

Effects of climate and topography on the diversity anomaly of plants disjunctly distributed in eastern Asia and eastern North America

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Abstract

Aim: Differences in physiography have been proposed to explain the diversity anomaly for vascular plants between environmentally similar regions of eastern Asia (EAS) and eastern North America (ENA). Here, we use plant species within disjunct genera to examine whether differences in topography contribute to the diversity anomaly and whether the richness–environment relationships differ between regions. Disjunct plants are used to ensure that the diversity anomaly relates to post-disjunction evolution and diversification rather than regional differences in clade ages or immigration.

Location: EAS and ENA.

Time period: Current.

Major taxa studied: Plant taxa disjunctly distributed in EAS and ENA.

Methods: We compiled county-level plant distribution data, and calculated species richness and variables of topography and climate within unit grid cells. We compared estimated coefficients of region effects among models, where richness was fitted with or without topography and climate. Topography and climate were also used to separately model within-region spatial diversity patterns using spatial simultaneous autoregressive error models.

Results: The coefficients of region effects varied from -0.776 for the model only including region to -0.309 when topography was controlled for, but remained significant. Climate dominated the spatial diversity patterns in ENA. In contrast, the influence of climate (14.2%) on species richness was weaker than that of topography (18.3%) in the warm area of EAS. Relations to elevation and temperature varied between regions, shifting between positive and negative relationships in several cases.

Main conclusions: Our results demonstrate that variability in local topography contributes to the strong regional anomaly in plant species richness between EAS and ENA. Nevertheless, the diversity anomaly persists after controlling for local topography and climate. EAS and ENA also exhibit contrasting richness–environment relationships, providing another divergent aspect between the EAS–ENA disjunct floras. Our findings highlight that regional differences in topography or other environmental factors may underlie the diversity anomaly.

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KEYWORDS

Asian bias, climate, disjunct plants, diversity anomaly, richness–environment relationships, topographic heterogeneity

1 | INTRODUCTION

In *On the origin of species*, Charles Darwin (1859) wrote

It is universally admitted, that in most cases the area inhabited by a species is continuous; and when a plant or animal inhabits two points so distant from each other, or with an interval of such a nature, that the space could not be easily passed over by migration, the fact is given as something remarkable and exceptional

Though Darwin did not use the term 'disjunct', he had foreseen the significance of spatial disjunctions for understanding mechanisms that generate and maintain biogeographic patterns of species distributions. During the 1800s, Darwin and Asa Gray corresponded specifically concerning the floristic similarity between eastern Asia and North America (Boufford & Spongberg, 1983). Since then, the similarities in climate and the close floristic relationships between eastern Asia (EAS) and North America have continued to attract the interest of generations of botanists and biogeographers (Boufford & Spongberg, 1983; Gray, 1878; Hong, 1993; Li, 1952; Qian & Ricklefs, 2000).

Many authors have compared the taxonomic richness of plants between EAS and North America, and demonstrated a floral diversity bias in favour of EAS. For example, Guo et al. (1998), Qian and Ricklefs (1999) and Qian (2002) detailed the diversity anomaly of vascular plants at the species level among both entire continental regions and their temperate climate zones. They postulated that this anomaly might result from multiple factors, particularly the highly heterogeneous topography of EAS (also see Qian, Fridley, et al., 2007). However, these works focused on the entire floras and did not account for the fact that some EAS clades were older than those in North America (Qian & Ricklefs, 1999). Asia has been considered as the birthplace of angiosperms (Takhtajan, 1969; Wu, 1980). Evidence showed that several of the oldest angiosperm fossils were found in China (e.g., *Archaeofructus*, a Jurassic angiosperm of approximately 125 million years old; Sun et al., 1998). EAS also served as the 'museum' to retain the late pre-Quaternary or Quaternary relict plants that used to have exotic or Asian origins and widespread distributions in the North Hemisphere (Chen et al., 2018; Manchester et al., 2009). Therefore, plants in EAS had more time for diversification compared with those in North America. An appropriate assessment of the plant diversity anomaly between EAS and North America should control for differences in evolutionary history between the floras of the two regions.

The shared plant genera with now disjunct distributions in EAS and eastern North America (ENA) make up an ideal set of taxa for

testing hypotheses relevant to diversity anomalies between continents with similar climates. The EAS–ENA disjunct genera are descendants of the widespread 'boreotropical' flora in the pre-Quaternary (Tiffney, 1985), which subsequently survived climate cooling during the late pre-Quaternary and Pleistocene in EAS and ENA to different extents (Guo & Ricklefs, 2000; Manchester et al., 2009). Meanwhile, the disjunct genera maintained their ancestral ecological distributions while independently evolving in the two regions (Qian & Ricklefs, 2004; Ricklefs & Latham, 1992). Therefore, regional differences in clade ages and immigration from other regions between EAS and North America could be minimized or ignored when focusing on the EAS–ENA disjunct plant genera and their constituent species, because the species in both EAS and ENA belong to the same set of boreotropical genera (Wolfe, 1975) and thus shared the same evolutionary history. Among the EAS–ENA disjunct plant genera, EAS has many more species than ENA does (e.g., Wu et al., 1994–2013). However, this diversity anomaly at the continental scale may or may not translate to species assemblages at local scales (e.g., ecological communities), depending on the degrees of overlap among species distributions within each continental region. When entire floras are analysed, the diversity anomaly observed at continental scales persists at local scales, where geographic samples of equal size and environment variations (e.g., topography and climate) are controlled for (Qian et al., 2017; Qian, White, et al., 2007). Accordingly, we predict that species within the EAS–ENA disjunct genera are also more diverse in EAS than in ENA after controlling for sampling areas (i.e., geographic units used in data analysis) of equal size, topography and climate (hypothesis H1).

