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RESEARCH ARTICLE

The relationship between niche breadth and range size of beech (*Fagus*) species worldwide

Qiong Cai[1,2] | Erik Welk[2,3] | Chengjun Ji[1] | Wenjing Fang[1] | Francesco M. Sabatini[3,2] | Jianxiao Zhu[1] | Jiangling Zhu[1] | Zhiyao Tang[1] | Fabio Attorre[4] | Juan A. Campos[5] | Andraž Čarni[6,7] | Milan Chytrý[8] | Süleyman Çoban[9] | Jürgen Dengler[3,10,11] | Jiri Dolezal[12,13] | Richard Field[14] | József P. Frink[15] | Hamid Gholizadeh[16] | Adrian Indreica[17] | Ute Jandt[2,3] | Dirk N. Karger[18] | Jonathan Lenoir[19] | Robert K. Peet[20] | Remigiusz Pielech[21] | Michele De Sanctis[4] | Franziska Schrodt[14] | Jens-Christian Svenning[22,23] | Cindy Q. Tang[24] | Ioannis Tsiripidis[25] | Wolfgang Willner[26] | Kubota Yasuhiro[27] | Jingyun Fang[1] | Helge Bruelheide[2,3]

[1]Department of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

[2]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

[3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[4]Department of Environmental Biology, University Sapienza of Rome, Rome, Italy

[5]Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain

[6]Research Centre of the Slovenian Academy of Sciences and Arts, Institute of Biology, Ljubljana, Slovenia

[7]University of Nova Gorica, Nova Gorica, Slovenia

[8]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

[9]Department of Silviculture, Faculty of Forestry, Istanbul University-Cerrahpasa, Sarıyer, Istanbul, Turkey

[10]Vegetation Ecology, Institute of Natural Resource Management (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland

[11]Plant Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), University of Bayreuth, Germany

[12]Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic

[13]Department of Botany, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

[14]School of Geography, University of Nottingham, Nottingham, UK

[15]National Institute for Research and Development in Forestry "Marin Drăcea", Cluj-Napoca, Romania

[16]Department of Biology, Faculty of Basic Sciences, University of Mazandaran, Babolsar, Iran

[17]Department of Silviculture, Transilvania University of Brasov, Brasov, Romania

[18]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[19]UR « Ecologie et Dynamique des Systèmes Anthropisés » (EDYSAN, UMR 7058 CNRS), Université de Picardie Jules Verne, Amiens, France

[20]Department of Biology, University of North Carolina, Chapel Hill, NC, USA

[21]Department of Forest Biodiversity, University of Agriculture, Kraków, Poland

[22]Centre for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus C, Denmark

[23]Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark

[24]Institute of Ecology and Geobotany, College of Ecology and Environmental Science, Yunnan University, Kunming, Yunnan, China

[25]Department of Botany, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

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[26]Department of Botany and Biodiversity Research, University of Vienna, Wien, Austria

[27]Faculty of Science, University of the Ryukyus, Nishihara, Okinawa, Japan

Correspondence
Helge Bruelheide, Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany.
Email: helge.bruelheide@botanik.uni-halle.de

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Abstract

Aim: This work explores whether the commonly observed positive range size–niche breadth relationship exists for *Fagus*, one of the most dominant and widespread broad-leaved deciduous tree genera in temperate forests of the Northern Hemisphere. Additionally, we ask whether the 10 extant *Fagus* species' niche breadths and climatic tolerances are under phylogenetic control.

Location: Northern Hemisphere temperate forests.

Taxon: *Fagus* L.

Methods: Combining the global vegetation database *sPlot* with Chinese vegetation data, we extracted 107,758 relevés containing *Fagus* species. We estimated biotic and climatic niche breadths per species using plot-based co-occurrence data and a resource-based approach, respectively. We examined the relationships of these estimates with range size and tested for their phylogenetic signal, prior to which a Random Forest (RF) analysis was applied to test which climatic properties are most conserved across the *Fagus* species.

Results: Neither biotic niche breadth nor climatic niche breadth was correlated with range size, and the two niche breadths were incongruent as well. Notably, the widespread North American *F. grandifolia* had a distinctly smaller biotic niche breadth than the Chinese *Fagus* species (*F. engleriana*, *F. hayatae*, *F. longipetiolata* and *F. lucida*) with restricted distributions in isolated mountains. The RF analysis revealed that cold tolerance did not differ among the 10 species, and thus may represent an ancestral, fixed trait. In addition, neither biotic nor climatic niche breadths are under phylogenetic control.

Main Conclusions: We interpret the lack of a general positive range size–niche breadth relationship within the genus *Fagus* as a result of the widespread distribution, high among-region variation in available niche space, landscape heterogeneity and Quaternary history. The results hold when estimating niche sizes either by fine-scale co-occurrence data or coarse-scale climate data, suggesting a mechanistic link between factors operating across spatial scales. Besides, there was no evidence for diverging ecological specialization within the genus *Fagus*.

KEYWORDS
climatic niche, co-occurrence data, deciduous species, *Fagus*, geographical range size, niche breadth, niche evolution, phylogenetic signal, temperate forest flora, vegetation-plot data

1 | INTRODUCTION

Geographical range size is generally defined as the 2-dimensional extent of the spatial distribution of a species based on latitudinal and longitudinal extents (Gaston, 1991), whereas a species' realized niche is widely understood as the n-dimensional hypervolume (Hutchinson, 1957) defined by the multi-dimensional range of abiotic and biotic conditions under which it can sustain natural populations (Blonder, 2018). The quantification and comparison of niche hypervolumes (hereafter niche breadth) have long been of interest to ecologists (e.g. Blonder et al., 2014; Fridley et al., 2007; Hutchinson, 1957; Junker et al., 2016; Kambach et al., 2019; Sexton et al., 2017; Smith, 1982). Properties like species' niche breadths and niche overlaps are proposed to affect co-occurrence patterns at the community level (Bar-Massada, 2015), and realized niche breadths are often used to define the degree of species specialization (Devictor et al., 2010). Since specialists (species with a narrow niche) are thought to be more vulnerable to current and future climate change than generalists (Devictor et al., 2010; but see Colles et al., 2009), determining species' niche breadth can help identify priority species for conservation actions (Boulangeat et al., 2012).

A positive relationship between range size and niche breadth has been proposed by the "niche breadth hypothesis" (Sheth et al., 2020). A wide niche allows a species to cope with a wide range of environmental conditions (Brown, 1984). Mechanistically, a wide niche breadth can be brought about either by generalistic genotypes or by many different particularly adapted genotypes that replace each other in different parts of the geographical range (i.e. geographical vicariants) (Sheth et al., 2020). Both mechanisms would be reflected in a larger distribution range. Most studies have confirmed such a positive correlation (Boulangeat et al., 2012; Brown, 1984; Kambach et al., 2019; Slatyer et al., 2013; Sporbert et al., 2019; Zelený & Chytrý, 2019). For example, in a study on about 1200 plant species in the French Alps, specialist species were found to be more geographically restricted than generalist species (Boulangeat et al., 2012). The same pattern was found in the Czech flora (Zelený & Chytrý, 2019). Similarly, Kambach et al. (2019) reported a positive relationship between niche breadth and geographical range size, both regionally (1255 plant species in the European Alps) and globally (180 plant species). Recently, a meta-analysis of 64 studies worldwide, found widespread convergence between geographical range size and niche breadth, even after taking into account differences in niche breadth measurements, taxonomic groups, spatial scales and sampling effects across studies (Slatyer et al., 2013). This has raised concerns for specialist species that might be disproportionally affected by habitat loss (Staude et al., 2020). However, contrasting patterns have also been observed (Kambach et al., 2019; Slatyer et al., 2013), potentially reflecting the multitude of factors affecting range size and realized niche breadth, such as dispersal abilities, regional availability of suitable niche space and historical events.

