

Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants

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Abstract

Aim: The plant species sharing ancestors now disjunctly distributed in eastern Asia (EAS) and eastern North America (ENA) have long been a biogeographic puzzle. Species within the EAS–ENA disjunct genera are presumed to exhibit niche conservatism, the tendency of closely related species to be more ecologically similar, reflecting lineages' common evolutionary history. However, the hypothesis has not been well examined at the species level.

Location: EAS and ENA.

Time period: Current.

Major taxa studied: Species within the EAS–ENA disjunct genera.

Methods: We compiled data on climate, species occurrence, growth form, and phylogeny to examine niche conservatism. We first built a phylogenetic tree to select intercontinental congeneric pairwise species and obtained their divergence times. We then quantified the observed niche overlaps with Schoener's *D*, which has a 0–1 range, based on species occurrence and climate of species' native ranges. To obtain projected distributions, each species' niche was projected to the non-native region using ensemble ecological niche models. Projected-related niche overlaps were then calculated using projected distributions and the corresponding climatic conditions.

Results: Average observed niche overlaps of congeneric pairwise species were relatively small: .124, .211 and .109 for all, herbaceous and woody species, respectively.

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Both observed and projected-related niche overlaps had significant negative relationships with divergence times of intercontinental congeneric pairwise species, with niche overlap for herbaceous species being higher than that for woody plants when controlling for divergence times.

Main conclusions: We conclude that the significant negative relationships between niche overlap and divergence times of congeneric pairwise species confirm niche conservatism among species of EAS–ENA disjunct plants and that the extent of niche conservatism is slightly different for herbaceous and woody plants. These findings suggest the potential role of allopatric speciation in EAS, and could help to understand the evolutionary history and the Asian-bias diversity pattern of the EAS–ENA disjunct plants.

KEYWORDS

divergence times, EAS–ENA plant disjunction, ensemble ecological niche models, niche conservatism, niche overlap, pairwise species

1 | INTRODUCTION

Exploring changes in distributions of living organisms during adaptation to environments over evolutionary time is vital for understanding the present biogeographic diversity patterns (Keil & Chase, 2019; Pennington et al., 2009; Pennisi, 2005). A long-held mystery in biogeography is the pre-Quaternary relictual plants that are now disjunctly distributed in eastern Asia (EAS) and eastern North America (ENA) at the genus level (Gray, 1878; Qian & Ricklefs, 2004; Torrey & Gray, 1843). The EAS–ENA disjunct plants first originated from temperate to subtropical forests, which were widely distributed in the Northern Hemisphere during the Palaeogene and Neogene, and migrated via the Bering and North Atlantic land bridges between Eurasia and Europe (Tiffney, 1985a; Wen, 1999; Wen et al., 2010; Wolfe, 1975). The plant relics, surviving subsequent climate oscillations in the Quaternary, diversified within each continent and led to the floristic diversity pattern seen today – species richness in EAS is two times greater than that in ENA for the EAS–ENA disjunct plant genera (Qian & Ricklefs, 2000). The common evolutionary ancestors, long independent within-continent evolutionary histories and the Asian-bias diversity pattern therefore give rise to an interesting question: are there similarities in environmental spaces among closely related lineages within the EAS–ENA disjunct plants as they independently evolved in EAS and ENA?

Niche conservatism, that is, the tendency of lineages to retain niches and ecological characters of ancestors over evolutionary time (Pearman et al., 2008; Wiens & Graham, 2005), has been suggested to occur among the EAS–ENA disjunct genera and their constituent species (Wen, 1999; Wen et al., 2010). Previous works detected strong parallelism in geographic and climatic distributions for disjunct genera in EAS and ENA, and reported an evolutionary conservatism (stasis) for the disjunct plants at the genus level (Qian & Ricklefs, 2004; Ricklefs & Latham, 1992). Specifically, compared

with woody genera, herbaceous genera were found to be more ecologically specialized and conserved, which may result from smaller sizes, shorter time for divergence and less selective pressure (Guo & Ricklefs, 2000; Qian & Ricklefs, 2004; Ricklefs & Latham, 1992). However, whether there exists niche conservatism for the EAS–ENA disjunct plants at the species level and whether niche conservatism differs between herbaceous and woody plant species have been largely unexplored.

Niche conservatism at the species level may help to understand biogeographic patterns and ecological processes from an evolutionary perspective. Accumulated evidence suggests niche conservatism as a contributing factor to the latitudinal diversity gradient, where species-rich regions in low latitudes are dominated by older clade organisms (Qian et al., 2013; Rosenzweig, 1995; Wiens & Donoghue, 2004). Organisms in climatically relatively stable regions (e.g., tropical regions) generally have higher survival possibilities (Hawkins et al., 2011; Kerkhoff et al., 2014). Niche conservatism could also contribute to an understanding of plant species with disjunct distributions. For example, closely related plant species from the Southern Hemisphere retained the evolutionary inertia of ancestral biomes during speciation processes and transoceanic colonization (Crisp et al., 2009). More importantly, studies of niche conservatism concerning taxa with close phylogenetic relationships can shed light on the conserved nature and general rules of adaptation to environments inherited from ancestors through lineage radiation or speciation processes like allopatric speciation (Crisp et al., 2009; Peterson, 2003; Wiens & Graham, 2005), which indicates species-specific evolutionary lability to new environments (Smith et al., 2018; Wiens et al., 2010).