Many hypotheses have been proposed to explain the continental-scale diversity anomaly in the EAS–ENA plant disjunction, including the Asian-origin hypothesis, that is, clades originating within EAS and subsequently spreading to ENA had more time for diversification in EAS (Donoghue & Smith, 2004; Xiang et al., 2004). However, differences in topographic or physiographic heterogeneity between the two continental regions might also be responsible, at least in part, for the diversity anomaly of the EAS–ENA disjunct plants between the two continental regions (Guo & Ricklefs, 2000). Topographic heterogeneity could act on species diversification in multiple ways, that is, allowing more species to coexist, promoting speciation, or reducing extinctions (Stein et al., 2014). Mountain building and the resulting rugged topography create dispersal barriers and form novel habitat types (Antonelli et al., 2018; Badgley et al., 2017). Such fragmented and diverse habitats promote spatial turnover of species adapted to different environments, increasing the number of coexisting species within a region (Kneitel & Chase, 2004). Meanwhile, populations isolated by topographic features could undergo allopatric speciation, accelerating the speciation rate (Graham et al., 2004;

Ricklefs, 2004; Schluter, 2009). Phylogenetic reconstructions suggest bursts of speciation are coincident with orogenic activities in mountain chains (Hughes & Atchison, 2015), such as the Hengduan Mountains (Ding et al., 2020; Xing & Ree, 2017). Topographically heterogeneous regions buffer climate change, as the topoclimatic variation shortens the distance required for species to track climate change, leading to reduced extinction (Dynesius & Jansson, 2000; Sandel et al., 2011). Accordingly, high topographic heterogeneity in EAS has been thought to contribute to its high species richness (Lu et al., 2018; Qian & Ricklefs, 2000). However, previous studies have not formally examined whether differences in topographic heterogeneity between EAS and ENA contribute to the diversity anomaly of the EAS–ENA disjunct plant genera. If topographic heterogeneity is the driver of high EAS richness, then the diversity anomaly among the EAS–ENA disjunct plants should be reduced or disappear when it is accounted for (hypothesis H2).

In addition to the diversity anomaly, the two regions may also exhibit different relationships between diversity and environmental factors, similarly reflecting differing evolutionary and diversification dynamics (Jiménez & Ricklefs, 2014; Ricklefs, 2004). Previous studies have shown that topography has a more important influence on the diversity patterns of entire regional and local floras in EAS than those in ENA (Qian, White, et al., 2007). Further, temperature and precipitation differ in importance as drivers of regulating species distributions and plant diversity in the two regions (Allen et al., 2002; Kreft & Jetz, 2007; Lu et al., 2018; Ricklefs et al., 2004; Wang et al., 2009). The different roles of topography and climate in driving species richness patterns may be partly due to their different geographic settings (e.g., more heterogeneous in EAS), different climate patterns (e.g., stronger monsoon climate in EAS) and different influences of past climates (e.g., stronger glacial climate effects in ENA). However, previous studies primarily have focused on the whole floras within regions and thus ignored the influence of different evolutionary histories between EAS and ENA on the diversity anomaly. Using congeners shared between eastern Asia and eastern North America, for example, EAS–ENA disjunct genera, to compare the relationships between species richness and environment allows one to control for differences in pre-disjunction evolutionary history between continents. Thus, we predict that there should be contrasting richness–environment relationships featuring different drivers between EAS and ENA for the EAS–ENA disjunct plant genera, reflecting differing evolutionary and diversification dynamics between the two continental regions (hypothesis H3).

In this study, we compiled data on county-level plant distributions, topography, and climate to explore the hypothesized diversity anomaly among the EAS–ENA disjunct plants and the richness–environment relationships in the two regions, at a 100-km spatial scale (10,000 km²) and at a 200-km spatial scale (40,000 km²). Specifically, we aim to test the following three hypotheses outlined above, that is, (a) species of the EAS–ENA disjunct genera are more diverse in EAS than in ENA after accounting for sampling areas, topography and climate (hypothesis H1); (b) the diversity anomaly among the EAS–ENA disjunct plants is reduced or disappears when

topographic heterogeneity is accounted for (hypothesis H2); (c) the richness–environment relationships and their driving factors differ between EAS and ENA (hypothesis H3). We used generalized linear models and spatial simultaneous autoregressive error models to relate richness in EAS and ENA to topography and climate. By comparing the effects of independent variables on the diversity patterns in EAS and ENA, we sought to understand which variables influenced the hypothesized contrasting richness–environment relationships in EAS and ENA.

2 | MATERIALS AND METHODS

2.1 | Study area

As EAS–ENA disjunct plant genera to a large extent occur in eastern China and the eastern United States (Li, 1952; Qian & Ricklefs, 2004), our study focuses exclusively on these two regions, hereafter denoted as eastern Asia (EAS; c. 6.4×10^6 km²) and eastern North America (ENA; c. 4.8×10^6 km²) (Figure 1). Though the climate is spatially more heterogeneous in EAS (Jiménez & Ricklefs, 2014), the similarities in latitudinal ranges and geographic locations relative to oceans give EAS and ENA generally comparable climate characteristics and spatial climatic patterns, for example, temperature and precipitation decrease from south-east to north-west (see Figure S1 in Supporting Information Appendix S1). Therefore, EAS and ENA are ‘natural laboratories’ for exploring factors underlying regional diversity anomalies (Qian & Ricklefs, 2000).

The boundaries of China and the United States were defined by data from Global Administrative Areas (<http://www.gadm.org/>). We used administrative maps containing county-level information, derived from the National Geomatics Center of China (<http://www.ngcc.cn/ngcc/>) and the United States Census Bureau (<http://www.census.gov/geo/>), to map and visualize the county-level distributions of species and genera as described below.

2.2 | Plant distribution data

We updated the checklist of the EAS–ENA disjunct genera compiled by Qian and Ricklefs (2004) based on the latest botanical information in the Flora of China (Wu et al., 1994–2013). When ranges of species distributions within a genus reached western North America, we excluded that genus from our analysis. All species in 53 EAS–ENA disjunct genera of vascular plants were included in this study. See Table S1 in Supporting Information Appendix S1 for the list of the EAS–ENA disjunct genera.

Distributions of the EAS–ENA disjunct plants were compiled from various sources. For species in the United States (ENA), county-level distribution data were collected from botanical publications listed in appendix A of Qian, White, et al. (2007) and the United States Department of Agriculture (USDA) Plants database (<https://plants.sc.egov.usda.gov/home>). Non-native species were