One reason why the positive niche breadth–range size relationship is not systematically observed in nature might stem from the many ways niche sizes are calculated. Numerous approaches have been proposed to estimate the realized niche breadth of species (Guisan & Zimmermann, 2000; Sexton et al., 2017). The resource-based method (Smith, 1982) determines niche breadth as the range of favourable conditions along certain environmental gradients, such as temperature, soil moisture and nutrients, and light availability. It estimates the Grinnellian niche (Grinnell, 1917; Grinnell & Swarth, 1913) and it is the most widely applied method. However, as the resulting niche breadth depends on the selection of niche axes, it will only represent a part of the whole multi-dimensional niche as defined by Hutchinson (Devictor et al., 2010).

As large distribution ranges involve a higher probability to include a higher variation in climatic conditions, a positive relationship between range size and climatic niche breadth would not be surprising (Slatyer et al., 2013). However, it is much less clear whether range size, as a global distribution characteristic, can be predicted from niche breadth estimates derived from the local scale of populations and the communities in which the populations occur (Kambach et al., 2019). Here, we focus on the community approach, which relies on the assumption that local-scale environmental conditions are reflected in community composition. At this scale, local interactions between species come into play, which can either reinforce broad-scale climatically induced patterns or blur them (Sheth et al., 2020). In the first case, a wider range of communities in which a species occurs would not only indicate the existence of higher environmental variation within the species' range, but also provide evidence that the species is able to compete with many other co-occurring species under these conditions. Thus, in this case the niche breadth–range size relationship would become clearer because environmentally unsuitable habitats within the species' range would remain unconsidered. Alternatively, local interactions might weaken the niche breadth–range size relationship, as the presence and abundance of the co-resident species might depend on different site factors than those relevant for the species under consideration.

One method to estimate this niche breadth based on community composition uses community turnover rates across plots (the taxonomic β-diversity) as a measure of species' niche breadth (Fridley et al., 2007; successively modified by Zelený, 2009 and Manthey & Fridley, 2009). The fundamental assumption of the co-occurrence-based (biotic) niche concept is that widespread species are generalists that should occur with a broader range of community compositions (i.e. in a higher number of different communities) compared to specialists, given an equal drawn number of plots in which the species occurs (Fridley et al., 2007). Overall, this method characterizes both the Grinnellian niche and the Eltonian niche (Elton, 1927), as it quantifies species' response to multi-dimensional environment gradients and considers species interactions as well (Devictor et al., 2010; Fridley et al., 2007). In addition, it can be applied where environmental information is unavailable. Resource-based and co-occurrence-based approaches differ in the dimensions measured and spatial scales, and can serve as complementary methods to estimate species' niches. While results based on the two approaches are not necessarily correlated (Emery et al., 2012; Pannek et al., 2016), a positive correlation is expected at broad spatial scales (Kambach et al., 2019).

Fagus is a key genus of the northern temperate forest flora. While phylogenetic relationships (e.g. Denk, 2003; Renner et al., 2016; Shen, 1992), climatic limits (Fang & Lechowicz, 2006), biogeographical history (Denk & Grimm, 2009) and community composition (e.g. Hukusima et al., 2013; Kavgaci et al., 2012; Willner et al., 2017) within the genus have been extensively studied, much less attention has been given to the range size and niche properties of the component species. This knowledge is valuable as it may help understand how *Fagus* species might respond to climate change. Increasing temperatures and more frequent extreme events, such as repeated heatwaves and summer droughts, have been projected for many mid-latitude regions (Booth et al., 2012; Geßler et al., 2007). *Fagus* species such as *F. sylvatica* and *F. grandifolia* are sensitive to high temperature and repeated drought events (Booth et al., 2012; Clark et al., 2011; Silva et al., 2012), and the distribution of European beech (*F. sylvatica*) has been projected to shift northward in a future climate (Kramer et al., 2010). Studying the relationship between range size and niche breadth could provide valuable information for predicting the future distribution of *Fagus* species (Sheth et al., 2020).

Species' responses to past environment changes could have been influenced dramatically by evolutionary processes (Kramer et al., 2010; Parmesan, 2006). Species differ in their environmental niche space because their ancestor populations were adapted to different conditions within the ancestral range, or the ancestor was sufficiently plastic to cope with different conditions (Bromham et al., 2020). In the course of speciation, we would expect that the descendant species share either a similar adaptation to local environment or the generalistic genotypic constitution with their ancestors. In both cases, the niche characteristics of closely related species should be more similar than those of more distantly related species (Losos, 2008). Consequently, it is important to analyse niche properties in a phylogenetic framework (Graham et al., 2004; Kozak & Wiens, 2010). Information as to which niche characteristics are more strongly affected by phylogenetic control might help establish hypotheses on the underlying mechanisms responsible for range dynamics and speciation and provide insights into the evolution of different niche axes (Emery et al., 2012; Evans et al., 2009). Variation among different *Fagus* species may be expected because of regionally varying palaeoclimatic forces on range dynamics (Dynesius & Jansson, 2000; Magri et al., 2006). In the genus *Fagus*, the widespread and dominant North American *F. grandifolia* belongs to a more ancestral clade compared to the non-dominant, regionally rare and small-ranged Chinese species (Oh et al., 2016; but see Renner et al., 2016 and Jiang et al., 2020). This phylogenetic pattern could suggest an evolutionary tendency towards ecological specialization.

As mentioned above, because species with larger ecological niches occur in a broader range of habitats, they tend to have larger distribution ranges and total population sizes. These conditions should provide higher chances for speciation events in quantitative and qualitative terms. A broader habitat range provides a higher probability for local adaptation processes. Such ecotypes have the chance to get isolated from the main population by ecological or spatial vicariance. The quantitative difference to small-ranged species provides a stochastically higher chance for such events as well as for long-distance dispersal events. This opens another possibility for speciation processes due to geographical isolation. Testing whether interspecific similarities of niche characteristics and phylogenetic relatedness are positively correlated (Blomberg et al., 2003; Losos, 2008; Wiens et al., 2010), could provide hints for evolutionary tendencies towards ecological specialization. In addition, identifying the key climatic factors for evolution and speciation of the *Fagus* species might also enhance our understanding on their response to climate change. So far, although several studies have explored the roles of climatic (e.g, Evans et al., 2009; Graham et al., 2004; Kozak & Weins, 2006) or habitat niche evolution (e.g., Emery et al., 2012) in speciation, this approach has rarely been applied to species' co-occurrence-based assessment of niche breadth.