Commonly used methods to examine niche conservatism for closely related taxa (like species), including those testing evolutionary phylogenetic signals (Blomberg & Garland Jr, 2002; Losos, 2008; Pagel, 1999) and estimating evolutionary rates (Wiens et al., 2010),

are mainly used for one or some lineages, but not for all taxa with close phylogenetic relationships. Alternatively, a negative relationship between niche or niche-related traits and phylogenetic distances could be considered as a 'phylogenetic signal' for the conserved niche. Such evidence has been found in broad-scale plant families (Su et al., 2020) and for a small number of species (Burns & Strauss, 2011), where richness and germination rates were used to represent the niche, respectively. Similarly, resemblances in distributions of closely related taxa can be used as a proxy to examine niche conservatism, that is, if the resemblances are negatively related to phylogenetic distances (Anacker & Strauss, 2014). Peterson et al. (1999) proposed 'reciprocal comparison' for sister taxon pairs, where the ecological niche of one species was used to predict the geographic distribution of another. Closely related birds, mammals, and butterfly species pairs exhibited reciprocal predictability where species' projected distributions showed consistence with geographic records of their sister species (Peterson et al., 1999). This method originally measured similarities in geographic distributions, and a more direct way would be to quantitatively measure overlaps in niche space across geographic ranges of pairwise species (Atwater et al., 2018; Broennimann et al., 2012; Warren et al., 2010; Wiens & Graham, 2005). Ecological niche models (ENMs) have been increasingly used to capture species' niche breadths and identify potentially suitable habitats using 'reciprocal comparison' (Hadly et al., 2009; Warren et al., 2008).

To test niche conservatism for species within the EAS-ENA disjunct plant genera, we compiled data on species occurrence, climate, growth forms, and phylogeny. We calculated niche overlaps of intercontinental congeneric pairwise species under the framework of 'reciprocal comparison'. Specifically, we focused on the following two questions: (a) to what degree are niches conserved among closely related species within the EAS-ENA plant disjunction; (b) do species of different growth forms, that is, herbaceous and woody plants, have different levels of niche conservatism? If niche conservatism exists in EAS-ENA disjunct plants at the species level, we would expect to observe negative relationships between niche overlaps and divergence times of pairwise species and the negative relationships to be stronger for herbaceous species than for woody plants because of the shorter divergence time in herbs (Anacker & Strauss, 2014; Burns & Strauss, 2011). This analysis provides evidence of niche conservatism for plant species within the EAS-ENA disjunct genera, deepening our understanding of the disjunction formation and present-day diversity patterns.

2 | MATERIALS AND METHODS

Our analysis took three steps to examine niche conservatism for species within the EAS-ENA disjunct genera (shown in Figure 1): (a) selecting intercontinental congeneric pairwise species containing one EAS species and one ENA species, based on a phylogenetic tree (see Supporting Information Appendix S1 for details), (b) fitting and evaluating the ENMs using species occurrence and climate data

through reciprocal comparison, and (c) quantifying niche overlaps and examining their relationships with divergence times of pairwise species.

2.1 | Study area

Following previous studies (Qian et al., 2017; Qian & Ricklefs, 2000, 2004; Wen et al., 2010), we used eastern China to represent eastern Asia (EAS), while south-eastern Canada and the eastern part of the United States constituted eastern North America (ENA) (Figure 2). Due to the dissimilar environmental conditions caused by the relatively long gradients within large areas, some provinces/states (e.g., Inner Mongolia, Ontario) were divided into subprovinces (Qian et al., 2019) (Table S1 in Supporting Information Appendix S2). EAS and ENA share similarities in decreasing gradients of temperature and precipitation from south-east to north-west (Mearns et al., 2009; Qin et al., 2016), resulting from similar latitudinal and longitudinal ranges and comparable geographic locations with east coasts facing large oceans (Figure 2).

2.2 | Species data

We updated the plant checklist with recorded growth forms from Qian and Ricklefs (2004) and distribution data mentioned below. Only genera whose species distributions did not reach far outside our study areas were retained. In total, 52 disjunct genera in EAS and ENA were included (Table S2 in Supporting Information Appendix S2).

For EAS species, we compiled county-level distributions in China based on the database described in Lu et al. (2018) and species checklists of counties, nature reserves and national parks (Qian et al., 2017). We also used georeferenced specimen records from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>) and the National Specimen Information Infrastructure of China (NSII, <http://www.nsii.org.cn/>). To correct for potential errors as a result of typographical errors or introduced plants records, we only used distribution records from provinces where species were regarded as native in the Flora of China (FOC; Wu et al., 1994-2013) and provincial floras (Liu et al., 2007). For species in ENA, local distribution data at the county levels were collected from botanical publications (Qian et al., 2007) and the United States Department of Agriculture (USDA) Plants database (<https://plants.sc.egov.usda.gov/home/>), complemented with records from GBIF. Distributions of introduced species in ENA were not included.

To reduce bias resulting from the administrative division of county-level data, species occurrences were converted to distributions in 100 km × 100 km grid cells under the Behrmann cylindrical equal-area projection. The centroids of grids were considered as species presence data. To yield robust projections (see Materials and methods below for details; Stockwell & Peterson, 2002; Wisz et al., 2008), only species with greater than 20 presence records