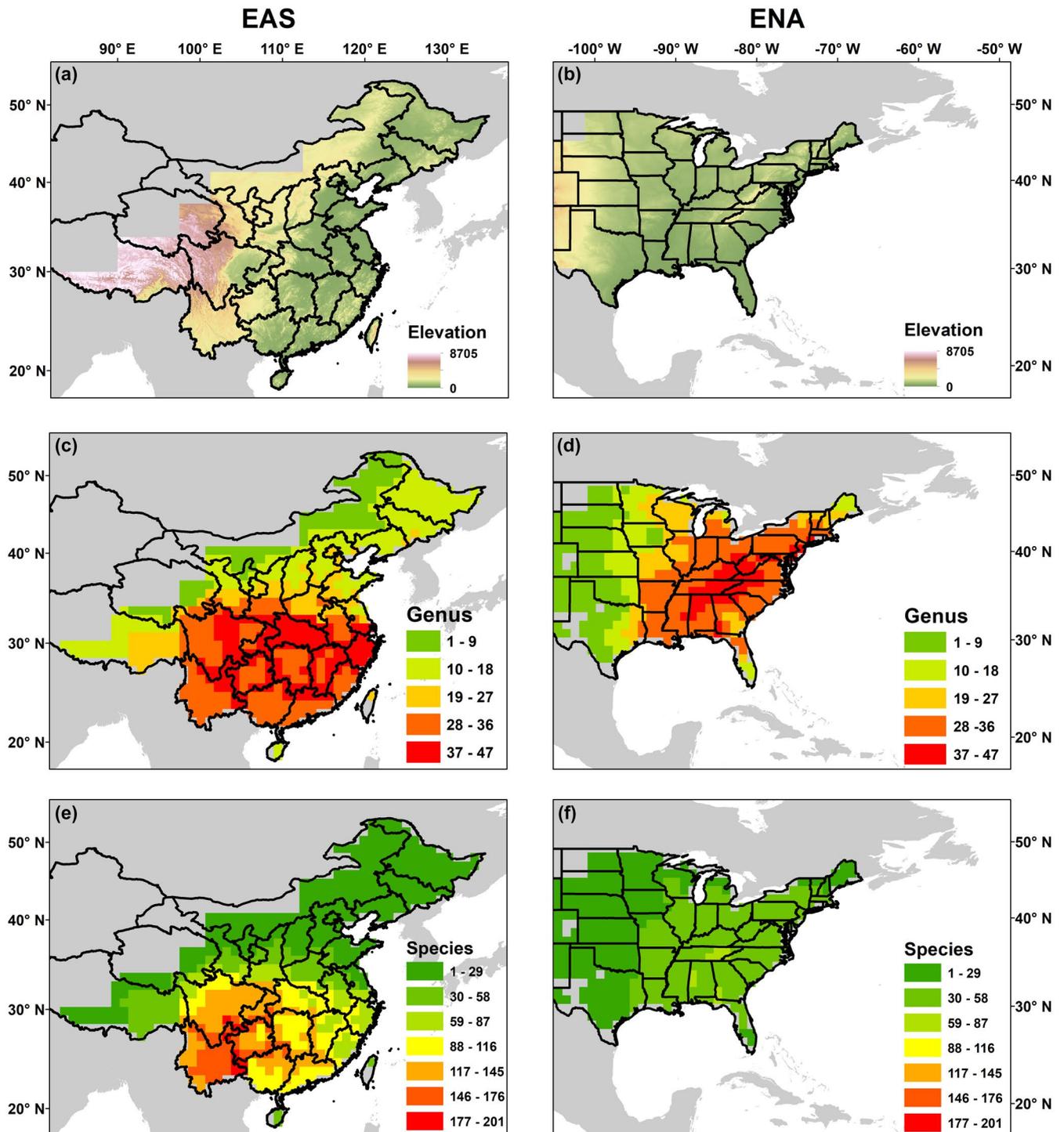


FIGURE 1 Study areas and spatial patterns of plant diversity in the eastern Asia–eastern North America (EAS–ENA) disjunct genera for grid cells of 100 km × 100 km. Colours ranging from dark green to white in EAS (a) and ENA (b) represent the change in elevation. Grid cells on the coastlines and on country borders with land areas $\leq 7,000$ km² were excluded from the distribution maps and analyses in this study. Panels (c) and (d), and panels (e) and (f) represent richness distributions of disjunct plants in EAS and ENA at the genus and species levels, respectively

excluded. County-level distributions were converted to distributions in 100 km × 100 km grid cells. For species in China (EAS), we first extracted 100 km × 100 km distributions from Lu et al.'s (2018) dataset and then improved the data by incorporating specimen records from the National Specimen Information Infrastructure of China

(NSII, <http://www.nsii.org.cn/>) and Flora of China (FOC; <http://foc.iplant.cn/>). We used only specimen records collected in the corresponding provinces to which species were found native based on FOC and provincial floras. Locality data from specimen records were converted to distributions in 100 km × 100 km grid cells. We then

checked the entire species list to exclude exotic species (whose distributions from collections or specimens were outside their native ranges). The final species data used in this study included 414 EAS species and 110 ENA species in the 53 EAS–ENA disjunct genera.

To compare spatial diversity patterns among disjunct plants in EAS and ENA, we generated range maps for each species and genus. Range maps at the species level consisted of grids with species occurrence records. A range map for each of the 53 disjunct genera was compiled from its constituent species within the EAS–ENA disjunct genera. The genus and species richness maps were derived by overlapping the range maps of genera and species, respectively, in the equal-area Behrman projection at a grid size of 100 km × 100 km. To reduce noise introduced by grid cells distributed on the coastlines and country borders, grid cells with land areas < 7,000 km² (i.e., < 70% of a full 100 km × 100 km grid) were excluded. The final distribution maps included 607 and 442 grid cells in EAS and ENA, respectively (Figure 1).

2.3 | Topography data

We assembled digital elevation model (DEM) data at a spatial resolution of 90 m at the equator from the NASA Shuttle Radar Topographic Mission (SRTM), which was accessible in CGIAR Consortium for Spatial Information (CGIAR-CSI; <https://srtm.csi.cgiar.org/>). 'No-data' gaps in the vicinity of Wisconsin and the Great Lakes were filled with data from the EarthEnv digital elevation model (<http://www.earthenv.org/DEM.html>).

We calculated the following nine indices in ArcGIS 10.3 (ESRI, Inc., Redlands, CA, USA) to characterize topographic heterogeneity (variation) for each 100 km × 100 km grid cell: mean elevation, elevation range, standard deviation of elevation, mean slope, mean aspect, projected area, surface area, curvature, and rugosity (the ratio of projected area to surface area). In addition, we calculated the topographic position index, which represents the difference in elevation between a focal cell and all neighbouring cells (Wilson et al., 2007) and was computed using the 'raster' package in R 3.6.1 (2019; <https://www.r-project.org/>). See Table S2 in Supporting Information Appendix S1 for a description of each topographic variable.

2.4 | Climate data

To characterize climates associated with local floras, bioclimatic variables (Table S2 in Supporting Information Appendix S1) were extracted from the 2.5-min-resolution WorldClim database (<http://www.worldclim.org/>; Hijmans et al., 2005) and averaged at each grain size using DIVA-GIS (<http://www.diva-gis.org/>) and ArcGIS. Previous analyses have shown that annual values (mean annual temperature and precipitation), seasonality (of temperature and precipitation), and extreme conditions of climate (minimum temperature of the coldest month and precipitation during the driest month)

strongly constrain the distributions of species (Qian et al., 2017; Zimmermann et al., 2009). Therefore, we calculated the mean values of these six climate variables at a 100-km spatial scale. We also calculated the standard deviation of mean annual temperature and precipitation within 100-km grid cells at 4 km × 4 km resolution to measure climate spatial heterogeneity. As a result, climate variables used in this study included six variables representing climate means and two variables representing climate heterogeneity.

