

## Research paper

## Phylogenetic diversity of eastern Asia–eastern North America disjunct plants is mainly associated with divergence time

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## ABSTRACT

The underlying causes of biodiversity disparities among geographic regions have long been a fundamental theme in ecology and evolution. However, the patterns of phylogenetic diversity (PD) and phylogenetic beta diversity (PBD) of congeners that are disjunctly distributed between eastern Asia–eastern North America (EA–ENA disjuncts) and their associated factors remain unknown. Here we investigated the standardized effect size of PD (SES-PD), PBD, and potentially associated factors in 11 natural mixed forest sites (five in EA and six in ENA) where abundant EA–ENA disjuncts occur. We found that the disjuncts in ENA possessed higher SES-PD than those in EA at the continental scale (1.96 vs –1.12), even though the number of disjunct species in ENA is much lower than in EA (128 vs 263). SES-PD of the EA–ENA disjuncts tended to decrease with increasing latitude in 11 sites. The latitudinal diversity gradient of SES-PD was stronger in EA sites than in ENA sites. Based on the unweighted unique fraction metric (UniFrac) distance and the phylogenetic community dissimilarity, PBD showed that the two northern sites in EA were more similar to the six-site ENA group than to the remaining southern EA sites. Based on the standardized effect size of mean pairwise distances (SES-MPD), nine of eleven studied sites showed a neutral community structure ( $-1.96 \leq \text{SES-MPD} \leq 1.96$ ). Both Pearson's  $r$  and structural equation modeling suggested that SES-PD of the EA–ENA disjuncts was mostly associated with mean divergence time. Moreover, SES-PD of the EA–ENA disjuncts was positively correlated with temperature-related climatic factors, although negatively correlated with mean diversification rate and community structure. By applying approaches from phylogenetics and community ecology, our work sheds light on historical patterns of the EA–ENA disjunction and paves the way for further research.

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## 1. Introduction

Eastern Asia (EA) and eastern North America (ENA) are home to two of the four major temperate forests in the Northern Hemisphere (Donoghue and Smith, 2004). The current floras in both regions are remnants of a formerly continuous temperate forest that spanned the Northern Hemisphere during the early Tertiary (Wolfe, 1975; Tiffney and Manchester, 2001). This continuous forest was ultimately fragmented by multiple processes through

geological time, including mountain building, desertification, and glaciation. From the time of Linnaeus to the present, the remarkable affinity of the EA and ENA floras has fascinated naturalists, evolutionary biologists, and ecologists, including Charles Darwin and Asa Gray (Li, 1952; Spongberg and Boufford, 1983; Qian, 2002; Wen et al., 2010). Approximately 65 seed plant genera are disjunctly distributed between EA and ENA, and these genera are referred to as 'EA–ENA disjuncts' (Wen, 1999). In EA, most EA–ENA disjuncts inhabit the Sino-Japanese forest (in the strict sense following Wu, 1998), whereas in ENA, EA–ENA disjuncts are more likely to be found in mixed forests along the Appalachian Mountains, but may occur in the Piedmont and Coastal Plain as well (Ying and Boufford, 1998; Milne and Abbott, 2002).

Although a high degree of overall similarity between the floras of EA and ENA has been well documented (Gray, 1878; Li, 1952), for the EA–ENA disjuncts, higher species richness is typically found in EA than in ENA (Wen, 1999; Xiang et al., 2004). This pattern has been referred to as the species diversity anomaly (Li, 1952; Qian and Ricklefs, 2000; Xiang et al., 2004), yet few explanations of this anomaly have been rigorously tested. Some have suggested that floristic regions in EA possess more complex habitats, larger spans of vegetational continuity, and more connections with tropical floristic elements than those in ENA (Wen, 1999; Milne and Abbott, 2002). Moreover, a higher rate of molecular evolution in EA has been proposed to be tightly linked to the species diversity anomaly in the EA–ENA disjuncts (Xiang et al., 2004), although recent work indicates that such a pattern does not hold for all disjunct genera (Melton et al., 2020).

In addition to species richness, phylogenetic diversity (PD; Faith, 1992) has been suggested as a complementary measurement for gauging biodiversity at the local and regional levels (Faith, 1992; Forest et al., 2007; Thuiller et al., 2011; Wang et al., 2013). However, PD will be positively correlated with species richness unless the tips have zero branch length or the ancestor of a tip has already been sampled, an observation made by various researchers (e.g., Lu et al., 2018; Allen et al., 2019). In this case, the standardized effect size of PD (SES-PD) has been proposed to estimate the difference between the observed PD and the expected PD (Webb et al., 2008; Mishler et al., 2014); this has become an increasingly popular measure (e.g., Speed et al., 2019; Aguilar-Tomasini et al., 2021). Research on inter-community phylogenetic dissimilarity, i.e., phylogenetic beta diversity (PBD), is also an important advance that permits a better understanding of how evolutionary and ecological factors shape current biodiversity (Webb et al., 2002; Hardy and Senterre, 2007; Graham and Fine, 2008). In a general sense, PBD is the phylogenetic distance between individual organisms between any two studied sites (Graham and Fine, 2008). For EA–ENA disjuncts, despite longstanding research interest in evolutionary biology and biogeography, no attempts have been made to examine SES-PD or PBD patterns across the disjunction. Some studies have reported regional PD in EA or ENA separately or have compared PD among sites between the two continents (e.g., Qian et al., 2017), but none emphasized the EA–ENA disjuncts.