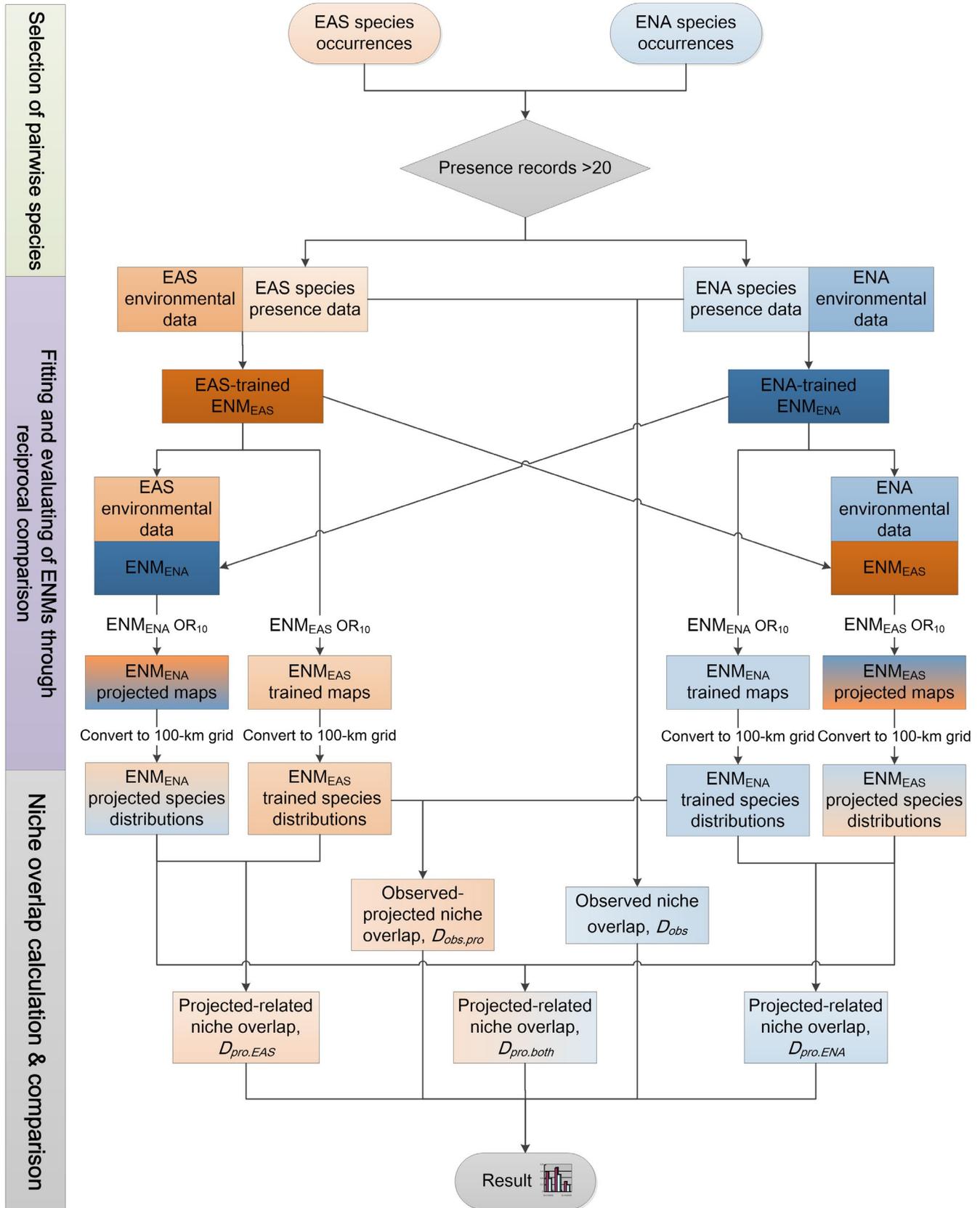


FIGURE 1 Workflow used in this study. ENM_{EAS} and ENM_{ENA} represent the ensemble ecological niche models (ENMs) trained in eastern Asia (EAS) and eastern North America (ENA), shown in warm and cold colours, respectively. OR₁₀ is an abbreviation for the 10% omission error rate of the evaluation data in ensemble ENMs; see Materials and methods for more details

