Coversheet

This is the accepted manuscript (post-print version) of the article. Contentwise, the accepted manuscript version is identical to the final published version, but there may be differences in typography and layout.

How to cite this publication
Please cite the final published version:


Publication metadata

Title: Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants
Author(s): Yin, X., Jarvie, S., Guo, W.-Y., Deng, T., Mao, L., Zhang, M., Chu, C., Qian, H., Svenning, J.-C., & He, F.
Journal: Global Ecology and Biogeography
DOI/Link: https://doi.org/10.1111/geb.13360

This is the peer reviewed version of the following article: Yin, X., Jarvie, S., Guo, W.-Y., Deng, T., Mao, L., Zhang, M., Chu, C., Qian, H., Svenning, J.-C., & He, F. (2021). Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants. Global Ecology and Biogeography, 30, 1990–2003., which has been published in final form at https://doi.org/10.1111/geb.13360. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be

General Rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognize and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the public portal.

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

If the document is published under a Creative Commons license, this applies instead of the general rights.

This coversheet template is made available by AU Library
Version 2.0, December 2017
enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley’s version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

General Rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognize and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

If the document is published under a Creative Commons license, this applies instead of the general rights.
Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants

Xue Yin¹,², Scott Jarvie²,³,⁴, Wen-Yong Guo²,³,⁵, Tao Deng⁶, Lingfeng Mao⁷, Minhua Zhang⁸, Chengjin Chu¹,*, Hong Qian⁹, Jens-Christian Svenning²,³, Fangliang He⁸,¹⁰

¹ State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou, 510275, China
² Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus, DK-8000, Denmark
³ Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus, DK-8000, Denmark
⁴ Otago Regional Council, Dunedin 9016, New Zealand
⁵ School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China
⁶ CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, 650201, China
⁷ Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and the Environment, Nanjing Forestry University, Nanjing, 210037, China
⁸ ECNU-Alberta Joint Lab for Biodiversity Study, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, East China Normal University, Shanghai, 200241, China
⁹ Research and Collections Center, Illinois State Museum, Springfield, IL 62703, USA
Acknowledgements

We thank Wolf Eiserhardt, Haibin Yu and Yonghua Zhang for discussions on phylogeny, Wang Li for assistance with spatial calculations, and Emilio Berti, Ming Ni and Wubing Xu for discussion about ecological niche models. We acknowledge support from Sun Yat-sen University, East China Normal University, China Scholarship Council (to XY), National Natural Science Foundation of China (31925027, 31622014 and 31570426 to CC), and the Natural Sciences and Engineering Research Council of Canada (FH). LM was supported by Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000), National Natural Science Foundation of China (31870506), Natural Science Foundation of Jiangsu Province (BK20181398). TD acknowledges financial support from the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0502), the Youth Innovation Promotion Association of Chinese Academy of Sciences (2019382), the Young Academic and Technical Leader Raising Foundation of Yunnan Province (2019HB039). JCS and WYG acknowledge financial support from the Danish Council for Independent Research | Natural Sciences to the TREECHANGE project (Grant 6108-00078B to JCS), and JCS and SJ acknowledge support from the Carlsberg Foundation through the Semper Ardens project MegaPast2Future (grant CF16-0005 to JCS). JCS also considers this work as a contribution to his VILLUM Investigator project “Biodiversity Dynamics in a
"Changing World” funded by VILLUM FONDEN (grant 16549).

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

Running title: Niche conservatism in disjunct plants

Abstract

Aim: The plant species sharing ancestors now disjunctly distributing 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.