During the last decades, extensive species co-occurrence data have been accumulated for forest stands in which the genus *Fagus* occurs. Combining *sPlot*—the global vegetation plot database (Bruelheide et al., 2019)—with an unpublished Chinese vegetation database, we extracted 107,758 relevés in which at least one *Fagus* species occurs. Using this unique dataset and the distribution data from Chorology Database Halle (http://chorologie.biologie.uni-halle.de//areale/), we estimated the range size and niche breadth of all extant *Fagus* species, and explored the relationship between them. Accordingly, we tested the following hypotheses: (H1) The commonly found positive relationship between range size and niche breadth applies to the genus *Fagus*; (H2) biotic and climatic niche breadths are correlated; and (H3) the *Fagus* species' niche similarities are positively correlated with phylogenetic relatedness. Although H1 is a general assumption in species distribution modelling, it has rarely been tested with different approaches to niche breadth estimation; doing so for all species of a key genus of northern temperate forests is, therefore, particularly valuable. Confirming H2 would demonstrate that fine-scale determinants of biotic niche breadth are transferable to the broad-scale characteristics represented by climatic niche breadth. Finally, the results on H3 would shed light on the evolution of *Fagus* species' niche properties, and thus improve our ability to model potential future changes of *Fagus* distributions.

2 | MATERIALS AND METHODS

2.1 | Study species

The genus *Fagus* includes widespread as well as relatively rare species distributed across the Northern Hemisphere, from eastern North America, Europe and western Asia to eastern Asia (Figure 1). There are four *Fagus* species in China (*F. engleriana*, *F. hayatae*, *F. longipetiolata*, *F. lucida*), with *F. longipetiolata* distributed in northern Vietnam and *F. hayatae* in Taiwan Island. Two species occur in Japan (*F. crenata*, *F. japonica*) and one on Ulleungdo Island in South Korea (*F. multinervis*) (Fang & Lechowicz, 2006; Oh et al., 2016). European beech (*F. sylvatica*) occurs in Europe, and *F. orientalis* in western Asia and southeast Europe (Willner et al., 2017). *Fagus grandifolia* is distributed in eastern North America, with *F. grandifolia* subsp. *mexicana* having a narrow, isolated range in the mountains of Mexico. It is noteworthy that the taxonomic status of the three geographically-isolated segregates (*F. multinervis*, *F. orientalis* and *F. grandifolia* subsp. *mexicana*) has been debated for a long time. In some studies, *F. multinervis* and *F. orientalis* have been treated as subspecies (Renner et al., 2016), while there are recent phylogenetic hypotheses that recognize *F. grandifolia* subsp. *mexicana* as a distinct species (Jiang et al., 2020).

2.2 | Datasets for niche breadth estimation

The data used were mainly obtained from *sPlot*—the global vegetation-plot database—which has a worldwide coverage

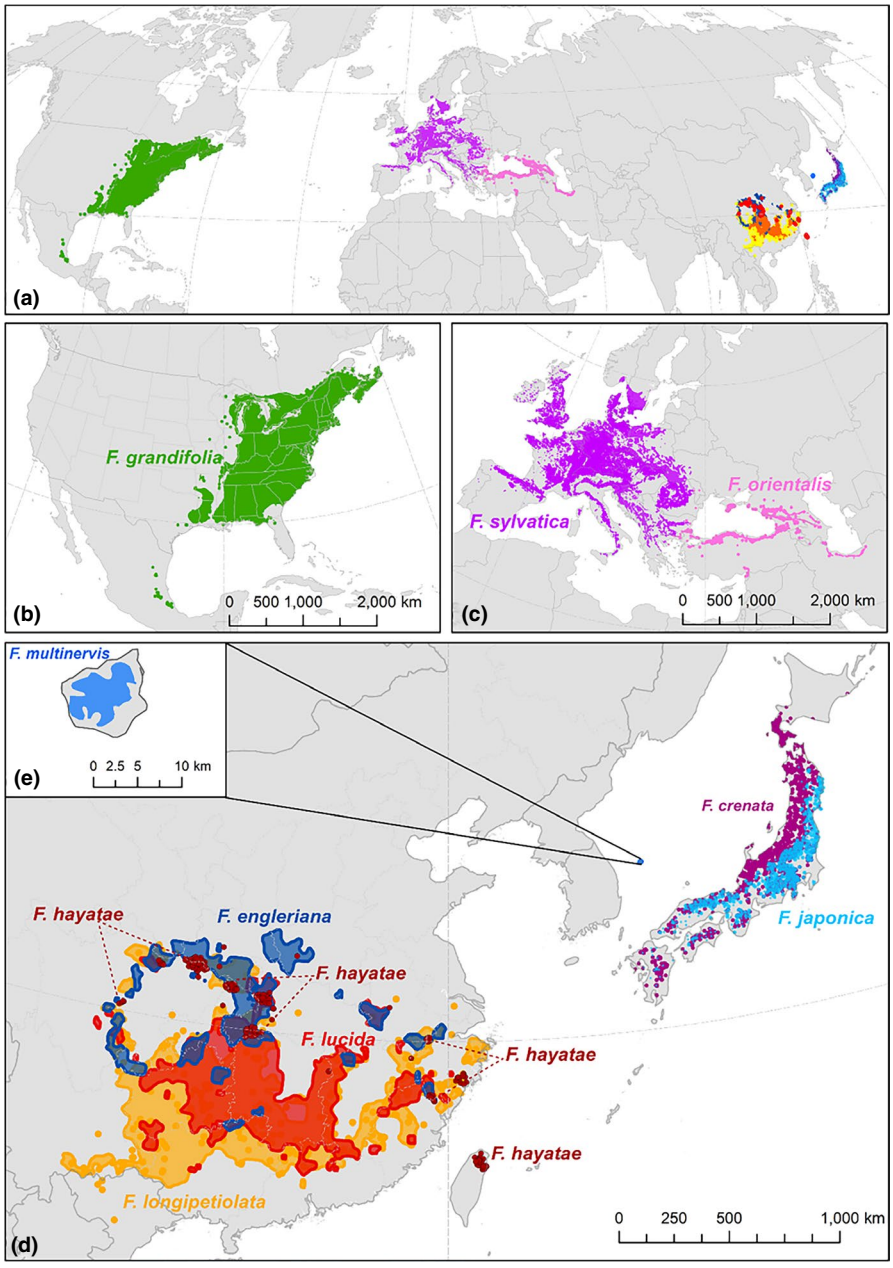

FIGURE 1 Range maps of the 10 extant *Fagus* species worldwide. The colour spectrum reflects the phylogenetic relationships of the 10 species (see Figure 5). (a) Global distribution of *Fagus* and detail enlargement for (b) North America; (c) Europe and West Asia; (d) East Asia; and (e) Ulleungdo Island in South Korea

and a standardized taxonomic nomenclature (Bruelheide et al., 2019). As data for *Fagus* in China were quite limited in *sPlot*, 219 additional *Fagus* plot data from China were added from our own unpublished field records. The taxonomic backbone of *sPlot* was used to harmonize the species nomenclature of these additional records. Species co-occurrences in the tree, shrub and herbaceous layer of each vegetation plot were used for co-occurrence-related analyses. Additionally, the spatial coordinates (latitude and longitude) of the plots were used to extract climatic attributes. As we were interested in estimating niche breadth from the full range of biotic constellations, we did not apply any minimum threshold for the cover of *Fagus* species in the plot records. Altogether, 107,758 vegetation plots in which at least one *Fagus* tree species occurs were obtained for the analyses (Figure S1, Table 1).