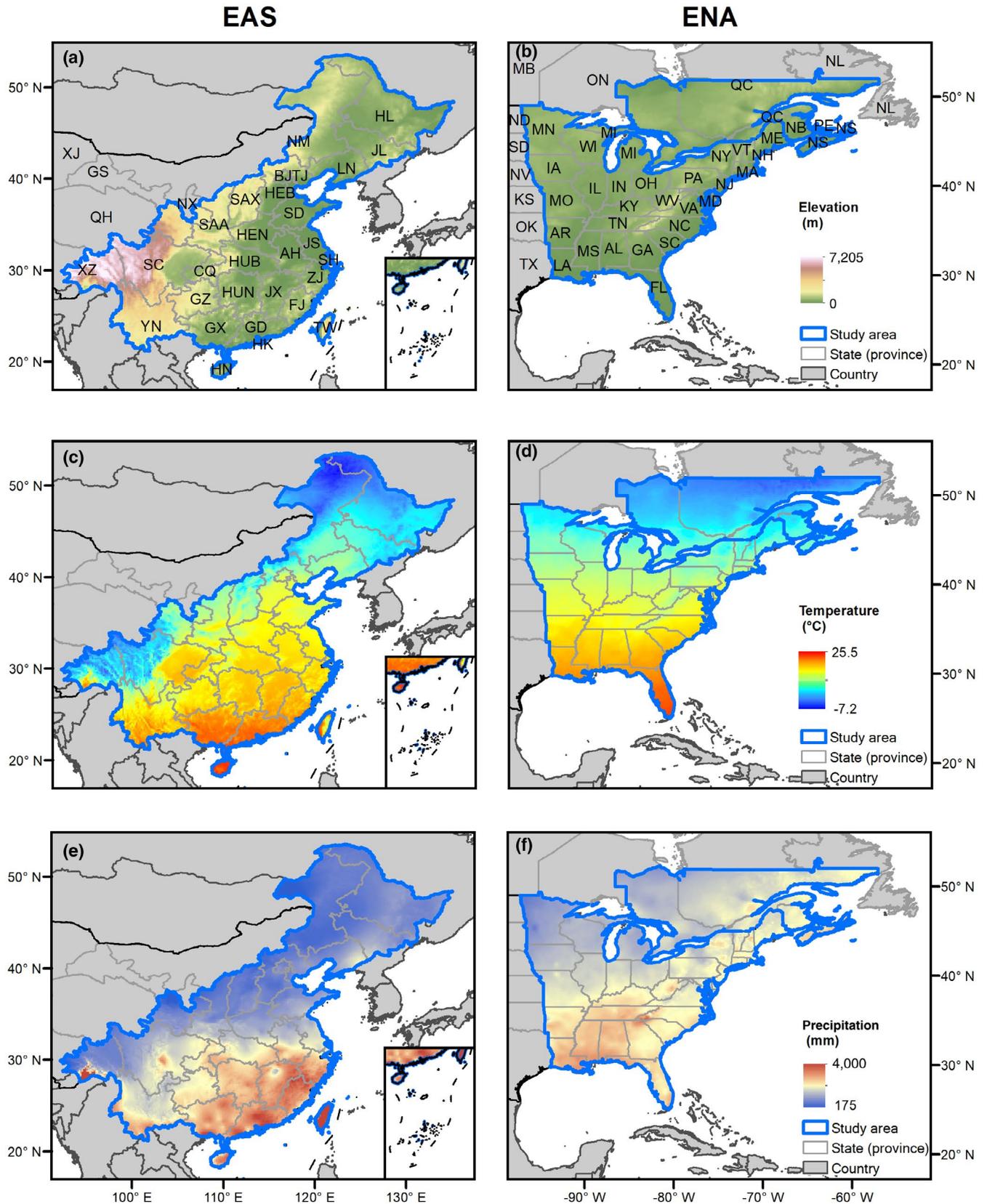


FIGURE 2 Elevation and climates of study areas in eastern Asia (EAS) and eastern North America (ENA). In (a) and (b), provinces or states are shown, with codes explained in Table S1 of Supporting Information Appendix S1. Colours ranging from dark green to red represent elevation. Mean annual values of temperature and precipitation of study areas are displayed in (c) and (d), and (e) and (f), respectively

were used. The final plant list included 48 genera, containing 283 and 91 species in EAS and ENA, respectively. The 20-presence-records threshold used in our study meets the lowest sample size limit suggested in the literature (e.g., Jiménez-Valverde, 2020) to produce ENMs of acceptable accuracy.

2.3 | Climate data

We used 19 bioclimatic variables from the WorldClim v.2 database at a 30-arc-second resolution (<http://worldclim.org/version2>; Fick & Hijmans, 2017). All climate rasters were resampled to the 100-km resolution using bilinear interpolation with ArcGIS 10.6 (ESRI, Inc., Redlands, CA) under the Behrmann projection. To reduce collinearity among variables, we conducted a principal components analysis (PCA) for the 19 bioclimatic variables (Legendre & Legendre, 2012). The first three principal components (PCs) explained 82.3% of the total variation in the climatic variables (Table S3 in Supporting Information Appendix S2). We thus retained the first three PCs for subsequent analyses. These analyses were conducted with the 'RStoolbox' package (Leutner & Horning, 2017) in R 3.6.1 (R Core Team, 2019).

2.4 | Fitting and evaluation of ecological niche models

In order to take account of model uncertainty, an ensemble approach was used for reciprocal comparisons of the ecological niche for pairwise species (Araújo & New, 2007). Hereafter, we use ENM_{EAS} and ENM_{ENA} to represent models trained in EAS and ENA, respectively. We used five predictive algorithms: bioclim, boosted regression tree (BRT), generalized additive model (GAM), maximum entropy (Maxent) and random forest (RF). The latter four algorithms need either background or pseudoabsence data. For BRT, GAM and RF, we generated 30 sets of pseudoabsence points, each of which has the same numbers as those for species' presence (Liu et al., 2019; Xu et al., 2019). For Maxent, we used 10,000 background points to characterize available environmental conditions (Phillips et al., 2006, 2009; Phillips & Dudik, 2008). All pseudoabsence and background points were randomly selected within 200 km of focal species' ranges, with points at the same locations as presence records being excluded (Barbet-Massin et al., 2012; Barve et al., 2011).

Performance of ensemble ENMs was evaluated with average of the area under the receiver operating curve (AUC; Swets, 1988), the continuous Boyce index (CBI; Hirzel et al., 2006), and true skill statistics (TSS; Allouche et al., 2006) via a five-fold cross-validation. Species data were split into five folds, 80% of which were used for fitting models and the remaining 20% for predicting models. This procedure was repeated five times, until each fold was used four times for model fitting and one time for model evaluation. AUC ranges from $\leq .5$ for models being no better than random

expectation to 1 for perfect predictions (Fielding & Bell, 1997). The CBI indicates how well models differentiate between presences and background sites. A negative CBI indicates that the model's output is negatively correlated with the true probability of presence. As CBI approaches 1, model performances increase (Hirzel et al., 2006). CBI was calculated using the 'enmsdm' package (Smith, 2018). TSS takes into consideration omission and commission errors, with values ranging from -1 to 1 (Allouche et al., 2006). Models with a TSS of 1 indicate perfect agreement. Specifically, we only included models in ensemble ENMs for which cross-validation gave TSS scores greater than .5. The selected ENMs were ensemble in the 'sdm' package (Naimi & Araújo, 2016), using the weighted-mean method with TSS as the weight. Performance of ensemble ENMs is provided in Figure S2 of Supporting Information Appendix S3.

We next projected ensemble ENMs into species' native regions. To threshold the projected probabilities layer into binary presence-absence trained maps, we used the 10% training threshold rule that the lowest 10% of predicted values were removed (OR_{10} ; Pearson et al., 2007). When ENMs were projected to the native regions of counterpart species, OR_{10} of trained ENMs was used to generate corresponding binary projected maps (Figure 1). All the binary trained and projected maps were resampled to 100-km resolution grids, centroids of which were used as trained and projected species distributions, respectively.

2.5 | Calculation and comparison of niche overlaps

To quantify niche overlap in environmental spaces between pairwise species, we calculated Schoener's D , a metric that ranges from 0 for no overlap to 1 for complete overlap (Broennimann et al., 2012; Schoener, 1968, 1970), using the 'ecospat' package (Di Cola et al., 2017). For each pair of intercontinental congeneric species, we calculated the following niche overlaps for species in all genera, as well as for species in herbaceous and woody genera separately.

