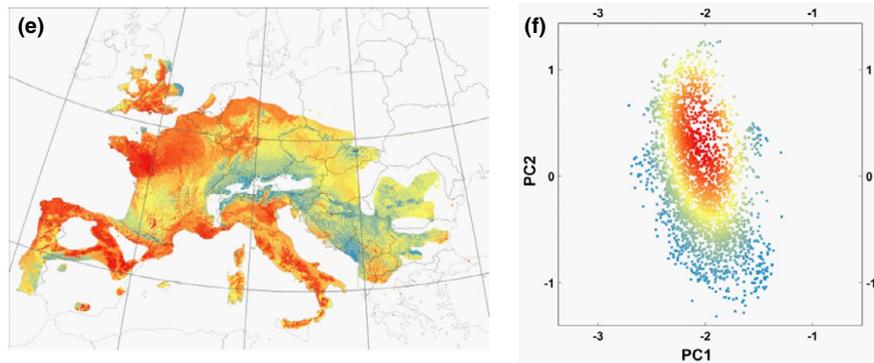


Range of *Inula conyzae* and location of vegetation plots

**Geographic and climatic centrality**

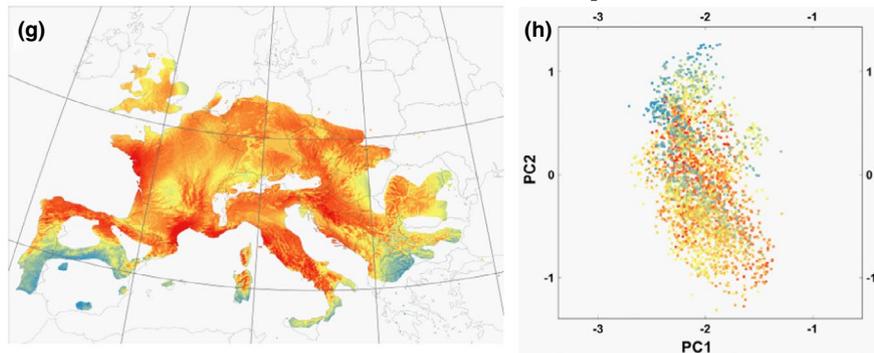


Distance to range centroid



Distance to niche centroid

**Climatic suitability**



Predicted climatic suitability

## 2.2 | Climatic niches

The multi-dimensional climatic space (or climatic niche) of each geographical range was determined using principal components analysis (PCA) of 19 bioclimatic variables from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 2.5-min cell resolution (Figure 2b; climatic niche of *Inula conyzae*). The common European climatic space is represented by the first two PCA axes, which explain 88.0% of the data variance. Unique PCA space locations were considered and counted as grid cells in climatic space. Species' niche size was calculated as the number of occupied grid cells in climatic space (see Appendix S2.1–2.3).

## 2.3 | Local abundance in vegetation plots

Local abundance values for a total of 744,513 vegetation plots were obtained from EVA (Chytrý et al., 2016) for the 517 study species in October 2015. For half of the plots, the recorded area was between 9 and 100 m<sup>2</sup> (25th and 75th percentiles) with a median of 25 m<sup>2</sup>. Data for subspecies were merged at the species level, and we matched synonymous species names according to (a) a taxonomic reference list for Germany (GermanSL version 1.2; Jansen & Dengler, 2008) and (b) for all taxonomic reference lists available via the R package 'taxize' (Chamberlain & Szöcs, 2013; R Core Team, 2018). We only included species that occurred in at least 100 vegetation plots in the EVA dataset, and plots with geographical location uncertainty of <10 km. The number of vegetation plots for each species ranged from 101 plots for *Malva pusilla* to 23,464 plots for *Plantago lanceolata*. For half of the studied species, the number of plots ranged between 631 and 4,531 plots (25th and 75th percentiles), with a median of 1,863 plots (see Appendix S1.3).

Cover-abundance values compiled in EVA that were based on different scales (e.g. Braun-Blanquet, 1951; Domin, 1928) were transformed to a common percentage scale (van der Maarel, 1979).