2.3 | Datasets for range size estimation

The geographical distribution of the 10 *Fagus* species (Figure 1) was based not only on the occurrence records described above but also on the data collected by the Chorology Working Group at the University of Halle-Wittenberg, Germany (Chorology Database Halle, CDH; http://chorologie.biologie.uni-halle.de//areale/), which has compiled a wide range of data sources. For example, distribution data of the Chinese *Fagus* species were primarily collected from '*Atlas of woody plants in China: distribution and climate*' (Fang et al., 2011). The data included polygon and point features. For methodological details, see Caudullo et al. (2017). For each *Fagus* species, the range size was calculated as the geographical area (km^2) of the range polygons in an equal-area cartographic projection (Lambert azimuthal equal-area projection). Isolated point clusters were converted to minimum convex polygons (MCPs).

TABLE 1 Geographical range sizes and plot information of the 10 extant *Fagus* species

Species	Plot number[a]	Range size (km^2)	Latitudinal range (°N)[b]	Longitudinal range
F. crenata	4811	1.6×10^5	31.5–42.7	130.1°E–142.1°E
F. engleriana	71	2.6×10^5	30.1–33.8	103.6°E–118.8°E
F. grandifolia	3574	2.1×10^6	19.6–46.1	68.2°W–97.0°W
F. hayatae	50	3.6×10^4	24.5–33.5	102.4°E–121.8°E
F. japonica	1187	8.0×10^4	32.4–40.0	131°E–141.9°E
F. longipetiolata	58	7.5×10^5	22.9–32.9	102.4°E–120.7°E
F. lucida	90	4.4×10^5	24.9–32.6	103.9°E–119.7°E
F. multinervis	35	3.7×10^1	37.49–37.53	130.8°E–130.9°E
F. orientalis	1316	1.7×10^5	36.0–50.4	21.5°E–53.1°E
F. sylvatica	97,045	1.3×10^6	37.7–57.5	5.3°W–28.3°E

[a]There are some plots with more than one *Fagus* species. Therefore, the sum of plot numbers in the table is greater than the total number of plots, which is 107,758.

[b]For *F. grandifolia*, the geographical range of plots excluding those in Mexico (19.6–19.7°N and 96.9–97.0°W) is 30.4–46.1°N and 68.2–94.3°W. For *F. hayatae*, the geographical range of plots in mainland China is 28.6–33.5°N and 102.4–120.7°E, and that of plots on Taiwan Island is 24.5–24.7°N and 121.3–121.8°E.

2.4 | Climate data

For the localities of all 107,758 selected plots, we extracted raster cell values from grid layers of the 19 bioclimatic variables (BIO01 to BIO19) provided by the CHELSA database (https://chelsa-climate.org/; Karger et al., 2017). The spatial resolution was 30 arc seconds, corresponding to about 0.64 km × 0.93 km = 0.6 km^2 at the average latitude of the plots (46.31°N). For those plots along the coastlines resulting to be located in the sea due to coarse location accuracy, we extracted the climate information of the closest terrestrial grid cells with the recorded elevation using the snap function in ArcGIS.

2.5 | Estimation of biotic (co-occurrence-based) niches from plot data

To estimate co-occurrence-based niche breadth, we generally followed the approach proposed by Fridley et al. (2007), which uses the taxonomic β-diversity metric among the set of plant communities (here, vegetation plots) in which a focal plant species occurs. To measure plot dissimilarity, we chose the multiple Simpson index (Baselga et al., 2007), which can disentangle changes in species composition caused by changes in species identities (species turnover) from those caused by species richness differences (nestedness effect), whilst being independent of the absolute species richness in the plots (Baselga et al., 2007; Manthey & Fridley, 2009). As the quantities of plots varied a lot among different *Fagus* species (Table 1), we conducted a resampling procedure to control for possible sample size effects. For each of the 10 *Fagus* species we calculated niche breadth 100 times by randomly drawing 20 plots with replacement out of the total number of plots that contain the focal species, and then taking the average dissimilarity value of the 100 iterations (Fridley et al., 2007; Pannek et al., 2016). We then calculated the variance of the dissimilarity values across the 100 runs. Results based on other dissimilarity indices for turnover calculations, i.e. the Jaccard and Sørensen index (Manthey & Fridley, 2009), are presented in the Supporting Information (Figure S2). The Sørensen index is a linear function of the multiplicative Whittaker's β-diversity metric (β_w), which eliminates possible effects of species pool sizes (Manthey & Fridley, 2009; Zelený, 2009).

2.6 | Estimation of climatic niches from plot data

We applied the method of dynamic range boxes (DRB) to estimate the climatic niche breadth since it has proven to be relatively robust to sampling effects and outliers, especially at high dimensionality (Junker et al., 2016). Accordingly, we calculated the realized climatic niche breadth based on the above-mentioned bioclimatic variables, using the R package 'dynRB' (Schreyer et al., 2018). To avoid bias related to inter-correlation, we excluded one of those variables with absolute pairwise correlation $r > 0.75$ and we thereby limited our selection to 10 variables as follows: BIO02 (Mean Diurnal Range); BIO03 (Isothermality); BIO05 (Max Temperature of Warmest Month); BIO06 (Min Temperature of Coldest Month); BIO07 (Temperature Annual Range); BIO08 (Mean Temperature of Wettest Quarter); BIO09 (Mean Temperature of Driest Quarter); BIO13 (Precipitation of Wettest Month); BIO15 (Precipitation Seasonality); and BIO17 (Precipitation of Driest Quarter). Original dimensions of the climatic variables were replaced with the first five principal components of a principal component analysis (PCA) (accounting for 91.8% of the variation) to avoid possible interdependence of predictors (Junker et al., 2016).

To limit pseudo-replication at a given site, in cases where two or more plots had identical spatial coordinates, only one plot was

selected randomly. As a result, the sample size for the climatic niche estimation was reduced to 61,717 plots. We used two different aggregation functions ('mean' and 'gmean', both included in the package 'dynRB') to compare the coordinate-wise volumes. Note that the 'product' method was omitted as it was not recommended by the authors (Junker et al., 2016). Results based on the 'mean' method are shown in the Supporting Information (Figure S3).

2.7 | Phylogenetic analysis

Before using phylogenetic methods to test whether specific macroclimatic traits are species-specific across genera, we ran a Random Forest (RF) analysis to select the key bioclimatic variables. Specifically, we quantified the discriminability of each bioclimatic variable range between the sister species. We employed two widely used variable importance measures: the mean decrease accuracy and mean decrease Gini index (Breiman, 2001). Only the plot data with distinct coordinates (n = 61,717) were used here.