Observed niche overlap (D_{obs}) was the overlaps observed based on species presence in EAS and ENA, whereas observed-projected niche overlap $D_{obs,pro}$ used trained distributions of focal species in their native regions (Figure 1). Observed-projected niche overlaps $D_{obs,pro}$ work as complements to the observed niche overlaps D_{obs} . Projected-related niche overlaps were generated through reciprocal comparison. Niche overlaps between trained ENM_{EAS} maps and projected ENM_{ENA} maps in EAS were defined as $D_{pro,EAS}$ and those in ENA as $D_{pro,ENA}$. $D_{pro,both}$ used projected maps in EAS and ENA.

Areas of projected maps could affect the calculation of projected-related niche overlaps. Species with small projected distributions (numbers of projected 100-km gridded presence smaller than five) were not used to measure niche overlap (Di Cola et al., 2017). Therefore, numbers of projected-related niche overlaps depended on areas of projected maps.

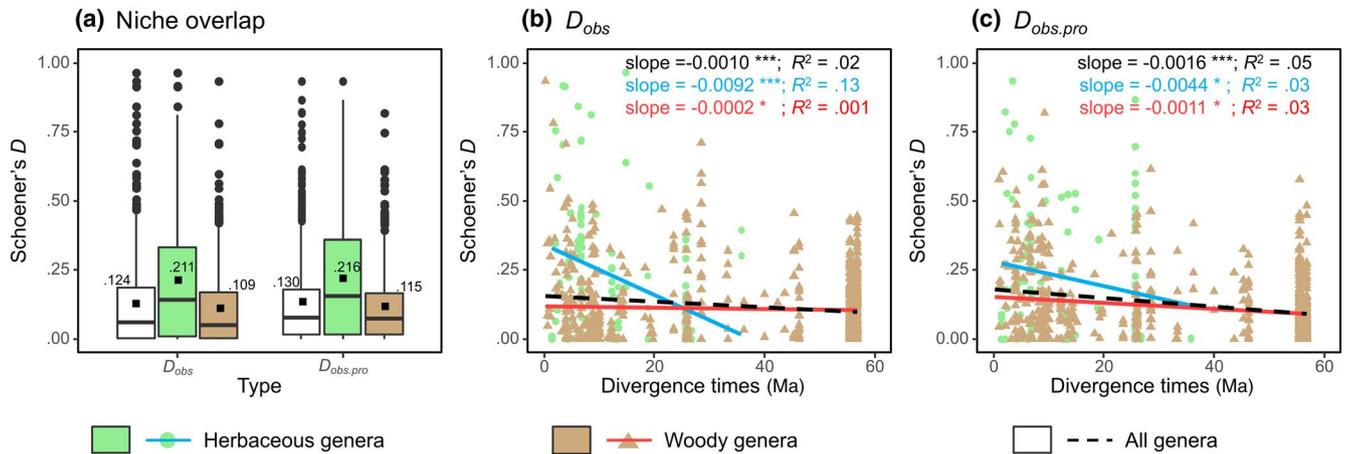


FIGURE 3 Values of observed-related niche overlaps and their relationships with divergence times of pairwise species for all, herbaceous and woody genera. D_{obs} refers to niche overlaps observed based on species presence data. $D_{obs.pro}$ stands for observed-projected niche overlap using trained species distribution from binary trained maps. In (a), square points and numbers in boxplots represent means of niche overlaps (measured as Schoener's D). In the scatter plots (b and c), lines are fitted with simple linear regressions to show relationships between observed-related niche overlaps and divergence times for herbaceous (green) and woody species (brown). *** $p < .001$. * $p < .05$

Linear models were used to examine the relationships between niche overlaps and divergence times of pairwise species. Slopes of linear relationships reflect how niche overlaps change with divergence times. To solve the pseudo-replication where a species may have two or more counterpart species, we randomly chose 100, 200 and 300 pairwise species from the entire 780 congeneric species pairs. In each replicate, we calculated the slope of regression lines between observed-related niche overlaps and divergence times for the randomly selected pairwise species. We compared the slopes of the 780 pairwise species with the simulated regression slopes.

2.6 | Sensitivity analysis

Climate and topography deeply influence species habitat suitability, and limit species distributions (Antonelli et al., 2018; Davis & Shaw, 2001). However, topography is less often used in ENMs than climate due to its indirect influences on species ranges (Austin, 2002; Guisan & Thuiller, 2005). Here, we did a sensitivity analysis to test whether the inclusion of topography better describes species niche spaces. We proposed two scenarios for the sensitivity analysis: a climate-only scenario that used climate variables to define niche spaces of species, and a climate-topography scenario using both climate and topography to calculate species' niches. We compared values of niche overlaps under the two scenarios and their relationships with the divergence times of pairwise species. Since results of the two scenarios were similar, we only report results of the climate-only scenario in the main text (description and results of the climate-topography scenario are provided in Tables S6, S7, S8, and Figures S5, S6, S7 of Supporting Information Appendix S4).

3 | RESULTS

3.1 | Divergence times of intercontinental congeneric pairwise species

Among the 780 selected pairwise species, mean and median values of divergence times were 31.12 and 26.03 million years ago (Ma), respectively (Figure S3 in Supporting Information Appendix S3). EAS species *Menispermum dauricum* and ENA congeneric species *Menispermum canadense* had the most recent divergence time of .165 Ma, while the largest divergence time of 56.83 Ma was found for paired species in *Magnolia* (Figure S1 in Supporting Information Appendix S1 and Figure S3 in Supporting Information Appendix S3). Divergence times of pairwise species for herbaceous plants (14.3 ± 9.7 Ma) on average were much younger than those for woody paired species (34.0 ± 21.9 Ma).