When more than one plot per species was present in a 2.5-min raster cell, we calculated mean values of abundance (%) to reduce effects of spatial autocorrelation and pseudo-replication. The percentage of grid cells with less than four plots ranged from 39.1% to 97.1% per species. For half of the studied species, the percentage of grid cells with less than four plots was between 66.7% and 77.4% (25th and 75th percentiles) with a median of 71.5%. The percentage of grid cells with more than 10 plots ranged from 0.0% to 28.6%. For half of the studied species, the percentage of grid cells with more than 10 plots was between 2.6% and 6.1% (25th and 75th percentiles), with a median of 4.3% (see Appendix S1.4). Information on source databases that provided vegetation-plot data is shown in Appendix S1.5.

## 2.4 | Distance from centre of the geographical range or climatic niche

To determine the centroids of each species' geographical range and climatic niche, all grid cells in which a species was indicated as present in the CDH database were considered. Geographical range

centroids were calculated as the arithmetic mean of spatial central coordinates of grid cells over the species' CDH geographical range. To determine species' niche centroids, the multivariate climatic space was translated into two-dimensional space (using PCA), and species' geographical occurrences were projected into this climatic niche space. Niche centroids were determined as the arithmetic mean of PCA-coordinates of the respective species' raster cell values. Geographical distance (in kilometres) from each respective EVA vegetation plot to the respective species' CDH range centre was determined using Haversine great circle geographical distance (Figure 2c and d). We calculated Mahalanobis distance to the climatic niche centroid as a measure in climatic space (Figure 2e and f). Mahalanobis distance is considered as a good proxy for marginality since it takes into account the covariance structure of the data (Osorio-Olvera, Soberón, & Falconi, 2019; Osorio-Olvera et al., 2020). For each species' vegetation-plot position, the distance to range or niche centroid was divided by the species-specific maximum distance to the range or niche centroid ( $\text{distance}/\text{distance}_{\text{max}}$ ). This standardization enabled and simplified comparison among the species in our study.

## 2.5 | Coarse-grain climatic suitability

We used species distribution modelling (SDM) to obtain spatial estimates of climatic suitability within each species' geographical range. SDMs estimate occurrence probabilities based on the relationship between species occurrence and environmental (climatic) characteristics. We used occurrence data from CDH and bioclimatic variables provided by the CHELSA project (Karger et al., 2017) at 2.5-min resolution as explanatory variables to build SDMs. The distribution range data of CDH are point-polygon maps covering the complete distribution of the recorded species. Apart from isolated or fragmented single occurrences (points), the areas outside the range polygons are proven to be 'absence areas' by accumulated regional expert knowledge, as documented in national to regional floristic atlases, floras or floristic inventories. Thus, pseudo-absences were sampled from bordering regions in geographical and climatic space. The general sampling approach is based on a climatic pre-stratification of the species' geographical range into differing climatic regions. A fixed number of presence and pseudo-absence samples were drawn randomly from each climatic region, irrespective of the size of the respective climatic region. As recommended by Barbet-Massin, Jiguet, Albert, and Thuiller (2012), we kept the number of selected pseudo-absence samples equal to the number of presence samples for all models, respectively (see Appendix S2.4 and 2.5).

SDMs estimate spatial predictions of environmental suitability from 0 (not suitable) to 1 (most suitable) (Figure 2g and h). We applied four different suitability modelling methods from the three main groups of modelling approaches (i.e. machine learning methods, statistical modelling and similarity methods). The methods we applied are 'bioclim' (similarity method), 'multivariate adaptive regression splines' (mars) (statistical modelling), 'random forest' (rf) and 'support vector machine' (svm) (machine learning methods). We used the area under the receiver operating characteristic (ROC) curve (AUC; Bradley, 1997) to calculate

model accuracy, within which high AUC values (i.e. those closer to 1) indicate a strong capacity for model discrimination (Bedia, Herrera, & Gutiérrez, 2013). Species distribution modelling was performed using the R package 'sdm' (version 1.0-67) (Naimi & Araújo, 2016). We fitted and evaluated the four models using 10 runs of subsampling replications withholding 30% samples as test data.

## 2.6 | Abundance versus range size, centrality and coarse-grain climatic suitability

We applied 'ordinary least squares' (OLS) linear regression models to examine the relationship of local abundance with range size, centrality and coarse-grain climatic suitability. We used 'linear quantile regression' to examine the relationship between centrality and coarse-grain climatic suitability to upper limits (90th quantile) of abundance values to test whether the relationships would be better described as 'triangular', as illustrated in Figure 1b and c. To estimate the overall trend across species, a meta-analysis was performed on species' slopes for each of the applied centrality and climatic suitability measures (Borenstein, 2009). We conducted a mixed-effect meta-analysis on the slopes and the associated variance of each of the centrality and suitability measures to calculate a summary effect size including species as a random factor. Quantile regressions were performed using the R package 'quantreg' (version 5.38) (Koenker, 2018) and the mixed-effect meta-analysis using the function 'rma' from package 'metafor' (Viechtbauer, 2010). All the analyses were rerun on a subset of the dataset, for which only grid cells with a minimum number of four occurrences of each species were included.