Method: 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 $D$, that has a 0–1 range, based on species occurrence and climate of species’ native ranges. To obtain projected distributions, species’ niche was projected to the non-native region by 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: 0.124, 0.211 and 0.109 for all, herbaceous and woody species, respectively. 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
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, Lavin, & Oliveira-Filho, 2009; Pennisi, 2005). A long 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 Paleogene and Neogene, and migrated via the Bering and North Atlantic land bridges between Eurasia and Europe (Tiffney, 1985a; Wen, 1999; Wen, Ickert-Bond, Nie, & Li, 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, i.e., the tendency of lineages to retain niches and ecological characters of ancestors over evolutionary time (Pearman, Guisan, Broennimann, & Randin, 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 differed 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 with older clade organisms (Qian, Zhang,
Zhang, & Wang, 2013; Rosenzweig, 1995; Wiens et al., 2010; Wiens & Donoghue, 2004).
Organisms in climatically relatively stable regions (e.g., tropical regions) generally have
higher survival possibilities (Hawkins, Rodriguez, & Weller, 2011; Kerkhoff, Moriarty, &
Weiser, 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
conserved nature and general rules of adaption 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, Godsoe, Rodríguez-Sánchez, Wang, & Warren, 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; M. 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 with phylogenetic distances could be considered as a ‘phylogenetic signal’ for the conserved niche. Such evidence have been found in broad-scale plant families (Su et al., 2020) and for a small number of species (Burns & Strauss, 2011), which used richness and germination rates to represent the niche, respectively. Similarly, resemblances in distributions of closely related taxa can work as a proxy to examine niche conservatism, i.e., if the resemblances are negatively related with phylogenetic distances (Anacker & Strauss, 2014). Peterson et al. (1999) proposed ‘reciprocal comparison’ for sister taxon pairs, where ecological niches of one species were used to predict 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, Soberón, & Sánchez-Cordero, 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, Ervine, &
Barney, 2018; Broennimann et al., 2012; Warren, Glor, & Turelli, 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, Spaeth, & Li, 2009; Warren, Glor, & Turelli, 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: 1) To what degree niches are conserved among closely related species within the EAS–ENA plant disjunction; (2) Whether species of different growth forms, i.e., 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 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 Fig.1): (1) selecting intercontinental congeneric pairwise
species which contains one EAS species and one ENA species, based on a phylogenetic tree 
(see Supporting Information Appendix S1 for details), (2) fitting and evaluating the ENMs 
using species occurrence and climate data through reciprocal comparison, and (3) quantifying 
niche overlaps and examining their relationships with divergence times of pairwise species.

2.1 | Study area

Following previous studies (Qian, Jin, & Ricklefs, 2017; Qian & Ricklefs, 2000, 2004; Wen 
et al., 2010), we used eastern China to represent eastern Asia (EAS), while southeastern 
Canada and the eastern part of the United States constituted eastern North America (ENA) 
(Fig. 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 shared similarities in decreasing gradients of temperature and 
precipitation from southeast to northwest (Mearns et al., 2009; Qin, Ding, & Mu, 2016), 
resulting from similar latitudinal and longitudinal ranges, comparable geographic locations 
with east coasts facing large oceans (Fig. 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, Yu, & Ma, 2007). For species in ENA, local distribution data at the county levels were collected from botanical publications (Qian, Fridley, & Palmer, 2007) and the USDA Plants database (https://plants.usda.gov/java/), 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 100×100 km grid cells under the Behrman cylindrical equal-area projection. The centroids of grids were considered as species presence data. To yield robust projections (see methods below for details) (Stockwell & Peterson, 2002; Wisz et al., 2008), only species with greater than 20 presence records were used. The final plant list included 48 genera, containing 283 and 91 species in EAS and ENA, respectively. The 20-presense-records-threshold used in our study meets the lowest sample size limit suggested in the literature (e.g., Jiménez-Valverde, 2020) to produce 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, California, USA) 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 for model uncertainty, an ensemble approach was used for reciprocal comparisons of the ecological niche for pairwise species (Araújo & New, 2007). Hereafter, we used ENM_EAS and ENM_ENA to represent models trained in EAS or 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, Newell, & White, 2019; Xu et al., 2019). For Maxent, we used 10,000 background points to characterize available environmental conditions (Phillips, Anderson, &
Schapire, 2006; Phillips et al., 2009; Phillips & Dudík, 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, Jiguet,
Albert, & Thuiller, 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, Le
Lay, Helfer, Randin, & Guisan, 2006), and true skill statistics (TSS; Allouche, Tsoar, &
Kadmon, 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 ≤ 0.5 for models being no better than
random expectation to 1.0 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 in to consideration
omission and commission errors, with values ranging from -1 to 1 (Allouche et al., 2006).
Models with TSS being 1 indicate perfect agreement. Specifically, we only included models
in ensemble ENMs where cross-validation with TSS scores were larger than 0.5. The selected
ENMs were ensembled 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
S1 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 (OR10; Pearson et al., 2007). When ENMs were projected to the native regions of counter species, OR10 of trained ENMs was used to generate corresponding binary projected maps (Fig. 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 (Fig. 1). Observed-projected niche overlaps $D_{obs.pro}$ works as complements to the observed niche overlaps $D_{obs}$. Projected-related niche overlaps were generated through reciprocal comparison. Niche overlaps between trained ENMEAS maps and projected ENMENA 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.