3.2 | Observed-related niche overlaps

We quantified the observed-related niche overlaps (D_{obs} and $D_{obs.pro}$) and their relationships with divergence times of pairwise species for all, herbaceous and woody genera, separately. Compared with D_{obs} , $D_{obs.pro}$ from trained maps consistently had higher mean Schoener's D values with herbs holding the highest value of .216 (Figure 3a). The mean of D_{obs} for all the disjunct genera was .124, which was higher than that for the woody genera (.109). There existed no significant differences in values between D_{obs} and $D_{obs.pro}$ (Wilcoxon tests, $p > .05$). Significantly negative relationships were found for D_{obs} and $D_{obs.pro}$ as functions of divergence times of pairwise species within all and herbaceous genera. For all the disjunct genera, the slope of linear regression for D_{obs} (-0.0010, Figure 3b) was similar

to that for $D_{obs,pro}$ (-0.0016 , Figure 3c). Regression slopes of the woody genera also shared similarities between D_{obs} (-0.0002) and $D_{obs,pro}$ (-0.0011). The smallest slope was -0.0092 for D_{obs} of herbs. The slopes of 780 pairwise species (-0.0010 for D_{obs} and -0.0016 for $D_{obs,pro}$, Figure 3b and c) were in the middle of density plots of slopes of simulated regressions (Figure S4 in Supporting Information Appendix S3), regardless of sample size.

3.3 | Projected-related niche overlaps

Three projected-related niche overlaps $D_{pro,EAS}$, $D_{pro,ENA}$ and $D_{pro,both}$ were measured. Different numbers of pairwise species were used in the calculations of projected-related niche overlaps, due to different areas of projected maps (pie charts in Figure 4; Table S4 in Supporting Information Appendix S3). Compared with $D_{pro,both}$, more paired species with large projected maps were used for projected-related niche overlaps, especially for $D_{pro,EAS}$ (395 and 339 pairwise species for all and woody genera, respectively; see Table S4 in Supporting Information Appendix S3). Intersections of species with large projected maps in EAS or ENA led to fewer pairwise species used for $D_{pro,both}$ (273 for all the disjunct genera, Table S4 in Supporting Information Appendix S3). Mean values of $D_{pro,EAS}$ were higher than $D_{pro,ENA}$ and $D_{pro,both}$, except for the herbaceous genera (.422 for $D_{pro,EAS}$ versus .431 for $D_{pro,ENA}$; Figure 4). Herbs had higher mean values of projected niche overlaps than those of woody species, the smallest being .136 for $D_{pro,both}$ for woody genera (Figure 4).

The slopes of linear regressions for projected-related niche overlaps ($D_{pro,EAS}$, $D_{pro,ENA}$ and $D_{pro,both}$) as a function of divergence times were consistently negative for the disjunct genera (Figure 4). As divergence times of pairwise species increased, projected-related niche overlaps for herbs decreased, especially for $D_{pro,both}$ (slope = -0.0151 , Figure 4f). Slopes of regression lines for all the disjunct genera remained around -0.0010 , regardless of the projected-related niche overlaps. The negative relationships between projected-related niche overlaps and divergence times of paired species for woody plants were only significant when ENM_{ENA} was projected to the environments in EAS (slope = -0.008 , $p < .05$; Figure 4g).

4 | DISCUSSION

Revealing similarities and differences in environmental spaces among species across evolutionary time is of vital significance to understanding diversity patterns (Wiens et al., 2010; Wiens & Graham, 2005) and to discovering mechanisms or processes driving diversity patterns (Peterson et al., 1999; Wiens, 2008). In this study, we combined species presence data, climate data and a dated phylogenetic tree to explore the niche conservatism of plant species within the EAS–ENA disjunct genera. We found both observed-related and projected-related niche overlaps were negatively correlated with

divergence times of intercontinental congeneric pairwise species (Figures 3 and 4), although the extent of negative relationships varied between herbaceous and woody plants. Our analysis helps to understand the evolutionary history of the EAS–ENA disjunct plants and highlights the important role of niche conservatism and potentially corresponding processes in shaping the Asian-bias disjunct plant diversity pattern (Qian & Ricklefs, 2000).

4.1 | Niche conservatism and allopatric speciation

Our study reveals that pairwise species with younger divergence times shared more resemblances in environmental spaces. The significantly negative trends showed niche conservatism in the EAS–ENA plant disjunction for both observed-related and projected-related niche overlaps, although the slopes of linear regressions for all the EAS–ENA disjunct genera differed only slightly from zero (-0.0010 to -0.0017 in Figures 3 and 4). Previous works claimed niche conservatism on continental scales resulting from physiological limitations to environments (Huntley et al., 1989; Svenning, 2003). However, for plant species within the EAS–ENA disjunct genera, niche conservatism may result from allopatric speciation (Wiens, 2004). The EAS–ENA plant disjunction dates back to the once widespread Arcto-Tertiary flora in the Eocene (Graham, 1993; Li, 1952; Tiffney, 1985a, 1985b). The Pacific Ocean divided the ancestors of disjunct plants into subgroups to adapt to their respective environments in EAS and ENA, which were further isolated by various topographic landforms within each region (Figure 1a,b). Therefore, the species of the EAS–ENA disjunct genera had high possibilities of resulting from vicariance and subsequent allopatric speciation caused by orogeny within each continent (Qian & Ricklefs, 2000). Since species' habitats tend to be restricted to their ancestors' distributions, a certain degree of niche conservatism is expected (Smith et al., 2018; Wiens, 2004; Wiens & Graham, 2005).

Orogeny caused by tectonic activities may drive allopatric speciation through niche conservatism (Hua & Wiens, 2013; Wiens & Graham, 2005). In contrast to ENA with its relatively simple topography (Hammond, 1964), EAS has a more complex topography as a result of the uplift of the Tibetan Plateau, which experienced localized uplift to near present height in the eastern part (e.g., the Hengduan Mountains) 8–10 Ma (Favre et al., 2015; Spicer et al., 2020). The niche conservatism found in the EAS–ENA disjunct plants and heterogenous topography in EAS suggest the potentially strong allopatric speciation in EAS. Coincidentally, we found a high frequency of pairwise species diversified 5–10 Ma (Figure S3 in Supporting Information Appendix S3), consistent with previous works (Donoghue & Smith, 2004; Wen, 1999; Wen et al., 2010; Xiang et al., 2004). This finding could indicate that the orogeny of the Tibetan Plateau and the Himalayas promotes speciation in EAS. Due to the isolated and heterogenous topography, vicariance and allopatric speciation may occur more often in EAS than in ENA, resulting in the Asian-bias diversity pattern (Qian & Ricklefs, 2000; Wen, 1999).