## 3 | RESULTS

### 3.1 | Abundance versus range size and niche size

Species' range size (no. of occupied grid cells) ranged from 1,202 in *Juniperus sabina* to 782,025 in *Stellaria media*. For half of the species, range size was between 74,867 and 476,865 (25th and 75th percentiles), with a median of 254,579 grid cells. Species' niche size (no. of occupied grid cells) ranged from 162 in *Scabiosa canescens* to 9,318 in

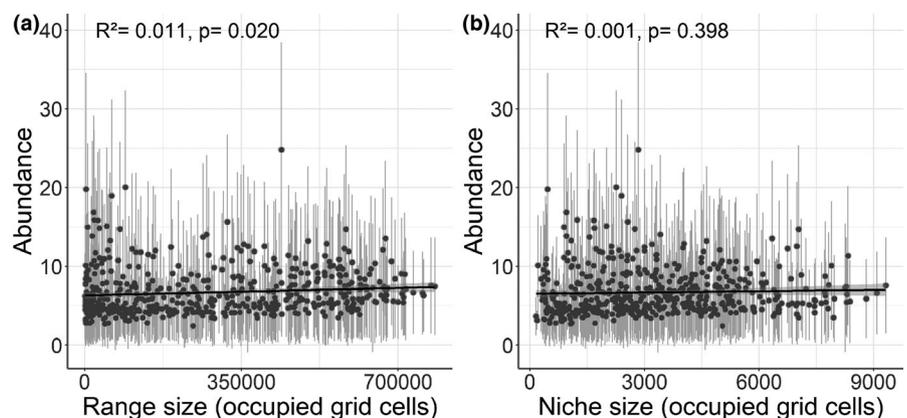
*Plantago major*. For half of the species, the niche size was between 1,657 and 4,614 (25th and 75th percentiles), with a median of 3,002 grid cells (see Appendix S3.1). There was a strong significant positive relationship between species range and niche size ( $R^2 = 0.616$ ,  $p$  value  $< .001$ , see Appendix S4.1). Species' local abundance (mean plot cover) was significantly, yet weakly, related to range size ( $R^2 = 0.011$ ,  $p$ -value = .020) but not to niche size ( $R^2 = 0.001$ ,  $p$  value = .398) (Figure 3a and b). For both relationships, we found high intraspecific variation in species' abundance values, as indicated by the width of the vertical error bars in Figure 3.