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 counter 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 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: the climate-only scenario that used climate variables to define niche spaces of species, and the climate–topography scenario using both climate and topography to calculate species’ niche. 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 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 million years ago (mya) and 26.03 mya, respectively (Fig. S2 in Supporting Information Appendix S3). EAS species *Menispermum dauricum* and ENA congeneric species *M. canadense* had the most recent divergence time of 0.165 mya, while the largest divergence time 56.83 mya were found for paired species in *Magnolia* (Fig. S1 in Supporting Information Appendix S1 and Fig. S2 in Supporting Information Appendix S3). Divergence times of pairwise species for herbaceous plants (14.3 ± 9.7 mya) on average were much younger than those for woody paired species (34.0 ± 21.9 mya).

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 0.216 (Fig. 3a). The mean of $D_{obs}$ for all the disjunct genera was 0.124, which was higher than that for the woody genera (0.109). There
existed no significant differences in values between $D_{\text{obs}}$ and $D_{\text{obs.pro}}$ (Wilcoxon tests, $p > 0.05$). Significantly negative relationships were found for $D_{\text{obs}}$ and $D_{\text{obs.pro}}$ as functions of divergence times of pairwise species within all and herbaceous genera. For all the disjunct genera, the slope of linear regression for $D_{\text{obs}}$ (-0.0010, Fig. 3b) was similar to that for $D_{\text{obs.pro}}$ (-0.0016, Fig. 3c). Regression slopes of the woody genera also shared similarities between $D_{\text{obs}}$ (-0.0002) and $D_{\text{obs.pro}}$ (-0.0011). The smallest slope was -0.0092 for $D_{\text{obs}}$ of herbs. The slopes of entire pairwise species (-0.0010 for $D_{\text{obs}}$ and -0.0016 for $D_{\text{obs.pro}}$, Fig. 3b and c) were in the middle of density plots of slopes of simulated regressions (Fig. S3 in Supporting Information Appendix S3), regardless of sample size.

### 3.3 | Projected-related niche overlaps

Three projected-related niche overlaps $D_{\text{pro.EAS}}$, $D_{\text{pro.ENA}}$ and $D_{\text{pro.both}}$ 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 Fig. 4; Table S1 in Supporting Information Appendix S3). Compared with $D_{\text{pro.both}}$, more paired species with large projected maps were used for projected-related niche overlaps, especially $D_{\text{pro.EAS}}$ (395 and 339 pairwise species for all and woody genera, respectively; see Table S1 in Supporting Information Appendix S3). Intersections of species with large projected maps in EAS or ENA led to fewer pairwise species used for $D_{\text{pro.both}}$ (273 for all the disjunct genera, Table S1 in Supporting Information Appendix S3). Mean values of $D_{\text{pro.EAS}}$ were higher than $D_{\text{pro.ENA}}$ and $D_{\text{pro.both}}$, except for the herbaceous genera (0.422 for $D_{\text{pro.EAS}}$ versus 0.431 for $D_{\text{pro.ENA}}$; Fig. 4). Herbs had higher mean values of projected niche overlaps than those of woody species,
the smallest reaching 0.136 for \( D_{pro.both} \) for woody genera (Fig. 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 (Fig. 4). As divergence times of pairwise species increased, projected-related niche

overlaps for herbs decreased, especially for \( D_{pro.both} \) (slope = -0.0151, Fig. 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, \( p < 0.05 \); Fig. 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 (Figs. 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 Figs. 3 and 4). Previous works claimed niche conservatism on continental scales resulting from physiological limitations to environments (Huntley, Bartlein, & Prentice, 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 dated 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 (Fig. 1a, b). Therefore, the species of the EAS–ENA disjunct genera had high possibilities to result from vicariance and subsequent allopatric speciation caused by orogeny within each continent (Qian & Ricklefs, 2000). Since species’ habitats tend to be restricted to the ancestors’ distributions, certain degree of niche conservatism is expected (Smith et al., 2018; Wiens, 2004; Wiens & Graham, 2005).