2.5 | Statistical analysis

2.5.1 | Species of disjunct genera are more diverse in EAS than in ENA (H1)

To generate unrelated synthetic variables representing topography and climate, we separately conducted two principal components analyses (PCAs) for topography and climate variables, combining grids in EAS and ENA together. Climate heterogeneity variables were not included in the climate PCA. The first three principal components (PCs) of each of the two PCAs explained 82.6% and 93.3% of the total variation in topography and climate, respectively (Table S3 in Supporting Information Appendix S1).

In order to test region effects on the hypothesized Asian diversity anomaly statistically, we fitted species richness in EAS and ENA within the 100-km grid cells using generalized linear models (GLMs) with the negative binomial family and a log-link function, following Ricklefs and He (2016). The link function for the negative binomial regression model is:

$$\mu = \exp(\beta_0 + \beta_{\text{region}} + \beta_{\text{Topo}} \text{Topo} + \beta_{\text{Clim}} \text{Clim} + \beta_{\text{rxT}} \text{region} \times \text{Topo} + \beta_{\text{rxC}} \text{region} \times \text{Clim}) \quad (1)$$

where μ is the mean of the negative binomial distribution. For simplicity, 'Topo' represents the first three PCs of topography; 'Clim' represents the first three climate PCs and two climate heterogeneity variables. The dummy variable 'region' (coded as 0 for EAS, and 1 for ENA) was included in the GLM to assess region effects (Qian et al., 2017; Ricklefs et al., 2004). Specifically, the estimated coefficients relating to region effects (β_{r} , β_{rxT} and β_{rxC}) were kept in the models when 'region' was coded as 1 for ENA, suggesting differences in region effects between EAS and ENA. To characterize regional differences in the relationships between species richness and environmental conditions, the interactions between region and topography, and between region and climate were included in the full model. We then selected the model with the lowest Akaike information criterion (AIC) as the best GLM through backwards stepwise selection (also used in the following analyses). Because we detected residual autocorrelation in the best GLM (Moran's I , using the R package 'spdep'; Bivand et al., 2013), we fitted spatial simultaneous autoregressive error models (SARs) for GLMs to remove the spatial autocorrelation in the error term (Kissling & Carl, 2008). We focused on the estimated parameters. If diversity in EAS were significantly higher than that in ENA, we would expect the coefficient β_{r} for 'region' in the above model to be significantly

negative. Coefficients for the interaction terms $\beta_{r \times T}$ (or $\beta_{r \times C}$) would indicate differences in relationships between topography (or climate) and richness between EAS and ENA.

2.5.2 | Topography explains the diversity anomaly (H2)

For the purpose of testing whether topography explains the diversity anomaly in the EAS–ENA disjunct plants, we used GLMs and SARs to fit species richness in EAS and ENA using the four models. Link functions are as follows.

$$\text{Model 1: } \mu = \exp(\beta_0 + \beta_r \text{region}) \quad (2)$$

$$\text{Model 2: } \mu = \exp(\beta_0 + \beta_r \text{region} + \beta_{\text{Topo}} \text{Topo}) \quad (3)$$

$$\text{Model 3: } \mu = \exp(\beta_0 + \beta_r \text{region} + \beta_{\text{Clim}} \text{Clim}) \quad (4)$$

$$\text{Model 4: } \mu = \exp(\beta_0 + \beta_r \text{region} + \beta_{\text{Topo}} \text{Topo} + \beta_{\text{Clim}} \text{Clim}) \quad (5)$$

where variables' meanings are the same as those in Equation 1. We compared the estimated coefficients of the region effect (β_r). If topography accounted for the diversity anomaly completely or partially, the absolute values of β_r would be smaller in models including topography than those without topography. Estimated coefficients of all the variables are shown in Tables S4 to S6 in Supporting Information Appendix S1.

2.5.3 | Richness–environment relationships and their driving factors differ between EAS and ENA (H3)

To model the richness–environment relationships in EAS and ENA separately, we used GLMs and SARs to regress species richness against the ten topography and eight climate variables. Pseudo- R^2 values of GLMs and SARs were calculated as the Pearson R^2 between the predicted and observed values, which were then adjusted by the numbers of predictors (Table S7 in Supporting Information Appendix S1). The fitted SARs included non-spatial trends and spatial signals (Kreft et al., 2010). The predicted richness, excluding spatial components in SARs, was entered as the new response variable to partition the contributions of topography and climate, using the 'vegan' package (Oksanen et al., 2011) in R 3.6.1 R Core Team, (2019).

To avoid multicollinearity among variables, we excluded topography and climate variables that had a variance inflation factor (VIF) larger than 10 (Dormann et al., 2013). Models with different sets of variables were selected for EAS and ENA to best characterize environmental conditions in each region (shown in Table S7 in Supporting Information Appendix S1). The full models for species richness in EAS and ENA included six and seven topography variables, respectively. Six and five climate variables were selected for full models within EAS and ENA, respectively. All the variables

were standardized to vary within the 0–1 range, using the formula $(x - x_{\min}) / (x_{\max} - x_{\min})$, so that the effect sizes of different variables could be directly compared. GLMs with the lowest AICs were further fitted using SARs to control for spatial autocorrelation in GLMs. We compared the effect sizes of variables based on the estimated coefficients from SARs, to determine the influential variables for species richness patterns in EAS and ENA. If EAS and ENA held contrasting richness–environment relationships, we would find that the relative roles of topography and climate differed between EAS and ENA and that the influential variables also differed.

2.5.4 | 'Masking' effect of excessively long environmental gradients

Previous studies have pointed out that, when analysing the effect of region on species richness in a model with environmental variables being included as covariates, excessively long environmental gradients can 'mask' the impact of region on species richness (Hawkins et al., 2003; Qian, White, et al., 2007; Whittaker & Field, 2000). Mean annual temperature had wider ranges in EAS (–6.8 to 24.1 °C) than in ENA (2.9 to 23.3 °C). Annual precipitation also had a similar difference in the range of values (63–2,698 mm in EAS versus 27–1,619 mm in ENA; Figure S1 in Supporting Information Appendix S1). Therefore, the relative contribution of climate to the spatial diversity patterns in EAS might be overestimated, whereas topographic effects on species richness might be underestimated (masked) as a result of the long climate gradients, particularly in EAS. Accordingly, the analyses could be biased due to the unbalanced climate gradients in the two continental regions.