### 3.2 | Abundance versus centrality in geographical space

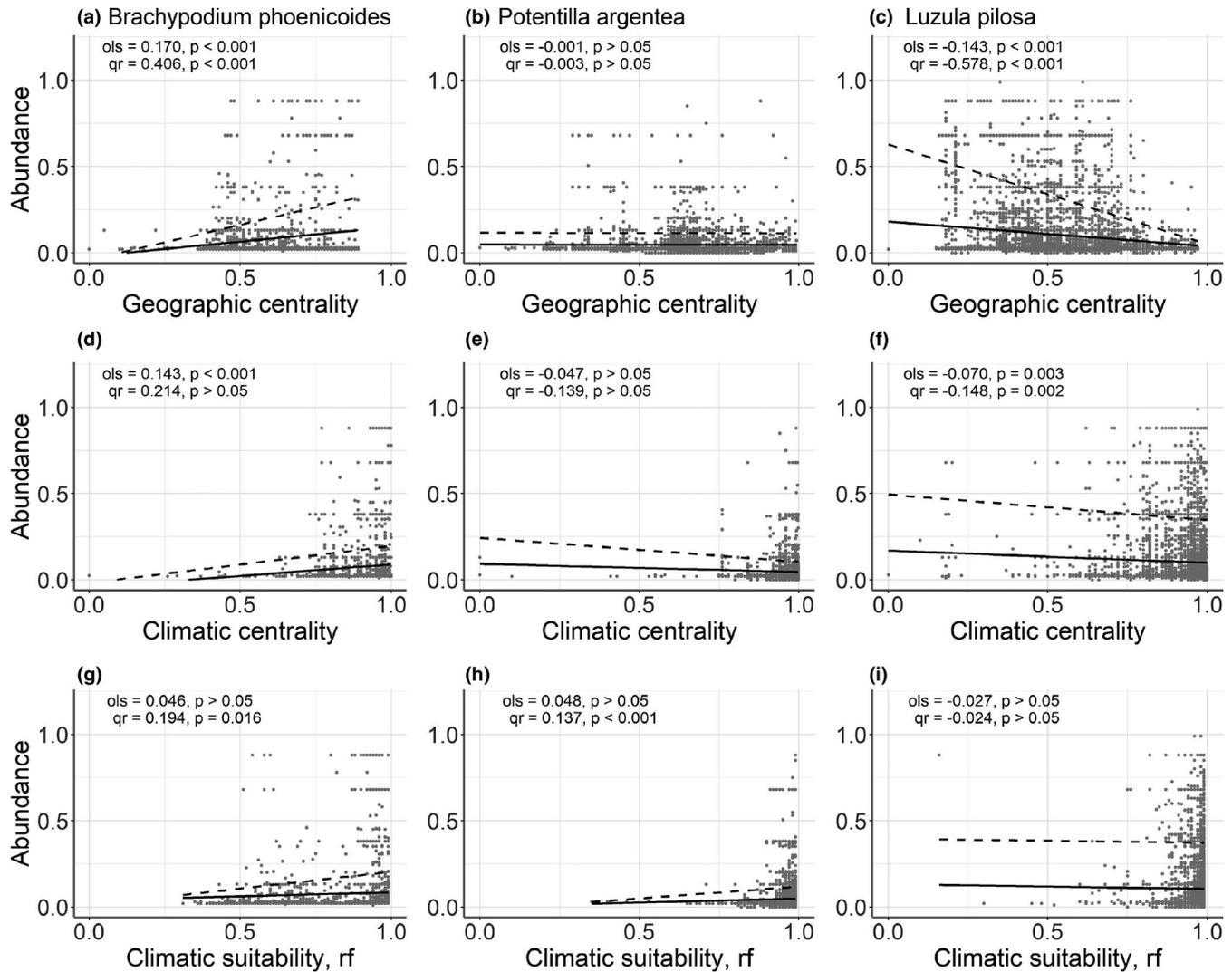
Across the 517 species, we found large variation in slopes of linear regressions relating abundance to the distance from the centre of geographical ranges, with species showing positive (e.g. *Brachypodium phoenicoides*), negative (e.g. *Luzula pilosa*) or no relationship (e.g. *Potentilla argentea*; Figure 4), ranging from  $-0.31$  to  $0.38$ , with a median of  $-0.03$  (Figure 5a). Similarly, diverse results were obtained using quantile regressions (90th quantile used to determine the upper limit of a triangular abundance–range centre relationship), with positive but also negative relationships ranging from  $-1.0$  to  $1.0$ , with a median of  $-0.08$  (Figure 5b). For 13.5% of the species, quantile regression revealed slopes not significantly different from 0 (Table 2). When we summarized the slopes of both linear and quantile regressions with a mixed-effect meta-analysis, we found that the overall mean slope across 517 species was slightly negative and significantly different from 0 in both OLS linear models and linear quantile regressions, with values averaging  $-0.04$  and  $-0.10$ , respectively (Table 3). This indicates that the distance of the plot location to the centre of the species' geographical range is a weak and variable predictor of local abundance.

### 3.3 | Abundance versus centrality in the climatic niche

Similar to the above-described analysis involving geographical space, we found large variation in regression slopes for the relationships between abundance and distance from the centre of climatic niches (Figure 5c and



**FIGURE 3** Absence of a relationship between species' mean abundance with (a) range size and (b) niche size at coarse (2.5 min) raster grain. Points indicate species' mean abundance values; grey error bars are standard deviations, and black solid lines are linear regressions