We calculated RF ensembles of recursive classification trees with the 'randomForest' package in R (Breiman, 2002). As settings, we used 10,000 iterations and the 'tuneRF' function to identify the 'optimal' number of input variables randomly chosen at each node. Since the number of plots per *Fagus* species varied considerably (n = 11 to 54,397), both a fixed sample size (n = 10) approach and a proportionate stratified sampling procedure (following the species sequence in Table 1, n = 3690; 40; 1840; 40; 1030; 50; 60; 10; 270; and 16,300, respectively, with replacement) were adopted. For comparison, a conservative variant with the fixed sample size of n = 10 was calculated. Out-of-bag (OOB) estimation of error rate was used to assess classification success and a permutation cross-validation test with 20% withhold test data was used to control for overfitting.

To assess whether niche breadth estimates as well as the least and most discriminating bioclimatic variables identified by the RF analysis (taking the 5th and 95th percentiles, respectively) are under phylogenetic control or show a random pattern of evolution, phylogenetic signals were tested across all 10 *Fagus* species. For each species, we calculated the biotic and climatic niche breadth estimates and the distinctive bioclimatic variables. Blomberg's K value is an indicator of the strength of the phylogenetic signal, which indicates strong phylogenetic control of characteristics when greater than one, and a random pattern of evolution when close to zero (Blomberg et al., 2003; Kembel, 2010). Blomberg's K values were calculated based on the phylogenetic trees as provided in Qian and Jin (2016) and Oh et al. (2016).

2.8 | Statistical analyses

We tested for differences in biotic niche breadth between the 10 *Fagus* species with a one-way analysis of variance (ANOVA) and Tukey's HSD post hoc tests, using an n = 100 random selection of plot records as replicates. To test hypothesis H1 (i.e. that range size is related to niche breadth) and H2 (i.e. that biotic and climatic niche breadths are correlated), we assessed the relationships between the different niche traits and range size by performing the phylogenetically corrected generalized least-squares (PGLS) regression using the R package 'caper' (Orme et al., 2018). Considering the relatively small sample sizes and the outlier species *F. multinervis*, we further assessed the relationships with a Spearman's correlation test. In addition, the PGLS regression and Spearman's correlation test were also performed when excluding *F. multinervis*. For hypothesis H3, which proposes that biotic and climatic niche breadths are non-randomly associated with phylogeny, we calculated the phylogenetic signal, using the 'picante' package in R (Kembel, 2010). Plotting of the phylogenetic signals was done with 'phylo4d' from the 'phytools' package (Revell & Revell, 2019). The RF analysis was done using the 'rf', 'rfUtilities', and 'randomForestExplainer' packages. All statistical analyses were conducted with R v3.5.1 (R Core Team, 2018), and further graphs were produced with the R package 'ggplot2' and ArcGIS 10.3.

3 | RESULTS

3.1 | Overall patterns of range sizes and niche breadths

Geographical range sizes of the 10 *Fagus* species differed by five orders of magnitude, ranging from 37 km^2 (*F. multinervis*) to 2.1×10^6 km^2 (*F. grandifolia*) (Table 1). Out of the four Chinese *Fagus* species (*F. longipetiolata*, *F. lucida*, *F. engleriana* and *F. hayatae*), *F. hayatae* had the smallest range size (3.6×10^4 km^2), but also a wide disjunction between the populations of mainland China and Taiwan. The ranges of the other three Chinese species were intermediate in size, but all were much smaller than those of *F. grandifolia* and *F. sylvatica* (1.3×10^6 km^2). *Fagus orientalis* (1.7×10^5 km^2) and the two Japanese *Fagus* species had larger, but still relatively small range sizes (8.0×10^4 and 1.6×10^5 km^2 for *F. japonica* and *F. crenata*, respectively) (Table 1). Despite some minor incongruences among different estimation methods, results obtained from the three co-occurrence approaches based on plot data were largely aligned, and so were the two climatic niche metrics calculated with different aggregation methods (Figures 2, 4g, S2, S3). Regarding the co-occurrence-based metric of niche breadth (multiple Simpson index), the Chinese *Fagus* species displayed the broadest biotic niches, while the *Fagus* species in Europe and West Asia had intermediate ones, and those in North America, Japan and Korea had relatively narrow niches (Figure 2). Similar patterns were observed based on the Jaccard and Sørensen index (Figure S2). In terms of climatic niche breadth, the Chinese species *F. hayatae* displayed the largest climatic niche breadth, followed by the West Asian and European *Fagus* species (*F. orientalis* and *F. sylvatica*). The North American and Japanese *Fagus* species had intermediate climatic niches, while the Korean species *F. multinervis* had the narrowest one (Figure 3). The aggregation method 'mean' resulted in a similar pattern (Figure S3). A PCA of the 10 climatic variables also showed that plots of *F. hayatae* had a wide range along the first two axes (Figure S4).

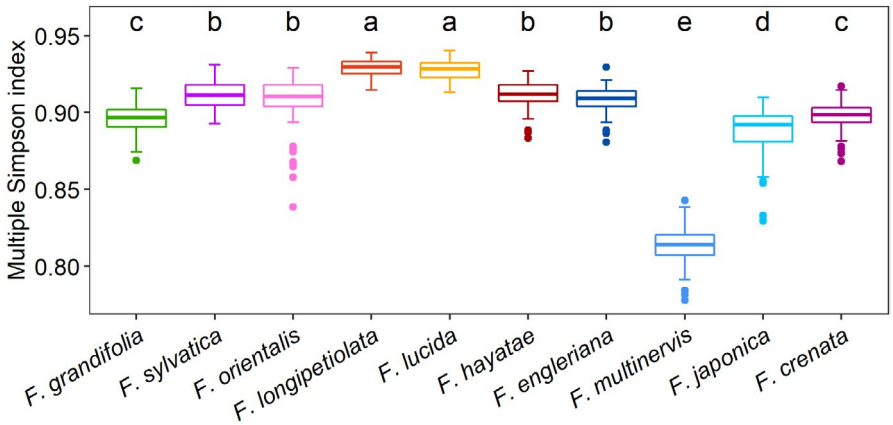

FIGURE 2 Co-occurrence-based niche breadths of the 10 extant *Fagus* species using multiple Simpson index for turnover calculations. The colour spectrum follows the distribution range maps (Figure 1). Different letters indicate significant differences according to a Tukey's HSD post-hoc test ($p < 0.05$)