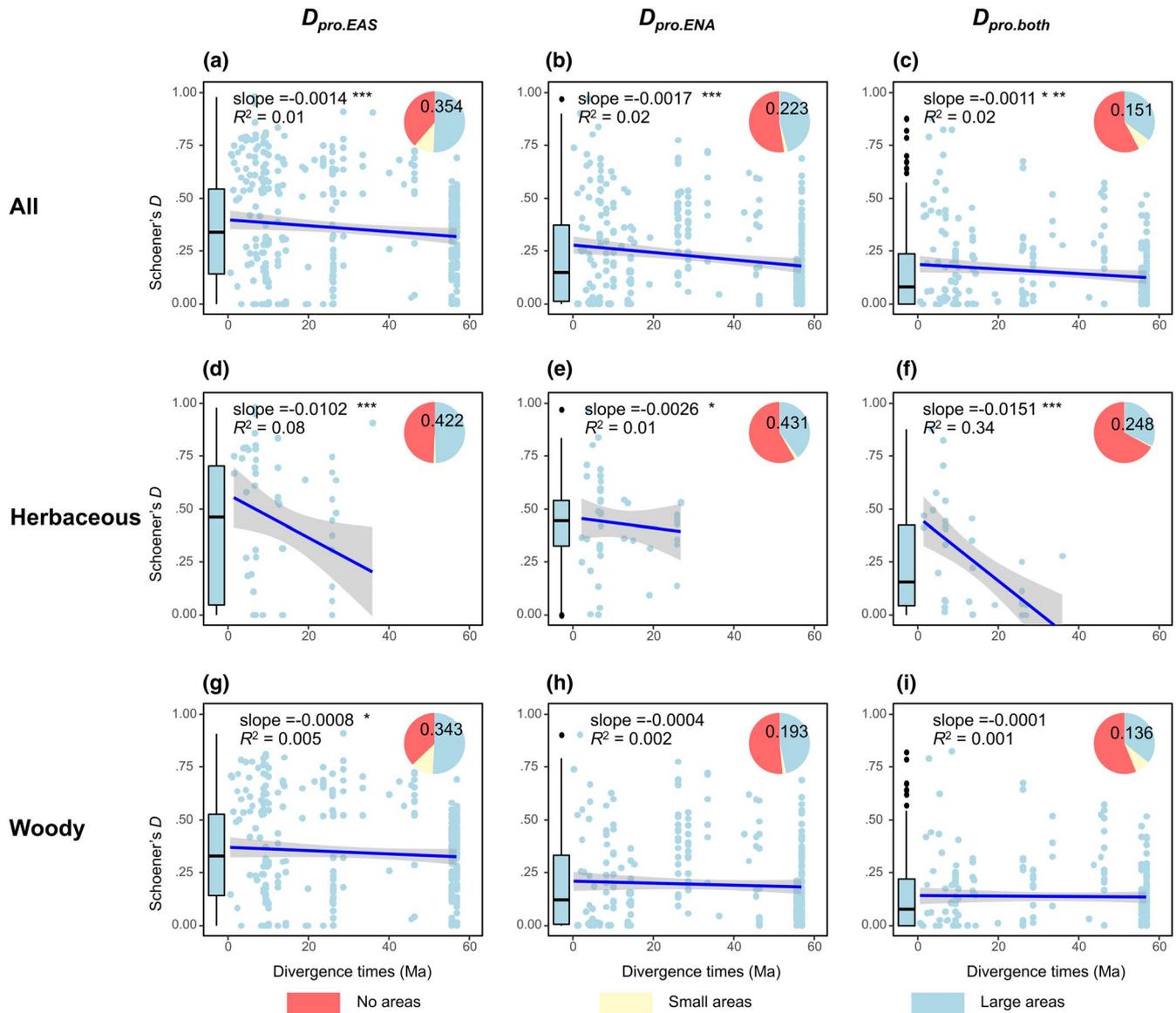


FIGURE 4 Relationships between projected-related niche overlaps and divergence times of pairwise species for all, herbaceous and woody genera. Boxplots show distributions of projected-related niche overlaps. Pink, light yellow and light blue colours represent projected-related species distributions with no, small and large ranges, respectively (detailed numbers shown in Table S4 of Supporting Information Appendix S3). Mean values of Schoener's D shown in the pie charts. 'No' and 'small areas' refer to no or small projected distributions of species that aren't used for niche overlap calculation; and 'large areas' stands for large projected distributions used for projected-related niche overlaps. $D_{pro.EAS}$ refers to niche overlaps using trained ecological niche model (ENM) map for eastern Asia (ENM_{EAS}) and projected ENM map for eastern North America (ENM_{ENA}) (a, d and g), and vice versa for $D_{pro.ENA}$ (b, e and h); $D_{pro.both}$ derived from projected map of ENM_{EAS} and ENM_{ENA} (c, f and i). Lines are the fitted simple linear regressions between projected-related niche overlaps and divergence times. *** $p < .001$. * $p < .05$

4.2 | Niche conservatism for herbaceous and woody species

Our analysis corroborated the existence of niche conservatism for both herbaceous and woody species in the EAS–ENA disjunct genera, though the conservatism for woody species was only detected using the observed-related niche overlap (Figure 3). Previous studies found the general existence of niche conservatism in disjunct genera for herbaceous and woody plants in EAS and ENA (Qian & Ricklefs, 2004; Ricklefs & Latham, 1992), and beech (*Fagus L.*)

in Europe and North America (Huntley et al., 1989). Here, we showed significant negative slopes of regression lines between niche overlaps and divergence times (Figures 3 and 4), suggesting that niches for herbaceous species were more highly conserved. Compared with woody species, herbaceous plants have much younger lineages so that it would be easier for herbs to keep stable niches of ancestors (Graham, 1993; Xiang et al., 2000). More importantly, herbs are often equipped with various strategies to cope with freezing cold conditions, for example, shortening life span, or overwintering as seeds or underground storage organs