**FIGURE 4** Examples of herbaceous species having positive (*Brachypodium phoenicoides*, left column), nearly absent (*Potentilla argentea*, middle column) and negative (*Luzula pilosa*, right column) relationships between local abundance and properties derived from distributions in the coarse-grain geographical and climatic space. Scatterplot and regression coefficients from OLS linear regression models (ols) and linear quantile regressions (qr, 90th quantile) between abundance and centrality in geographical space (a–c), centrality in climatic space (d–f), and predicted climatic suitability from model ‘random forest’ (rf) (g–i). Bold lines represent the 50th quantile regression (regression from linear model); the dashed line represents the 90th quantile regression

d). Slopes from linear models ranged from  $-0.30$  to  $0.29$  with a median of  $-0.02$ , while slopes from the quantile regression ranged from  $-1.00$  to  $0.89$  and had a median of  $-0.01$ . For 24.1% of the species, quantile regression slopes were not significantly different from 0 (Table 2). Summarized in a mixed-effect meta-analysis, the overall mean slope was slightly negative and significantly different from 0 in both linear models and quantile regressions, with means of  $-0.03$  and  $-0.08$ , respectively (Table 3). Again, this points to a weak and considerably varying relationship.

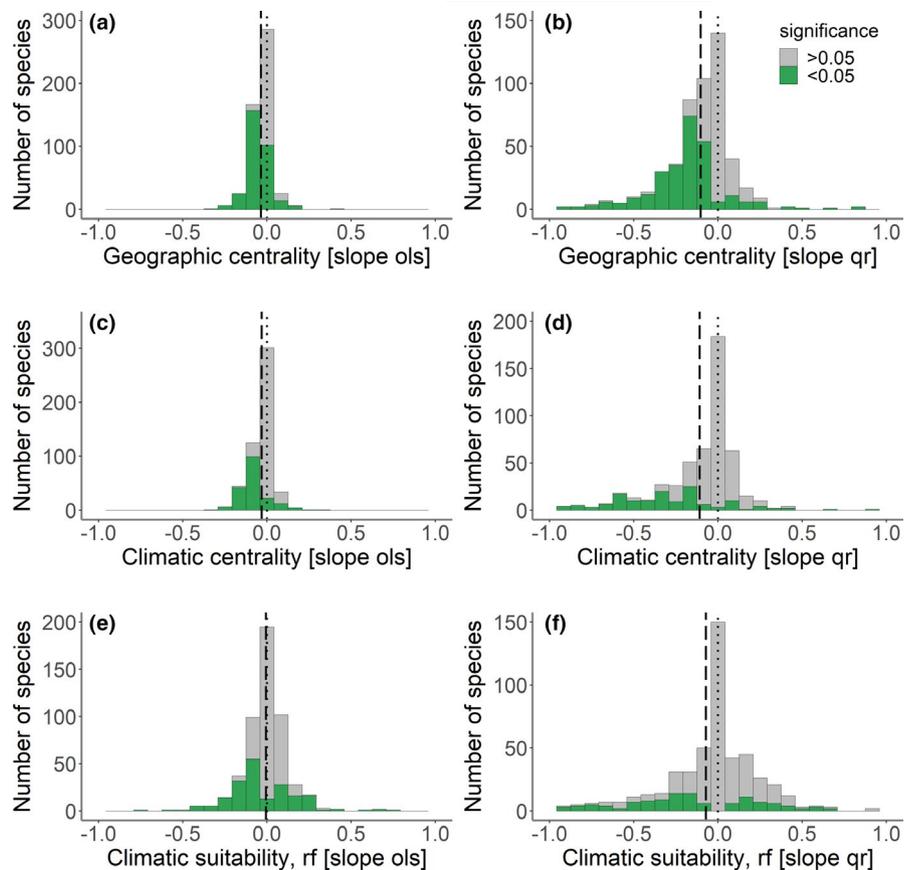
### 3.4 | Abundance versus coarse-grain climatic suitability

The four SDM techniques (‘bioclim’, ‘mars’, ‘rf’, ‘svm’) predicted similar maps of coarse-grain climatic suitability (Figure 2g and h). According

to AUC scores, all techniques had high success rates, with AUC values averaged over 517 species being 0.947, 0.930, 0.916 and 0.718 for ‘bioclim’, ‘mars’, ‘rf’ and ‘svm’, respectively. Importantly, when predicted climatic suitability was used as a predictor of abundance, we found no general relationship, irrespective of the SDM technique used. Specifically, both OLS linear regression and linear quantile regression showed a number of relationships with both positive and negative slopes, as well as no relationship. For some of the species, linear quantile regression revealed no relationship (slope = 0) between abundance and climatic suitability (Table 2, Figure 5e and f, Appendix S4.2).