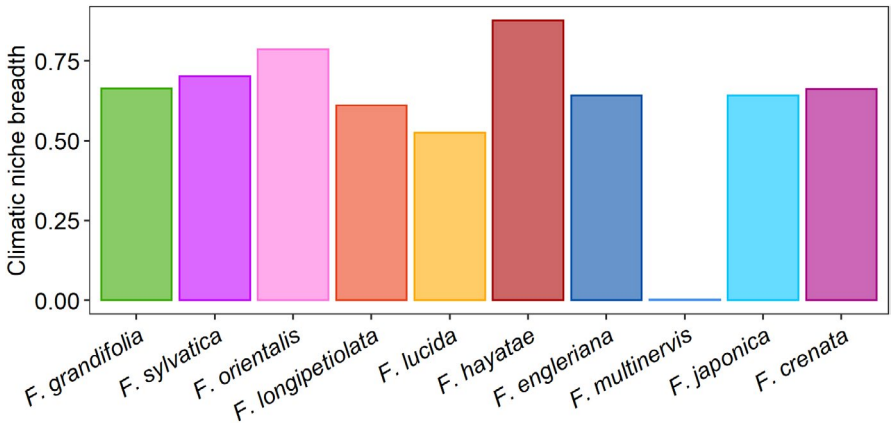

FIGURE 3 Climatic niche breadths of the 10 extant *Fagus* species based on the resource-based method of dynamic range boxes (DRB). The aggregation method used was 'gmean' (Junker et al., 2016). The colour spectrum follows the distribution range maps (Figure 1)

3.2 | Relationships between range sizes and niche breadths

According to the PGLS regression and Spearman's correlation test, neither the biotic nor the climatic niche breadth estimate was related to range size ($p > 0.05$; Figure 4a–b, g). Although log-transformed range size exhibited a positive relationship with both biotic and climatic niche breadth (R^2 ranging from 0.57 to 0.87, $p \leq 0.01$; Figure 4c–d), these relationships were strongly determined by the influential point of *F. multinervis*. When excluding *F. multinervis*, the relationships were not significant any more ($p > 0.05$; Figure 4c–d). The biotic niche breadth estimates were significantly correlated with the climatic niche breadth values based on PGLS regression (R^2 ranging from 0.43 to 0.72, $p < 0.05$; Figure 4e–f). However, these relationships were also strongly influenced by *F. multinervis* (Figure 4e–f). Both PGLS regression excluding *F. multinervis* and the Spearman's correlation test (Figure 4g) exhibited no significant relationships between the two niche breadth measures ($p > 0.05$).

3.3 | Phylogenetic analyses of climatic tolerances and niche properties

The RF analysis successfully classified the species by climate with an out-of-bag (OOB) error rate of 11.1% when using a fixed sample size (n = 10), but reaching an OOB error rate of 1.95% when using proportional sample sizes. Similar values were obtained with the cross-validation approach when withholding 20% test datasets (9.86% and 2.03%, respectively). For both sampling strategies, the bioclimatic variable BIO03 (Isothermality, which is the mean diurnal range of temperature divided by the annual range of temperature, i.e. BIO02/BIO07) had the strongest importance for discriminating the species, as it returned the largest decrease in accuracy and increase in Gini node impurity when excluded (Figure S5). In contrast, the exclusion of the bioclimatic variable BIO06 (Minimum temperature of the coldest month) had the lowest importance (Figure S5).

Blomberg's *K* values were smaller than one for all the biotic and climatic niche characteristics as well as the two aforementioned bioclimatic variables (BIO03 and BIO06). No biotic or climatic niche characteristics were significantly different from a random distribution ($p > 0.1$; Figure 5), suggesting that we cannot conclude that these characteristics are phylogenetically conserved within the genus *Fagus*. Rather, small and large niche breadths are distributed randomly among the clades within *Fagus*.

4 | DISCUSSION

Contrary to our first hypothesis and the commonly reported positive relationship between range size and niche breadth (Boulangeat

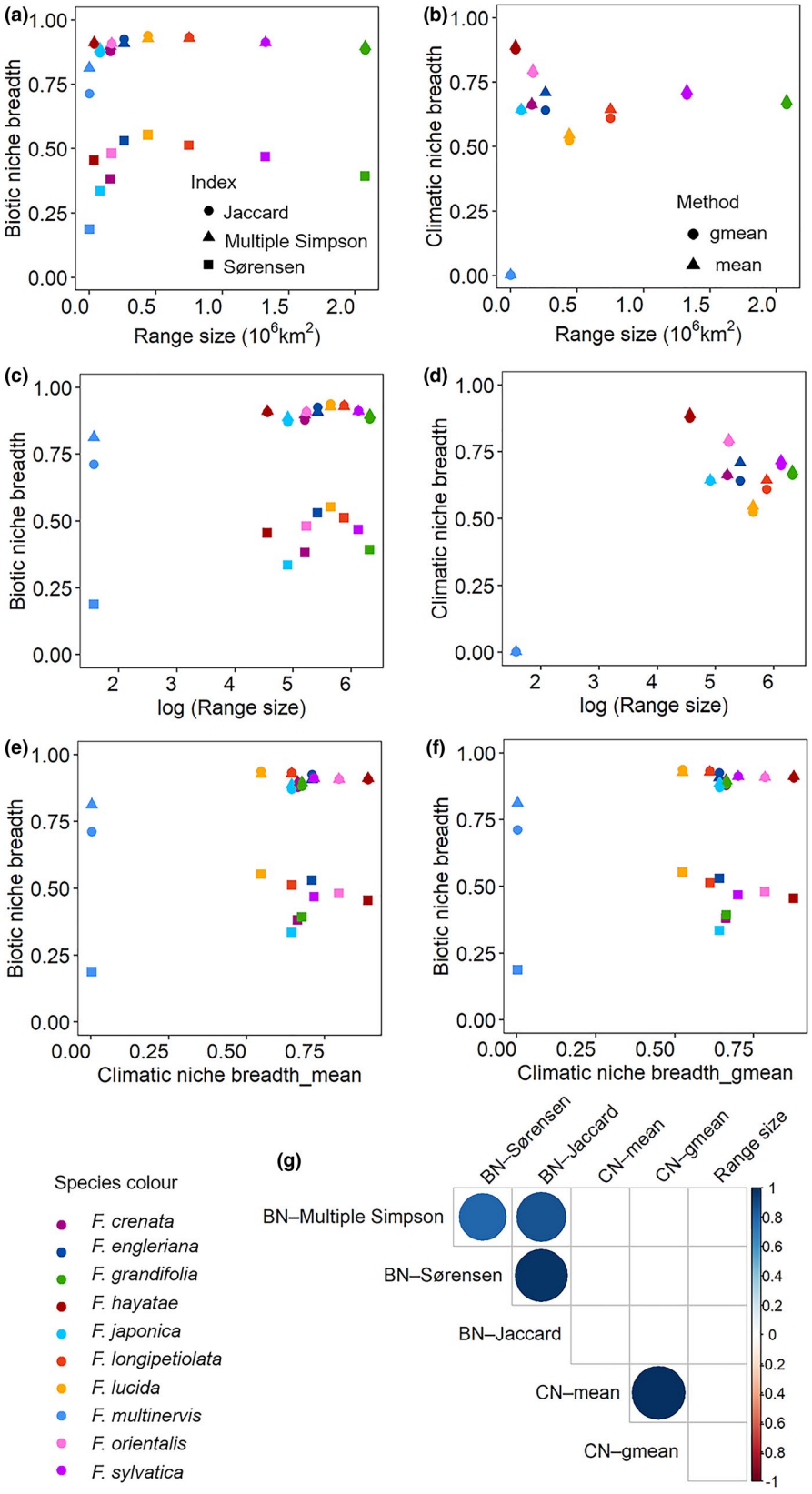

FIGURE 4 Relationships between different niche breadths and range size (a–b) or log-transformed range size (c–d), and between biotic and climatic niche breadth (e–f). Panels a–f are based on the phylogenetically corrected generalized least-squares (PGLS) regression and panel g is based on the Spearman's correlation test ($p < 0.05$). Considering the outlier point of *Fagus multinervis*, fitted lines and coefficients of the PGLS regression of the 10 *Fagus* species are not shown in panels c–f. Multiple Simpson, Jaccard and Sørensen are different indices for biotic niche estimation. Mean and gmean represent different aggregation methods for climatic niche estimation and refer to the arithmetic and the geometric mean of the different niche dimensions, respectively. The acronyms BN and CN mean biotic niche and climatic niche, respectively