Orogeny caused by tectonic activities could 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 mya (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 potential strong allopatric speciation in EAS. Coincidently, we found a high frequency of pairwise species diversified 5-10 mya (Fig. S2 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 patterns (Qian & Ricklefs, 2000; Wen, 1999).

4.2 | Niche conservatism for herbaceous and woody species

Our analysis corroborated the existences 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 (Fig. 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 (Figs. 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, Soltis, Soltis, Manchester, & Crawford, 2000). More importantly, herbs are often equipped with various strategies to cope with freezing cold conditions, e.g., shortening lifespan, 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 favor 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, Mao, Sandel, Swenson, & Svenning, 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 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. $D_{\text{pro.}EAS}$, the projected niche overlap using projected ENM$_{ENA}$ maps and trained ENM$_{EAS}$ maps, had the most pairwise species (395 for $D_{\text{pro.}EAS}$ vs 356 and 273 for $D_{\text{pro.}ENA}$ and $D_{\text{pro.both}}$, respectively; Fig. 4 and Table S1 in Supporting Information Appendix S3). Since a species would only occupy area suitable
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 could not find suitable environmental conditions in the
projected regions, compared with their native environments in trained areas. 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 species’ small niche spaces (Pagel et al., 2020; Slatyer, Hirst, &
Sexton, 2013). Correspondingly, there were more EAS species with no and small projected
ranges than ENA species (Table S2 in Supporting Information Appendix S3), implying that
EAS offers more unique, heterogeneous environmental conditions, which would be absent
from ENA. This finding was strengthened by taking topography into consideration, where
more rugged topography in EAS had greater effects on heterogeneity of environmental niche
than that in ENA (Fig. 2). Wider niches enabled EAS species to separately distribute among
niche axes, promoting coexistences 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, Hedenäs,
Broennimann, Guisan, & Vanderpoorten, 2021; van Proosdij, Sosef, Wieringa, & Raes,
2016). Given this concern would also exists 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 occurrences records less than 30. Most of species within the EAS–ENA disjunct plants have a greater number of occurrence records than the 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 for 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 for the 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 certain 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.

**Data Accessibility 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 (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;
(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).

**References**

models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*,
43(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Anacker, B. L., & Strauss, S. Y. (2014). The geography and ecology of plant speciation:


distributions are strongest in poorly dispersed and highly persistent plant species. 

*Proceedings of the National Academy of Sciences of the United States of America,* 117(7), 3663–3669. https://doi.org/10.1073/pnas.1908684117


Torrey, J., & Gray, A. (1843). A flora of North America: containing abridged descriptions of all the known indigenous and naturalized plants growing north of Mexico, arranged according to the natural system. In *Wiley & Putnam* (Vol. 2). https://doi.org/10.1086/325163


Figure 1 Workflow used in this study. $\text{ENM}_{\text{EAS}}$ and $\text{ENM}_{\text{ENA}}$ represent the ensemble ecological niche models (ENMs) trained in eastern Asia (EAS) and eastern North America (ENA), shown in warm and cold colors, respectively. OR$_{10}$ is an abbreviation for the 10% omission error rate of the evaluation data in ensemble ENMs; see Methods for more details.
Figure 2 Elevation and climates of study areas in EAS and ENA. In (a) and (b), provinces or states are shown, with codes explained in Table S1 of Supporting Information Appendix S1. Colors 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.
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). ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$. 
Figure 4 Relationships between projected-related niche overlaps and divergence times of pairwise species for all, herbaceous and woody genera. Boxplots showed distributions of projected-related niche overlaps. Pink, light yellow and light blue colors represented projected-related species distributions with no, small, and large ranges, respectively (detailed numbers shown in Table S2 of Supporting Information Appendix S3). Mean values of Schoener’s $D$ shown in the pie charts. ‘No’ and ‘small areas’ refers 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 ENM$_{EAS}$ map and projected ENM$_{ENA}$ map (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. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$. 