The integration of community ecology with phylogenetics enables the interpretation of biodiversity patterns and the tracing of community assembly in an evolutionary context (Webb et al., 2002; Emerson and Gillespie, 2008; Graham and Fine, 2008). The standardized effect size of mean pairwise distances (SES-MPD, or  $-1$  times the Net Relatedness Index) and the standardized effect size of mean nearest taxon distances (SES-MNTD, or  $-1$  times the Nearest Taxon Index) quantify the distribution of taxa in a sample relative to a species pool based on a null model (Webb, 2000; Webb et al., 2002), permitting inferences about possible processes of community assembly (Webb et al., 2002; Vamوسي et al., 2009; Graham et al., 2018; Ramm et al., 2018). Employing these community ecology

approaches can further facilitate our investigation of PD patterns in EA–ENA disjuncts.

Several studies indicate that multiple factors, including climatic factors, diversification rate, divergence time, and community structure, can all play interconnected roles in shaping diversity patterns (e.g., Qian et al., 2015; Rao et al., 2018; Shrestha et al., 2018). The well-known latitudinal diversity gradient hypothesis, i.e., that diversity decreases from the equator to the poles (Rosenzweig, 1995; Mittelbach et al., 2007), has received significant attention (Wiens and Donoghue, 2004; Donoghue, 2008; Wang et al., 2010; Condamine et al., 2012; Kissling et al., 2012; Kerkhoff et al., 2014). However, few studies have attempted to test the latitudinal diversity gradient hypothesis in different floristic components, particularly with a focus on the EA–ENA disjuncts. In addition, to our knowledge, no previous study has attempted to explore the correlation between PD and either diversification rate or divergence time. Thus, the EA–ENA disjunction provides the opportunity to explore the relative roles of climatic factors, diversification rate, divergence time, and community structure in impacting SES-PD patterns in the context of ancient historical connections between forests in EA and ENA.

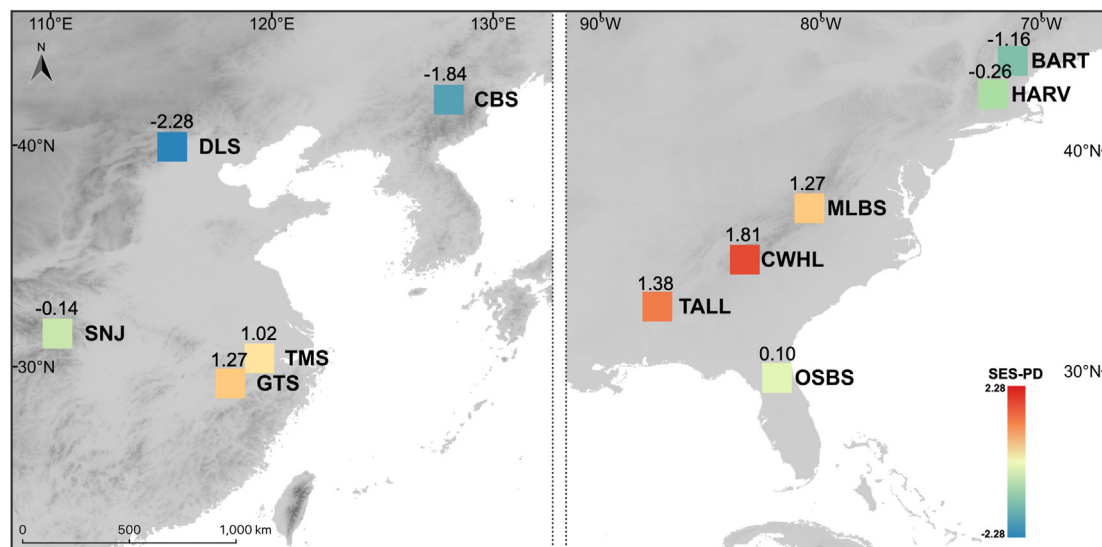
Within the regions of the Sino-Japanese forests of EA and the deciduous forests of ENA, where most EA–ENA disjuncts occur, we selected 11 mixed mesophytic forest sites (five in EA and six in ENA) as our study system. These sites contain significant community components of the EA–ENA disjuncts (263 spp. from 61 genera in EA and 128 spp. from 55 genera in ENA) and span a similar latitudinal range (EA: 29.24°–42.06° N; ENA: 29.69°–44.06° N). In the present study, we aim to 1) examine SES-PD and PBD patterns of the EA–ENA disjuncts and the community structure of 11 forests, and 2) investigate which factors played major roles in impacting contemporary SES-PD patterns observed in EA–ENA disjuncts.