To minimize this 'masking' effect, considering that the vast majority of genera and species of the EAS–ENA disjunct plants were restricted to warm latitudes of the two continental regions (Figure 1; also see Qian & Ricklefs, 2004), we identified one-third of the warmest grid cells in the southern part of each region (denoted as 'warm area' to be distinguished from the 'entire' study area). Within these two warm areas, temperature gradients across the 203 EAS grids and the 148 ENA grids are similar (14.6–24.1 °C in EAS and 14.8–23.3 °C in ENA). We conducted two sets of the above-mentioned analyses: one for the 'entire' study area and the other for the subset 'warm area'.

After controlling for the long climate gradient, the full models of how topography and climate influenced species richness included seven and eight topography variables in warm areas of EAS and ENA, respectively. Six climate variables were retained to model species richness in warm ENA (Table S7 in Supporting Information Appendix S1).

We repeated the above analyses for species diversity data at the grain size of 200 km × 200 km. Because the results were qualitatively similar to those at the scale of 100 km × 100 km grids, we only report the results for 100 km × 100 km grids in the main text and include the details for 200 km × 200 km grids in Supporting Information Appendix S2 (see Tables S8 to S15 and Figures S3–S5 for the corresponding results).

3 | RESULTS

3.1 | EAS harbours higher species richness (H1)

With a mean of 63.23 (\pm 51.89 SD) species per grid cell, EAS species richness, ranging from 1 to 201 per grid cell, decreased from topographically complex regions in the south-west to flat areas in the north-east (Figure 1e). In contrast, richness in ENA ranged from 1 to 66 per grid cell with mean species richness being 29.09 (\pm 19.03 SD; Figure 1f).

When the dummy variable 'region' was included in a model to assess spatial differences in species richness, we detected a significant region effect for the entire area ($\hat{\beta} = -1.923$, $p < .001$; Table 1), indicating that species diversity in EAS greatly exceeded that in ENA. The region effect favouring EAS remained significant when the study area was constrained to the warm region of each continent ($\hat{\beta} = -3.074$, $p < .001$; Table 1).

3.2 | Topography partially explains the diversity anomaly (H2)

To examine the role of topography in explaining the diversity anomaly, we compared coefficients of the region effect (β_r) derived from different models. A significant region effect was detected regardless of the analysis areas and models (Table 2). This was consistent with results found in Table 1 that EAS harboured higher species richness. Compared with models only including region, the absolute values of coefficients for Model 2 with the addition of topography decreased from .776 to .309 and from 1.201 to .917 for the entire and warm area, respectively (Table 2). When climate variation was controlled for in Models 3 and 4, the region effects measured by the coefficient β_r got amplified to some extent. However, the role of topography in the diversity anomaly persists. Compared with Model 3, the absolute value of β_r in Model 4 was slightly reduced (1.404 vs. 1.531 and 2.265 vs. 2.276 for the entire and warm area, respectively; Table 2).

3.3 | Different richness–environment relationships between EAS and ENA (H3)

Taking the interaction between region and topography into consideration, the coefficients for the first PC (PC1) of topography differed between EAS and ENA for the entire ($-.145$ vs. $.149$, $p < .001$) and warm areas ($-.113$ vs. $.320$, $p < .001$; Table 1). Since topography PC1 was negatively related to topographic heterogeneity (mean slope, mean elevation; Table S3 in Supporting Information Appendix S1), the negative topography PC1–richness relationships in EAS actually represents a positive relationship between EAS species richness and topographic heterogeneity. In contrast, species richness in ENA was directly negatively related to topographic heterogeneity. Similar results were also found for the interactions between region and climate PC2 for the warm areas (Table 1).

The spatial patterns of species richness for the EAS–ENA disjunct plants were separately fitted with topography and climate variables. The two factors statistically accounted for 74.6% and 84.9% of the variation in the entire EAS and ENA, respectively. 31.8% and 28.0% of the variation in the two regions were explained by climate (Figure 2a and b). Topography alone explained 10.5% of the spatial variation in EAS species richness, far exceeding that in ENA (.6%; Figure 2b); 56.3% of the variation in the species richness pattern of ENA was jointly explained by climate and topography (Figure 2b).

We also partitioned the effects of topography and climate in warm areas, and these variables accounted for more variation in species richness in ENA (89.8%) than in EAS (54.5%) (Figure 3a and b). Compared with the results for the entire study area, the effect of topography was consistently negligible in ENA (.1%), while variance explained by climate was slightly enhanced (33%, Figure 3b). Importantly, topography accounted for more variation in species richness in the warm EAS area than climate did (18.3% vs. 14.2%, Figure 3a).

To explore factors influencing spatial diversity patterns of the EAS–ENA disjunct plants, we compared standardized effect sizes of variables deriving from SARs. As shown in Figures 2c and 3c, mean elevation (ME) and elevation range (ER) were the most influential, positively affecting the species richness in the entire EAS (standardized effect size, $\hat{\beta} = 1.53$, $p < .001$) and warm EAS ($\hat{\beta} = 0.92$, $p < .001$), respectively. In contrast, mean elevation was negatively related to the spatial diversity patterns in ENA, especially in warmer areas ($\hat{\beta} = -3.47$, $p < .001$; Figure 3d). Among the climate variables, annual mean temperature (MAT) had a positive relationship with EAS species richness ($\hat{\beta} = 2.51$, $p < .001$; Figure 2c) and was negatively correlated with species richness in ENA (Figures 2d and 3d).

4 | DISCUSSION

4.1 | Disjunct genera are more diverse in EAS than in ENA

Comparing diversity of disjunct taxa in different regions (e.g., EAS and ENA) can inform us of the relative importance of regional and local mechanisms in shaping diversity patterns (Ricklefs, 1987, 2004). Eastern Asia and eastern North America are ideal model regions for this purpose since their common evolutionary histories date back to the Holarctic palaeoflora in the pre-Quaternary (Tiffney, 1985). However, most previous work concerning the EAS–ENA plant disjunction was limited to particular taxa (e.g., Nie et al., 2008 for *Magnolia*; Chen et al., 2019 for *Liriodendron*) and cannot be considered broadly representative. In this study, we combined topography and climate data to statistically examine differences in diversity among disjunct genera between the environmentally similar but geographically separated regions, EAS and ENA. After controlling for the area of geographic samples (i.e., equal-area samples), topography and climate, we observed that species richness per grid cell was, on average, higher in EAS than in ENA, both for the entire regions and for warm study areas (Table 1 and Figure 1). Similar results were also found in any of the