Summarized in a mixed-effect meta-analysis, the overall mean slope was slightly negative for all applied SDM methods in OLS linear regression models and linear quantile regressions. The overall mean slope was significantly different from 0 for ‘bioclim-’, ‘svm-’ and

**FIGURE 5** Frequency distributions for 517 vascular plant species of slopes from OLS linear regressions (ols) (left) and linear quantile regressions (qr; 90th percentile) (right) between mean species local abundance and distance to range centroid (a and b); distance to niche centroid (c and d), and climatic suitability predicted from model 'random forest' (rf) (e and f). Green bars represent significant slope values. The dotted line represents slope = 0; the dashed line represents the average slope



'rf'-based predictions in OLS linear regressions and for all models in quantile regression, indicating a slightly negative trend in local plot abundance with increasing coarse-grain climatic suitability, which again points to a weak and heterogeneous relationship. The analyses were rerun on a subset of the dataset that included only grid cells with a minimum number of four occurrences for each species, which revealed similar results (see Appendix S4.3 and 4.4).

## 4 | DISCUSSION

In our attempt to link species' local abundance to their distribution at coarse resolution and broad extents in geographical and climatic space we tested for three macroecological relationships: (a) the abundance–range size relationship, (b) the abundance–range centre relationship and (c) the abundance–suitability relationship.

For (a), we found no empirical association between species' local abundance and the size of the species' geographical range or the size of its climatic niche estimated at a coarse spatial grain. For (b), contrary to some of our expectations, we found that, on average, species' local abundance was not related to distance with respect to the centre of its geographical range or climatic niche; however, a generally weak and slightly negative relationship indicates substantial variation, with many species having strong positive or strong negative forms of the relationship. For (c), we again unexpectedly found species' local abundance to be nearly unrelated to its predicted climatic suitability, notwithstanding the weak negative trend

and, again, considerable variation. As such, despite the significant statistical associations discussed below, most of the relationships were weak and highly variable. While this finding contradicts some early macroecological propositions (Brown, 1984), it accords with some more systematic and data-intensive empirical evaluations that often showed similarly noisy and weak relationships (Dallas & Hastings, 2018; Gaston et al., 1997; Köckemann, Buschmann, & Leuschner, 2009).

Whereas our study tested the relationships on a large group of herbaceous plant and shrub species predominantly over their full distributional ranges, many other studies focused on popular taxa and functional species groups (e.g. trees and amphibians, VanDerWal et al., 2009; mammals and trees, Dallas & Hastings, 2018; birds, Osorio-Olvera et al., 2020), or they were restricted to specific geographical regions (e.g. Australian rainforest, VanDerWal et al., 2009; China, Ren et al., 2013).

Overall, we offer two general and plausible explanations for our results. First, that processes driving species' local abundance can differ from those driving occupancy across their geographical or climatic space (Bradley, 2016; Mertes & Jetz, 2018; Shmida & Wilson, 1985; Wiens, 1989). Continental-scale presence or absence of species may be primarily shaped by broad-scale environmental conditions (e.g. climate), historical factors (Brändle & Brandl, 2001) and long-distance dispersal limitation. In contrast, species' abundance at the local scale may be more influenced by abiotic microhabitat characteristics such as soil or microclimatic conditions (De Frenne et al., 2013; Köckemann et al., 2009), or the prevailing

Measure	Slope OLS linear regression		Slope linear quantile regression (90th quantile)		
	[+] slope	[-] slope	[+] slope	[-] slope	no slope
Geographical centrality	6.2	54.0	6.2	45.8	13.5
Climatic centrality	3.9	32.5	4.3	23.4	24.1
Suitability bioclim	13.0	34.6	10.4	29.0	17.7
Suitability mars	17.2	22.8	11.8	18.8	14.7
Suitability rf	13.5	24.2	8.5	17.6	20.9
Suitability svm	10.8	28.0	7.4	22.6	14.6

**TABLE 2** Regression slopes derived from OLS linear regression models and quantile regressions (90th quantile) between species' local abundance and the six measures for distance and suitability applied (distance to range centroid, distance to niche centroid, predicted climatic suitability from 'bioclim', 'mars', 'rf' and 'svm') for 517 vascular plant species. The percentage of all 517 species included in this study showing significant ( $p < 0.05$ ) positive, negative or no slope