## 2. Materials and methods

### 2.1. Compilation of species lists

Eleven mixed forest sites were selected for the present study. The EA sites, from south to north, are Gutianshan (GTS), Tianmushan (TMS), Shennongjia (SNJ), Donglingshan (DLS), and Changbaishan (CBS) (Fig. 1). All EA sites are nature reserves in China. The ENA sites, from south to north, are Ordway-Swisher Biological Station (OSBS), Talladega National Forest (TALL), Coweeta Hydrologic Laboratory (CWHL), Mountain Lake Biological Station (MLBS), Harvard Forest (HARV), and Bartlett Experimental Forest (BART) (Fig. 1); all ENA sites except CWHL are part of the National Ecological Observatory Network (NEON) system (<https://www.neonscience.org/about-neon-field-sites>). All 11 sites are located in protected areas and represent natural ecosystems.

Given that plant specimen records remain incomplete in public databases for EA sites and few ENA sites had complete species checklists, we compiled lists of seed plant species for each site as follows. For EA sites, a checklist of all seed plant species for each site was obtained from the relevant literature (Lou and Jin, 2000; Fu, 2002; Liu, 2007; Ding, 2010; Zhou, 2010). For the ENA sites, seed plant species lists for OSBS, TALL, CWHL, and HARV were generated from voucher specimens housed at the University of Florida Herbarium (FLAS; <https://www.floridamuseum.ufl.edu/herbarium>), a floristic database (Jenkins and Motzkin, 2009) for HARV, and published local floras from the 1980s (Beckett and Golden, 1982). For MLBS and BART, we downloaded the shapefiles of polygons from the MLBS official website resources (<https://mlbs.virginia.edu/maps>) and NEON (<https://www.neonscience.org/field-sites/bart>), respectively. Then, we queried the Global Biodiversity Information Facility database (GBIF; <https://www.gbif.org>) and the Integrated Digitized



**Fig. 1.** Standardized effect size of phylogenetic diversity (SES-PD) of EA–ENA disjuncts among 11 seed plant communities. GTS: Gutianshan; TMS: Tianmushan; SNJ: Shennongjia; DLS: Donglingshan; CBS: Changbaishan; OSBS: Ordway-Swisher Biological Station; TALL: Talladega National Forest; CWHL: Coweeta Hydrologic Laboratory; MLBS: Mountain Lake Biological Station; HARV: Harvard Forest; BART: Bartlett Experimental Forest.

Biocollections repository (iDigBio; <https://www.idigbio.org>) with these two polygons using the R packages ‘spocc’ (Chamberlain, 2018) and ‘ridigbio’ (Michonneau et al., 2016). We identified all seed plants within the two polygons using the R packages ‘sp’ (Pebesma and Bivand, 2005; Bivand et al., 2013), ‘spocc’ and ‘wicket’ (Keyes, 2017), as well as QGIS software (QGIS Development Team, 2019). All names in the resulting species lists for each site were validated and reconciled via The Plant List (<http://www.theplantlist.org>) using the R package ‘Taxonstand’ (Cayuela et al., 2019). Finally, all species names for the 11 sites resolved from the procedures above were compiled as a complete species list for all sites with duplicates removed, which resulted in 5306 unique seed plant names as the total species pool for EA–ENA disjuncts.

## 2.2. Community phylogeny reconstruction

To ensure that the SES-PD values for EA–ENA disjuncts across 11 sites originated from the same phylogenetic framework, we sub-setted the broadly inclusive dated seed plant phylogeny from Smith and Brown (2018) via functions from Phyx (Brown et al., 2017) and OpenTree PY Toys ([https://github.com/blackrim/opentree\\_pytoys](https://github.com/blackrim/opentree_pytoys)) based on the complete species list with 5306 unique names generated above, following the procedures mentioned in Allen et al. (2019), Jantzen et al. (2019), and Li et al. (2019). The final cleaned, dated tree with 5306 seed plant species from all 11 sites was used for all the analyses in this study. The branch length of this 5306-tip tree is in units of time (million years, Myr), and the clades containing the EA–ENA disjunct species are fully bifurcated.