Variable	Entire area			Warm area		
	β	SE	$p (> z)$	β	SE	$p (> z)$
Intercept	4.097	0.04	***	4.586	0.066	***
Region	-1.923	0.102	***	-3.074	0.17	***
Topography						
Topo_PC1	-0.145	0.022	***	-0.113	0.017	***
Topo_PC2	-0.063	0.012	***	-0.028	0.015	ns
Topo_PC3	-0.043	0.012	***	-0.023	0.017	ns
Climate						
Clim_PC1	0.389	0.012	***	0.058	0.025	*
Clim_PC2	0.097	0.027	***	0.092	0.027	**
Clim_PC3	-0.165	0.04	***	-0.08	0.101	ns
MAT_std	-0.561	0.256	*	-	-	-
AP_std	-1.539	0.213	***	-1.448	0.198	***
Interaction						
region \times Topo_PC1	0.294	0.042	***	0.433	0.078	***
region \times Topo_PC2	-	-	-	0.202	0.061	**
region \times Topo_PC3	-	-	-	-0.52	0.12	***
region \times Clim_PC1	-0.062	0.02	**	0.385	0.064	***
region \times Clim_PC2	-0.804	0.042	***	-0.432	0.061	***
region \times Clim_PC3	-	-	-	-1.125	0.263	***
region \times MAT_std	-1.096	0.649	ns	-	-	-
region \times AP_std	1.439	0.756	ns	1.439	0.756	*

Note: The dummy variable 'region' is coded as 0 for EAS and 1 for ENA. The first three principal components (PCs) of topography and climate are respectively denoted as Topo1, Topo2, Topo3 and Clim1, Clim2, Clim3 (see Materials and methods for details about what these Topo and Clim variables represent). MAT_sd and AP_sd are the standard deviations of mean annual temperature (MAT) and annual precipitation (AP), respectively. Significance levels:

*** $p < .001$; ** $p < .01$; * $p < .05$. ns = not significant.

Model	Entire area			Warm area		
	β	SE	$p (> z)$	β	SE	$p (> z)$
1	-0.776	0.055	***	-1.201	0.061	***
2	-0.309	0.063	***	-0.917	0.081	***
3	-1.531	0.051	***	-2.276	0.066	***
4	-1.404	0.055	***	-2.265	0.064	***

Note: Richness is separately modelled with region (Model 1), region and topography (Model 2), region and climate (Model 3), and all the three factors (Model 4). Significance level:

*** $p < .001$.

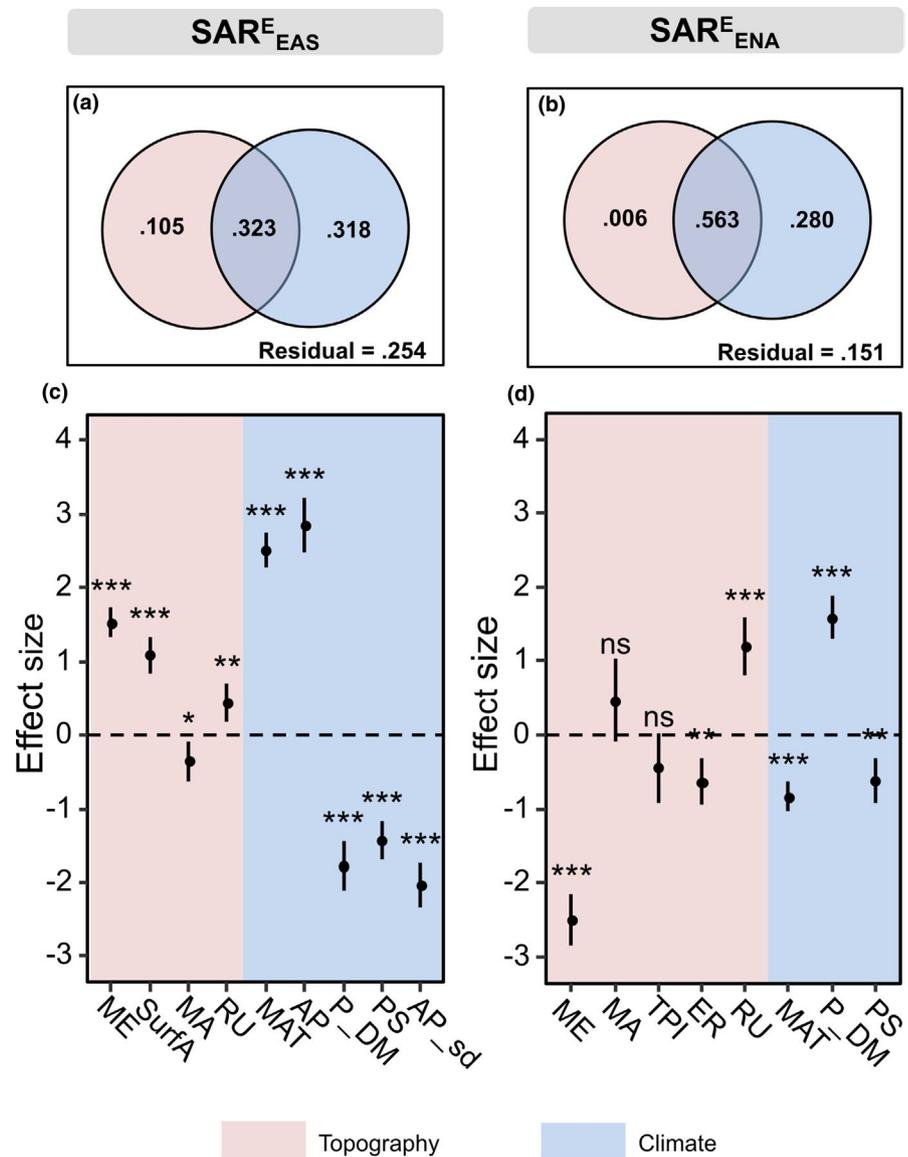
models with or without topography and climate (Table 2). This Asian-bias diversity pattern among the EAS-ENA disjunct plants is consistent with previous findings for vascular plant species (Guo & Ricklefs, 2000; Guo et al., 1998; Qian & Ricklefs, 1999). One potential cause for the broadly documented diversity anomaly is the different evolutionary histories of Asia and North America (for example, eastern Asia has more pre-Quaternary plant relics than does eastern North America; Qian, 2001). Using EAS-ENA disjunct genera in our analysis, we control

for differences in pre-disjunction evolutionary histories between the two continental regions. Our results, based on several statistical approaches, show that the diversity anomaly favouring Asia, observed at the continental scale in previous studies (e.g., Guo et al., 1998; Qian & Ricklefs, 1999), has also emerged in equal-area assemblages at much smaller spatial scales (10,000 and 20,000 km²), after controlling for differences in pre-disjunction evolutionary history between these two continents, thus supporting our hypothesis H1. Therefore, other

TABLE 1 Spatial autoregression for modelling the region effect on the species diversity patterns of eastern Asia-eastern North America (EAS-ENA) disjunct plants in the entire and warm areas

TABLE 2 Estimated coefficients of region effects for models in the entire and warm areas

FIGURE 2 Partitioning of variance (a and b) and effects of topography and climate (c and d) on the diversity patterns of the eastern Asia–eastern North America (EAS–ENA) disjunct plants for the entire study area using spatial simultaneous autoregressive error models (SARs). 'E' in the superscript represents the entire study region. The numbers in the Venn diagrams are exclusive. Abbreviations: ME = mean elevation; SurfA = surface area; MA = mean aspect; TPI = topographic position index; ER = elevation range; RU = rugosity; MAT = annual mean temperature; AP = annual precipitation; P_DM = precipitation of driest month; PS = precipitation seasonality; AP_sd = standard deviation of annual precipitation. Significance level: *** $p < .001$. ** $p < .01$. * $p < .05$. ns = not significant



ecological and regional factors (e.g., regional-scale topography) likely have played an important role in generating the diversity bias favouring eastern Asia.