et al., 2012; Brown, 1984; Kambach et al., 2019; Sheth et al., 2020; Slatyer et al., 2013), we found no significant relationship between range size and the biotic and climatic niche breadth estimates for the species in the globally important tree genus *Fagus*. Setting possible methodological issues aside (see Appendix 1 in the Supporting Information), there are many biological, geographical and historical factors that might affect the niche breadth–range size relationship for these closely related species, such as dispersal ability

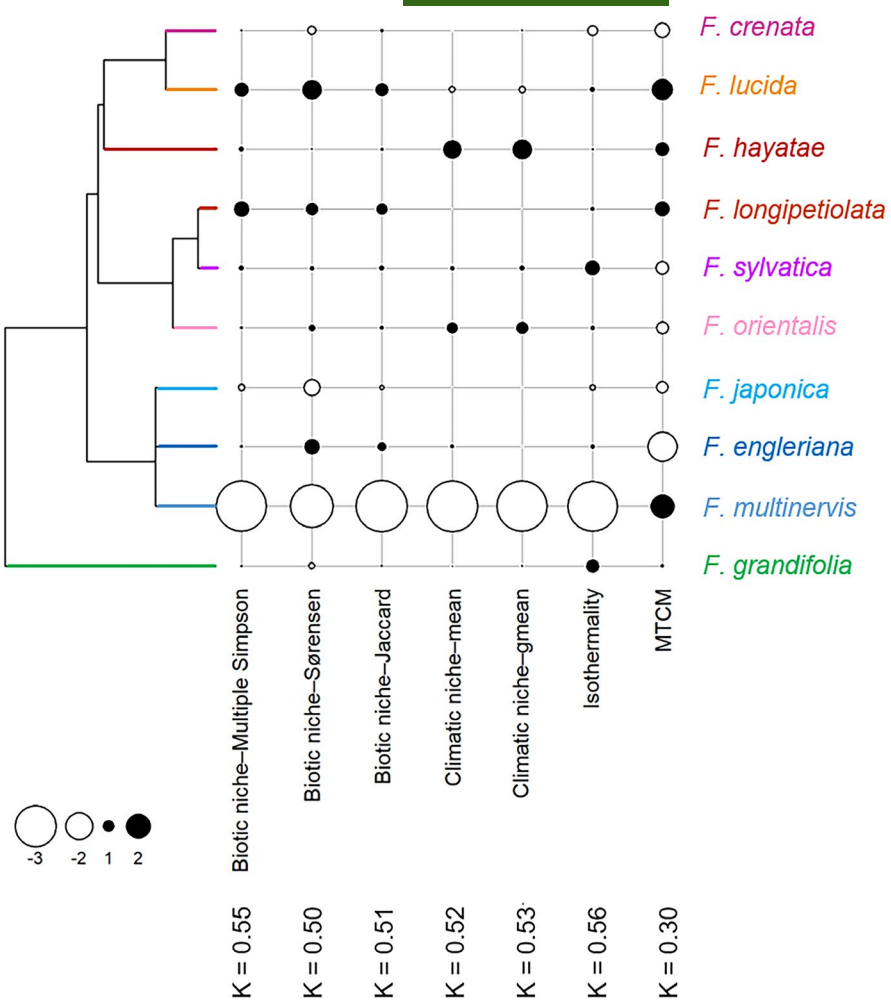

FIGURE 5 Different characteristics and their phylogenetic signal for the 10 extant *Fagus* species, measured by Blomberg's *K*. If *K* is significantly larger than one, the characteristic is regarded as phylogenetically conserved (Blomberg et al., 2003). Blomberg's *K* was not statistically significant ($p > 0.05$) for any characteristic. The phylogenetic tree is based on results provided in Qian and Jin (2016) and Oh et al. (2016). The size/colour of the circle represents the scaled and centred value of the corresponding characteristic. The acronym MTCM means minimum temperature of the coldest month

or biotic interactions with other species, the regional availability of suitable niche space or differences in landscape heterogeneity, evolutionary processes or historical events, as well as human impacts (Boulangeat et al., 2012; Lambdon, 2008; Sillero, 2011; Slayter et al., 2013; Wandrag et al., 2019).

The North American species *F. grandifolia* probably represents a member of the oldest clade (Renner et al., 2016). However, its large distribution and its relatively low niche breadth may, to a large extent, represent lower spatial species turnover and environmental heterogeneity in eastern North America in comparison to Europe and East Asia. It is well-established that the diversity of angiosperms in eastern China is larger than in eastern North America (e.g. Qian et al., 2005). *Fagus hayatae* has a very disjunct distribution with two subranges in mainland China and Taiwan Island, and thus, covers a broad, yet disjunct range of climatic conditions (Hukusima et al., 2013; Shen, 1992; Shen et al., 2015). *Fagus orientalis*, although with a distinctly narrower range size compared to *F. grandifolia* and *F. sylvatica*, covers diverse climatic zones from the Balkan mountain ranges to the southern Euxinian, Colchic, Eastern Mediterranean and Hyrcanian regions (Crimea, North Turkey, Caucasus, isolated patches in southern Turkey and North Iran), in combination with steep elevational gradients (Gholizadeh et al., 2020; Kavgaci et al., 2012; Shen, 1992). For example, in the Hyrcanian area, *F. orientalis* grows between around 300 to 2700 m a.s.l., covering a broad range of climatic conditions (from warm and humid to cool and dry) (Gholizadeh et al., 2020). Similarly, *F. sylvatica* has a broad ecological amplitude and a wide range of habitats in Europe (Magri, 2008; Ujházyová et al., 2016; Willner et al., 2017). The *Fagus* species in Korea (*F. multinervis*) and Japan (*F. crenata* and *F. japonica*) have narrower biotic and climatic niche breadth, consistent with these species being limited to isolated islands, especially for *F. multinervis*, endemic to Ulleungdo Island (Hukusima et al., 2013).