Measure	Slope (SE) $p$ value	
	OLS linear regression	Linear quantile regression (90th quantile)
Geographical centrality	-0.036 (0.002)***	-0.100 (0.008)***
Climatic centrality	-0.032 (0.003)***	-0.081 (0.009)***
Suitability bioclim	-0.013 (0.002)***	-0.036 (0.005)***
Suitability mars	-0.005 (0.006)	-0.043 (0.015)**
Suitability rf	-0.010 (0.005)*	-0.031 (0.011)**
Suitability svm	-0.029 (0.004)***	-0.092 (0.013)***

**TABLE 3** Slopes of the mixed-effect meta-analysis for linear models and quantile regressions (90th quantile) between species' local abundance and the six measures for distance and suitability applied (distance to range centroid, distance to niche centroid, predicted climatic suitability from 'bioclim', 'mars', 'rf' and 'svm'); summary effect size (SE) is given in brackets;  $p$  values: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$

disturbance regimes or successional stages (Meurant, 2012; Morris, Ehrlén, Dahlgren, Loomis, & Louthan, 2020). Furthermore, biotic interactions may strongly influence local species' abundance (Dallas & Hastings, 2018; Moeslund et al., 2017).

The second explanation emphasizes the central role of temporal scale and short-term stochasticity (Lande et al., 2003), which can particularly disrupt patterns of local abundance, thereby disconnecting them from coarse-grain occurrence patterns, which are driven by long-term average conditions. This acknowledges that vegetation plots only reflect abundance at any one point in time (and thus vary within and across years, e.g. due to stochasticity), while species' coarse-grain occurrence patterns, and any derived assumptions on their climatic niches, represent long-term averages.

We consider both explanations to be plausible as that they can explain results associated with the three examined relationships, and because the grain of the vegetation plots is particularly small and thus potentially highly sensitive to both local spatial variation of microhabitats and short-term stochasticity. This is also supported by the observed high variation of abundance values around the determined relationships (see Figure 4).

Our results have several important practical implications: The first concerns the interpretation of SDMs, which have become an essential tool in conservation planning and assessment (Peterson et al., 2011) and have been used to identify priority species and regions (Hoffmann et al., 2010). Species' coarse-grain occurrence and local abundance do not frequently display similar patterns, and they often do not even correlate well (Mi, Huettmann, Sun, & Guo, 2017).

In a study by Johnston et al. (2015), locations that had been prioritized for conservation by SDMs based on species' occurrence only showed 10%–58% overlap with locations prioritized by Species Abundance Models (SAMs) based on species' abundance. They conclude that SDMs do not typically identify locations of highest abundance that are crucial for the conservation of populations. Our results support this conclusion as we found no clear correlation between coarse-grain climatic suitability predicted by SDMs and local species' abundance. Since most conservation strategies are implemented at the local scale, we highlight the need to check predictions made at a global or regional scale and their transferability to the local scale, as previously proposed by Guerrero, McAllister, Corcoran, and Wilson (2013).

Another practical implication concerns rarity as a proxy for threat or conservation status. Our results indicate that for European plants, range size, especially when used as the only proxy for local abundance, seems to be a weak predictor of local rarity. Species with small ranges may be locally abundant, while those with large ranges may be locally rare. Thus, we argue that range size and local abundance should be independently considered when developing conservation measures for species or habitats.

In conclusion, we found conflicting evidence for some of the hypothesized links between species' coarse-grain distribution and local abundance, which may be due to the nature of dispersal barriers across Europe. In addition, we note that the size of the vegetation plots used can make species' abundance values more or less sensitive to local microhabitat variation and stochasticity. These results call into question any assumptions made on species' abundance at

the local scale, particularly where predictive SDMs on coarse-grain occurrence data were used. As such, we recommend that further detailed investigations of the processes driving species' local abundance in relation to their geographical range are required, particularly to better inform conservation measures.

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## AUTHOR CONTRIBUTION

MS and EW conceived the study with considerable input by HB and PK. GS and MS harmonized data retrieved from EVA and CDH. MS carried out statistical analyses with support by GS. MS produced the graphs. MS and PK wrote the paper, MS led the writing. All other authors contributed data. All authors contributed to the writing of the manuscript.

## DATA AVAILABILITY STATEMENT

All data are available as Supporting Information.

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#### BIOSKETCH

Maria Sporbert is interested in the biogeography of European vascular plant species. This work represents a component of her PhD work at Martin-Luther University Halle on the relationship between plant species' geographical distribution at broad extents, local abundance and the role of functional traits.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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