4.2 | Topography partially explains the diversity anomaly

Our results corroborate the hypothesis that the more complex topography in EAS could partially account for the Asian bias in diversity (Qian & Ricklefs, 2000). After controlling for topography, the region effect became substantially reduced, albeit it remained important (Table 2). Hence, topographic heterogeneity at the level of grid cells contributes to the regional diversity anomaly, but does not fully explain it. In contrast, the increase in the magnitude of the region effect between Models 1 and 3 (Table 2) indicates that climate does not help explain the diversity anomaly. The stronger region effects in Models 3 and 4 (Table 2) might be explained as follows: EAS and ENA

differ in richness–environment relationships (i.e., hypothesis H3, see the discussion below), but when the interaction between region and environment is not included in these models, this difference can only be captured in the region term.

The remaining region effect must reflect other factors. One possibility would be regional-scale topographic complexity, that is, at a broader spatial scale than the grid-cell level topographic heterogeneity. EAS has highly varied landforms and complex topography (Figure 1), partly resulting from the uplift of the Qinghai-Tibetan plateau and Hengduan Mountains (maximum elevation > 4,500 m; Elsen & Tingley, 2015; Spicer et al., 2003). In contrast, the topography in ENA is relatively flat, with the highest Appalachian mountains not exceeding 2,100 m (Hammond, 1964). Recent studies have emphasized a relationship between orogenic activity and high speciation rates of plant taxa (Antonelli et al., 2009; Ding et al., 2020; Hughes & Eastwood, 2006; Xing & Ree, 2017). The more active tectonics (e.g., mountain uplift) in EAS promote geographic isolation and allopatric speciation (Qian et al., 2017), leading to higher speciation rates

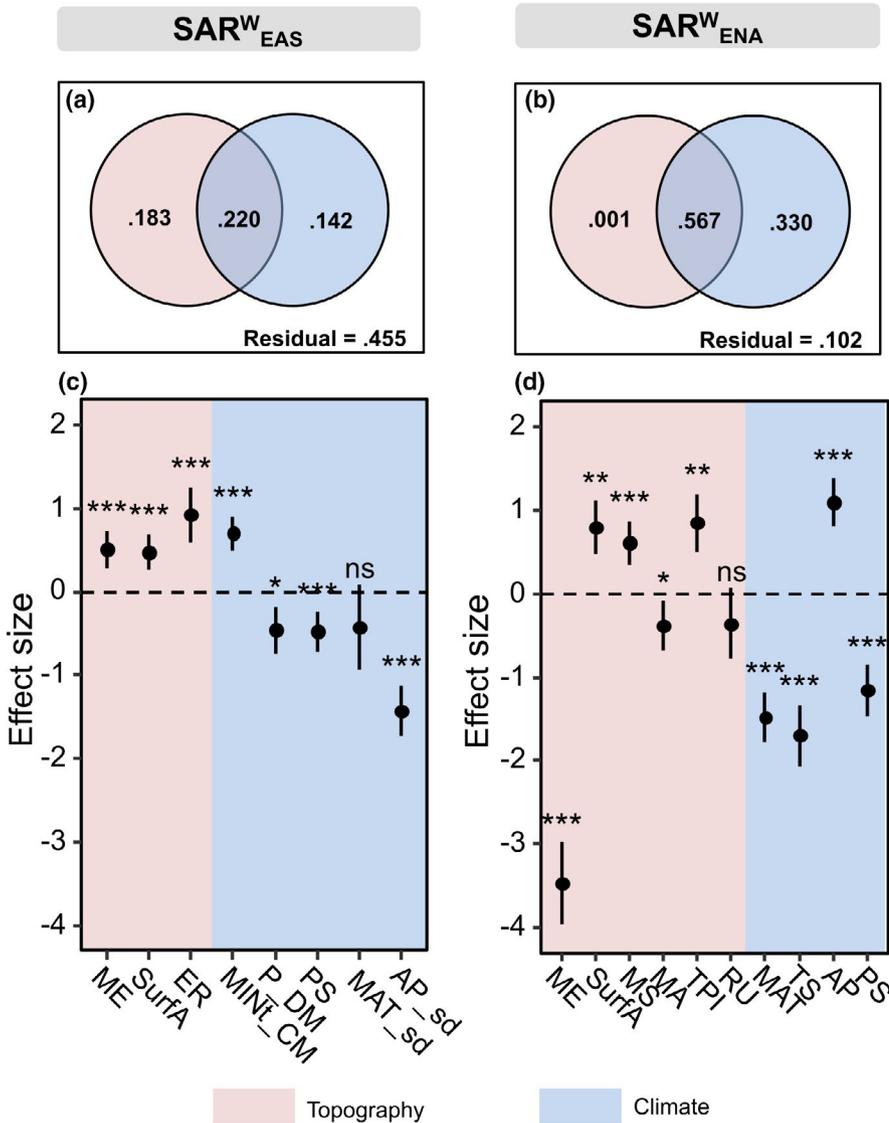


FIGURE 3 Partitioning of variance (a and b) and effects of topography and climate (c and d) on the diversity patterns of the eastern Asia–eastern North America (EAS–ENA) disjunct plants for the warm area using spatial simultaneous autoregressive error models (SARs). ‘W’ in the superscript represents the warm area. The numbers in the Venn diagrams are exclusive. Abbreviations: ME = mean elevation; SurfA = surface area; MS = mean slope; MA = mean aspect; TPI = topographic position index; ER = elevation range; RU = rugosity; MAT = annual mean temperature; TS = temperature seasonality; MINT_CM = minimum temperature of coldest month; AP = annual precipitation; P_DM = precipitation of driest month; PS = precipitation seasonality; MAT_sd = standard deviation of mean annual temperature; AP_sd = standard deviation of annual precipitation. Significance level: ****p* < .001. ***p* < .01. **p* < .05. ns = not significant

associated with more complex topography compared with ENA. Indeed, the warm south-western area of EAS, which has both complex topography and high species richness, is considered as an evolutionary ‘cradle’ for speciation and diversification (Figure 1; Lu et al., 2018; Yu et al., 2019). The more complex topography at the regional level within EAS could also have provided greater survival possibilities, for example, through the Plio-Pleistocene glaciations (Dynesius & Jansson, 2000). As both new species and relicts could subsequently spread across the region (e.g., Kou et al., 2016), these regional-level topographic effects could contribute to a higher species richness than predicted from grid-cell topographic heterogeneity.