The distribution of *Fagus* was severely influenced by the Quaternary historical events in the Northern Hemisphere (Huntley et al., 1989; Liu et al., 2003; Magri, 2008). Following the early Quaternary, the geographical range of *Fagus* dramatically shrunk and shifted southwards during the glacial periods, although the history of *Fagus* species during the interglacials before the Holocene remains unclear (Hukusima et al., 2013; Huntley et al., 1989; Liu et al., 2003; Magri, 2008; Magri et al., 2006). After the Last Glacial Maximum, northward or northwestward re-immigration of *Fagus* from the southern refugia happened in North America, Europe and Japan (Huntley et al., 1989; Liu et al., 2003; Magri, 2008), despite strong dispersal limitations (Saltré et al., 2013). In China, however, the northward postglacial migration of *Fagus* was limited by the monsoon climate with early-season aridity, which restricted the

distribution ranges of the Chinese species to the subtropical region only (Liu et al., 2003; Shen et al., 2015).

Human activities might have affected the distribution and community composition of *Fagus* forests to a certain degree. For example, *F. sylvatica* forests in Europe have been managed for a long time as beech is an important economic tree for wood production, especially in northern-central Europe (Magri, 2008). Activities such as livestock grazing and disturbance of the preceding forests by fire before *Fagus* became established have promoted the spread of *Fagus* in northern Europe (Bradshaw et al., 2010).

Overall, these idiosyncratic impacts on range dynamics differed from those factors affecting niche breadth, as witnessed by the absence of a significant correlation. Our study, with a sample size of 10 species, suffers from low statistical power and does not preclude finding such a relationship across species within other genera. It would be, therefore, interesting to benchmark our finding that different factors drive range size and biotic niche width independently on a larger dataset.

Additionally, the lack of relationship between range size and niche breadth might also suggest that the prevalent processes of community assembly differ across *Fagus* species. In most communities, both deterministic and stochastic processes are at work simultaneously (Stegen & Hurlbert, 2011). Thus, a low taxonomic turnover (β-diversity), such as in *F. grandifolia* stands in North America, might reflect a low impact of stochastic processes, but might also be brought about by deterministic processes such as strong environmental filtering under homogeneous climatic conditions. In contrast, high β-diversity, such as for the *Fagus* stands in China, might indicate that stochastic processes dominate (Daniel et al., 2019), resulting from the more pronounced geographical isolation and more glacial refuge areas in China. However, the same pattern could also be caused by deterministic processes with different environmental filtering regimes under heterogeneous climatic conditions.

4.1 | Correlations between niche concepts

The co-occurrence-based biotic niche breadth estimates were uncorrelated with the climatic niche breadth estimates, incongruent with our second hypothesis (H2). Although positive relationships have been observed in previous studies (Kambach et al., 2019; Pannek et al., 2016), it has to be admitted that the two adopted niche concepts differ greatly in dimensions and spatial scales and thus are not necessarily correlated (Emery et al., 2012; Pannek et al., 2016). The incongruence of results based on different indices of realized niche breadth suggests that these indices carry complementary information.

4.2 | No phylogenetic signal for niche properties in *Fagus*

Our results suggest dynamic development of the biotic and the climatic niches, which does not seem to be related to the rooting depth and phylogenetic distance of the respective clades (Losos, 2008; Wiens et al., 2010), in contrast with our hypothesis H3. Considering the lack of a clear phylogenetic signal towards ecological specialization, we conclude that the complex phylogeographical history of the genus *Fagus* does not allow us to find support for the stated "specialization hypothesis". In previous studies, both divergent (e.g. Evans et al., 2009; Graham et al., 2004) and conserved (e.g. Kozak & Wiens, 2006; Peterson et al., 1999) climatic niches have been related to speciation processes. For *Fagus*, factors such as vicariance and geographical barriers might have resulted in the evolution of biotic and climatic niche properties. For example, the three species in the subgenus *Engleriana* (*F. japonica*, *F. engleriana* and *F. multinervis*) are closely related and speciated later than the other Chinese species (Renner et al., 2016), probably as a result of limited gene flow between separated islands (Japan and Ulleungdo Island in South Korea) and isolated mountain ranges (Oh et al., 2016). Having evolved from a common ancestor species, such geographical separation and differences in available niche space may result in the development of different biotic and climatic niches.

Cold tolerance has been regarded as a key trait for the geographical distribution patterns of trees (Hawkins et al., 2014; Wiens & Donoghue, 2004). The monthly mean of the minimum daily temperatures (BIO06) has been used to represent the cold tolerance of tree species for which large scale physiological data are usually hard to obtain (Hawkins et al., 2014). The RF classification analyses revealed that cold tolerance did not discriminate the species, suggesting it might be conserved across the whole *Fagus*-clade, possibly representing an ancestral adaptation. Uniform cold tolerance across the genus is consistent with Blomberg's *K*, revealing the absence of a phylogenetic signal within the genus. However, testing for conservatism at the genus level would require a broader taxonomic scope, for example, by including the whole Fagaceae family. Nevertheless, genus-level conservatism is suggested by the consistent association of *Fagus* with mesic temperate climates, relative to the broader distribution of the family.

5 | CONCLUSIONS

We estimated the biotic and climatic niche breadths of all 10 extant *Fagus* species and examined their relationships with range size. Biotic and climatic niche breadth were uncorrelated with range size and phylogeny, and also incongruent with each other. Furthermore, there was no evidence for evolutionary tendencies towards ecological specialization in the younger *Fagus* clades occurring in East Asia. We conclude that within widespread groups of related species such as in the *Fagus* genus, general macroecological patterns such as the range size–niche breadth relationship might be overridden by different regionally available niche space opportunities, differences in landscape heterogeneity and Quaternary histories.

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ORCID

Qiong Cai https://orcid.org/0000-0002-7173-1447
Erik Welk https://orcid.org/0000-0002-2685-3795
Francesco M. Sabatini https://orcid.org/0000-0002-7202-7697
Zhiyao Tang https://orcid.org/0000-0003-0154-6403
Fabio Attorre https://orcid.org/0000-0002-7744-2195
Andraž Čarni https://orcid.org/0000-0002-8909-4298
Milan Chytrý https://orcid.org/0000-0002-8122-3075
Süleyman Çoban https://orcid.org/0000-0003-1570-9795
Jürgen Dengler https://orcid.org/0000-0003-3221-660X
Richard Field https://orcid.org/0000-0003-2613-2688
Ute Jandt https://orcid.org/0000-0002-3177-3669
Dirk N. Karger https://orcid.org/0000-0001-7770-6229
Jonathan Lenoir https://orcid.org/0000-0003-0638-9582
Robert K. Peet https://orcid.org/0000-0003-2823-6587
Remigiusz Pielech https://orcid.org/0000-0001-8879-3305
Michele De Sanctis https://orcid.org/0000-0002-7280-6199
Franziska Schrodt https://orcid.org/0000-0001-9053-8872
Jens-Christian Svenning https://orcid.org/0000-0002-3415-0862
Cindy Q. Tang https://orcid.org/0000-0003-3789-6771
Ioannis Tsiripidis https://orcid.org/0000-0001-9373-676X
Wolfgang Willner https://orcid.org/0000-0003-1591-8386
Helge Bruelheide https://orcid.org/0000-0003-3135-0356

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BIOSKETCH

Qiong Cai is interested in plant community ecology, especially that of the genus *Fagus*. This work is the result of a co-operation project during her one-year visit at the Institute for Biology, Department of Geobotany, Martin-Luther-University Halle-Wittenberg.

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SUPPORTING INFORMATION

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

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