(Qian et al., 2017; Zanne et al., 2014). This explanation is supported by more northern distributions of herbs than woody plants in EAS and ENA (Qian & Ricklefs, 2004). Herbaceous species were also found to favour specialized edaphic space and microhabitats (Ricklefs & Latham, 1992). If this was the case, one would expect that herbaceous species could shift their niches by exploiting microrefugia due to their smaller statures, or by senescing constructed aboveground tissues (Feng et al., 2016; Qian et al., 2017; Zanne et al., 2014). Therefore, more recent divergence times and less selective pressure may enable herbaceous species to retain trait legacies inherited from common ancestors and present a conserved niche during the diversification on different continents (Guo & Ricklefs, 2000; Qian & Ricklefs, 2004; Smith, 2018; Wiens, 2004; Wiens & Graham, 2005).

4.3 | Niche conservatism and Asian-bias disjunct plant diversity pattern

Our results for projected-related niche overlaps used different numbers of pairwise species due to projected maps with different areas. $D_{pro,EAS}$, the projected niche overlap using projected ENM_{ENA} maps and trained ENM_{EAS} maps, had the most pairwise species (395 for $D_{pro,EAS}$ versus 356 and 273 for $D_{pro,ENA}$ and $D_{pro,both}$, respectively; Figure 4 and Table S4 in Supporting Information Appendix S3). Since a species would only occupy suitable areas within its niche range (Atwater et al., 2018), areas of projected maps could reflect the extent to which projected regions contained subsets of species' niche spaces. Species with no projected ranges suggested that they possibly failed to find suitable environmental conditions in the projected regions. Although large geographic range sizes did not guarantee large niche spaces due to little environmental heterogeneity across geographic distributions, small range sizes of species were generally positively correlated with small niche spaces (Pagel et al., 2020; Slatyer et al., 2013). Correspondingly, there were more EAS species with no and small projected ranges than ENA species (Table S5 in Supporting Information Appendix S3), implying that EAS offers more unique, heterogeneous environmental conditions, which are less likely to be found in ENA. This finding was strengthened by taking topography into consideration, where more rugged topography in EAS had greater effects on the heterogeneity of environmental niches than that in ENA (Figure 2). Wider niches enabled EAS species to separately distribute among niche axes, promoting coexistence of more species (Levine & HilleRisLambers, 2009; Silvertown, 2004; Wright, 2002), which may partially explain the EAS–ENA disjunct plant diversity patterns.

4.4 | Small sample sizes and model performance

The performance (or accuracy) of ENMs has previously been found to be influenced by the number of occurrence records, especially small sample sizes (Collart et al., 2021; van Proosdij et al., 2016).

Given this concern would also exist with our ensemble ENMs of focal species within the EAS–ENA disjunct plants, we used a sample size of > 20 occurrence records. A recent study suggested that the lowest sample size limit to produce acceptable accuracy was within the range of 20 to 30 occurrence records (Jiménez-Valverde, 2020). In our analyses, 38 of 283 (13.42%) and 10 of 91 (10.99%) species in EAS and ENA had fewer than 30 occurrence records. Most of the species within the EAS–ENA disjunct genera have a greater number of occurrence records than the recommended lowest sample size limit. Therefore, the sample size should not influence the model performance of our ensemble ENMs.

5 | CONCLUSION

In summary, we for the first time examined the niche conservatism of closely related plant species within the EAS–ENA disjunct genera. Our results showed that niche overlap between intercontinental congeneric pairwise species had significantly negative relationships with their divergence times, regardless of whether the observed-related niche overlaps based on species occurrence data or the projected-related ones derived from reciprocal comparisons were used. Notably, niche spaces were more conserved for herbaceous than for woody species among the EAS–ENA disjunct genera, consistent with previous works on these disjunct genera (Qian & Ricklefs, 2004; Ricklefs & Latham, 1992). Niche conservatism plays an important role in driving speciation processes like allopatric speciation (Wiens, 2004; Wiens & Graham, 2005). Therefore, niche conservatism in the EAS–ENA plant disjunction stresses the potential role of allopatric speciation in shaping the disjunct plant diversity patterns, which has been suggested to account for the EAS–ENA disjunct plant diversity patterns for years (Wen, 1999; Xiang et al., 2004), but has not been tested until now. In addition to allopatric speciation, the wider niche spaces in EAS may more strongly drive species diversification in EAS than in ENA, as suggested by more EAS species with no or small projected distributions in ENA. Our study can be extended to other niche characteristics of lineages within a particular region and deepen the understanding of niche conservatism in EAS–ENA disjunct plants, which could be used to predict their distributions in the face of climate change.

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AUTHOR CONTRIBUTIONS

FH and XY conceived the study. XY, HQ, TD, LM and MZ compiled the data. HQ and TD constructed the phylogeny. XY carried out the analyses, with advice from SJ, WYG and JCS on ecological niche models. XY and CC wrote the first draft, with substantial input from all authors.

DATA AVAILABILITY STATEMENT

All data used in this study have been published. Details about data sources are cited in the article, including regional and local checklists and floras (Q.-R. Liu et al., 2007; Qian et al., 2017), plant distributions in 100-km grid cells (Lu et al., 2018; http://www.darwintree.cn/resource/spatial_data); the Flora of China (Wu et al., 2013; http://www.efloras.org/flora_page.aspx?flora_id=2), the USDA Plants database (<https://plants.usda.gov/java/>), Global Biodiversity Information Facility (<http://www.gbif.org>), National Specimen Information Infrastructure (www.nsii.org.cn), and WorldClim v.2 database (<http://worldclim.org/version2>).

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BIOSKETCH

Xue Yin is currently a PhD candidate and 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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