4.3 | Contrasting richness–environment relationships in EAS and ENA reflect different richness-driving factors in the two regions

Our analyses were consistent with the prediction of hypothesis H3, that EAS and ENA held contrasting richness–environment

relationships. The relative importance of topography and climate to the within-region spatial diversity patterns differed in EAS and ENA. Climate was identified as the most important driver influencing the richness–environment relationships within ENA, with the variance explained by topography being less than 1% (Figures 2b and 3b). The climate-dominated richness–climate relationships in ENA remained relatively stable irrespective of the ranges of the ENA climate gradients. However, the effect of climate on the richness in EAS was weaker in the warm area and less than that of topography (Figure 3a).

Specifically, the relationships between species richness and topography differed, in both direction and magnitude, between EAS and ENA (Table 1). For example, increases in mean elevation promoted species richness in EAS, but constrained species richness in ENA. These findings were reinforced by our results on factors driving the spatial diversity patterns, where topography variables performed quite differently between EAS and ENA (Figures 2 and 3). This may reflect the fact that more area in North America was covered by ice during the Last Glacial Maximum (LGM), potentially leading to fewer

relict species in montane regions (Dyke & Prest, 1987). In addition, evidence showed that topographically flat ENA had a relatively high velocity of climate change, as well as low proportions of endemic species, compared with heterogenous EAS (Sandel et al., 2011). Therefore, the diversity anomaly could also be attributed to fewer extinctions in EAS as a result of topographic heterogeneity. The high elevations and complex topography in EAS could increase the diversity of habitat types for plants and limit the range sizes of many species (Jetz & Rahbek, 2002), leading to high local endemism and thus strengthening the Asian diversity bias. For example, 47% of the 414 species in EAS occupied fewer than 50 grids at the 100-km scale (small range sizes), while the percentage of such restricted species was much lower (33%) in ENA (Figure S2 in Supporting Information Appendix S1). The more small-range EAS species took full use of diverse and unique niche space, increasing spatial turnover and coexisting species in EAS.

The contrasting richness–environment relationships could also possibly have resulted from different effects of climate cooling during the LGM in the two continental regions. Ice coverage at that time extended approximately as far south as 38 degrees north latitude in North America (Dyke & Prest, 1987). These ice sheets constrained the extent of suitable habitat for plants and hampered the geographic shifting of plant distributions. Plant species in ENA likely dispersed slowly, with relatively low post-glacial migration rates, and did not reach equilibrium with climate (Seliger et al., 2021), as was also the case in Europe (Svenning & Skov, 2004, 2005, 2007). In contrast, eastern Asia lacked large-scale ice sheets, although permafrost covered Asia south to 40° N (Beijing area; Rapp, 2012). Considering the existence of a much greater area of subtropical climate in EAS compared to ENA (Qian & Ricklefs, 2004), EAS populations had more space to move south and could more easily survive the glacial period, likely leading to fewer extinctions in EAS (Guo & Ricklefs, 2000; Manchester et al., 2009).

Our results also support the hypothesis that different factors influenced diversity patterns in EAS and ENA. As shown in Figures 2 and 3, the sets of factors influencing diversity differ between EAS and ENA. Generally, temperature-related variables had a positive influence on species richness in EAS and a negative influence in ENA (Figures 2 and 3). In addition, variables representing seasonally extreme conditions of precipitation significantly constrained the spatial diversity patterns of EAS plant species. With large areas being covered by the monsoon climate in EAS, the precipitation in EAS showed great spatial and seasonal variation (Fu et al., 2008). Distributions of plant species are restricted, in part, by their physiological tolerance of desiccation (Zimmermann et al., 2009). Therefore, it is not surprising that species of EAS–ENA disjunct plants were deeply affected by precipitation in EAS. Specifically, precipitation seasonality exhibited a negative relationship with species richness regardless of the extent of study regions (Figures 2 and 3). This is remarkably consistent with the finding that precipitation seasonality is the most important climatic factor in determining the distribution patterns of tree species richness on a global scale (Ricklefs & He, 2016) and in eastern North America (Xing & He, 2018). We also found that the standard

deviation of annual precipitation was only retained in models for EAS species richness (Figures 2a and 3a). The greater climate heterogeneity in EAS was associated with stronger effects on corresponding species richness patterns. Overall, the spatial diversity patterns of species in EAS among the EAS–ENA disjunct plants were deeply affected by topography (e.g., mean elevation), climate heterogeneity, and precipitation-related variables, while temperature was strongly associated with species richness in ENA, perhaps overall reflecting the flatter topography in ENA.

4.4 | Conclusion

Our results corroborate the previously reported diversity anomaly between EAS and ENA, showing that it also applies to EAS–ENA disjunct plant taxa and persists after controlling for variation within grid cells in topographic heterogeneity, climate gradients, and regional climate differences. We furthermore found contrasting richness–environment relationships between EAS and ENA, suggesting their current richness is shaped by differing drivers. The greater regional-level topographic complexity in EAS relative to ENA could explain greater species richness in EAS after accounting for grid-cell climate and topography, through positive effects on speciation and reduced extinction coupled with subsequent re-expansions of new and relict species. The steeper slope of the topography–species richness relationship in EAS compared with that in ENA could potentially also reflect such an effect on the regional species pool (as found in Europe, Svenning et al., 2009). Contrasting richness–climate relationships between EAS and ENA could potentially also reflect such an effect. In a broader perspective, our results highlight how regional differences in the topography or other environmental factors acting across multiple spatial scales may underlie regional diversity differences.

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AUTHOR CONTRIBUTIONS

FH, HQ, RR and XY conceived the study. XY, HQ, XS, MZ and LM compiled the data. XY and FH carried out the data analysis. XY, HQ, JCS and FH led the writing with input from all authors.

DATA AVAILABILITY STATEMENT

The data for reproducing the results at the spatial scales of 100 and 200 km are available at <https://doi.org/10.5061/dryad.bzkh1898t>

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BIOSKETCH

Xue Yin is currently a PhD candidate who is interested in patterns and mechanisms associated with the disjunct plants in eastern Asia and eastern North America.

SUPPORTING INFORMATION

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

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