## 2.3. Calculation of SES-PD and PBD and inference of community structure

Two matrices were generated for SES-PD calculation of the EA–ENA disjuncts: one at the continental level and the other at the site level. For both matrices, species were scored either as EA–ENA disjuncts [1] or not [0] based on the EA–ENA disjunct genera list from Wen (1999). SES-PD was calculated from the observed PD based on a null model that randomized the tip labels of the phylogeny 999 times as  $[\text{SES-PD} = (\text{PD}_{\text{observed}} - \text{PD}_{\text{randomized}}) / \text{sd} \text{PD}_{\text{randomized}}]$  using the R package ‘picante’ (Kembel et al., 2010).

Further, in order to test the latitudinal diversity gradient hypothesis, we calculated the Pearson correlation coefficients (Pearson’s  $r$ ) between SES-PD and latitude using the R package ‘stats’ (R Core Team, 2018).

For PBD, based on the species list of the EA–ENA disjuncts at the site level generated above, we calculated both the unweighted unique fraction metric (UniFrac) distance and the phylogenetic community dissimilarity (PCD), given that the statistical power of different metrics may differ under different scenarios (Ives and Helmus, 2010). The UniFrac distance can be calculated as the sum of the branch lengths two communities share on a phylogenetic tree. If two communities shared no common species, and their clades are separate and only joined at the base of the phylogenetic tree, the UniFrac distance would reach its maximum (Lozupone and Knight, 2005). Meanwhile, PCD can be partitioned into two components, the first is a nonphylogenetic component that reflects shared species between communities, and the second comprises a phylogenetic component that shows the evolutionary relationships among non-shared species (Ives and Helmus, 2010). The unweighted UniFrac distance between communities was calculated using the R package ‘picante’ with the ‘unifrac’ function, and PCD was calculated using the R package ‘phyr’ with the ‘pcd’ function (Li et al., 2020).

The inference of community structure was based on the complete seed plant species list for each site. Compared to other indexes, SES-MPD (the standardized effect size of mean pairwise distances, or  $-1$  times the Net Relatedness Index) may better demonstrate overall community structure (Kress et al., 2009; Graham et al., 2018). Hence, SES-MPD was used for interpreting community structure in this study. SES-MPD was calculated under the same null model with SES-PD as  $[\text{SES-MPD} = (\text{MPD}_{\text{observed}} - \text{MPD}_{\text{randomized}}) / \text{sd} \text{MPD}_{\text{randomized}}]$  via the R package ‘picante’ (Kembel et al., 2010). All calculations were based on the phylogenetic tree with 5306 tips as described above.

## 2.4. Assembly of climatic data

To investigate whether and how climatic factors relate to SES-PD patterns at the 11 studied sites, we downloaded 19 bioclimatic variables from 1970 to 2000 from the WorldClim database version 2 (Fick and Hijmans, 2017; <http://www.worldclim.org/>) with the

finest resolution (30 arc-seconds spatial resolution, ~1 km at the equator). The 11 sites were divided into 1 km × 1 km grids to fit the resolution of climatic data. Values of bioclimatic variables were extracted based on the centroids of each grid cell using the R packages ‘raster’ (Hijmans, 2019), ‘rgdal’ (Bivand et al., 2019), and ‘sp’ (Pebesma and Bivand, 2005; Bivand et al., 2013). Values of bioclimatic variables were standardized (mean to 0 and standard deviation to 1) in R (R Core Team, 2018) before downstream analyses. To avoid multicollinearity among the 19 variables, we performed a principal component analysis (PCA) using the R package ‘stats’ (R Core Team, 2018) to extract the first and the second principal components (PC1 and PC2) of the climatic variables.

### 2.5. Inference of divergence time and diversification rate

We inferred the divergence time and the diversification rate of the EA–ENA disjuncts based on the dated tree with 5306 tips as described above. For the divergence time, we summarized the species tip age, each of which was determined by the age of the closest node defined by the most recent common ancestor (MRCA) based on any given species tips in the final tree (also see Sun et al., 2020). Then, the mean tip age (mean divergence time) was summarized for the EA–ENA disjuncts at each site. For the

**Table 1**  
A summary of frequently-used acronyms in the present study.

Acronym	Full Name
EA	eastern Asia
ENA	eastern North America
SES-PD	the standardized effect size of phylogenetic diversity
PBD	phylogenetic beta diversity
PCD	the phylogenetic community dissimilarity
UniFrac	the unique fraction metric
SES-MPD	the standardized effect size of mean pairwise distances
CBS	Changbaishan
DLS	Donglingshan
SNJ	Shennongjia
TMS	Tianmushan
GTS	Gutianshan
BART	Bartlett Experimental Forest
HARV	Harvard Forest
MLBS	Mountain Lake Biological Station
CWHL	Coweeta Hydrologic Laboratory
TALL	Talladega National Forest
OSBS	Ordway-Swisher Biological Station

**Table 2**  
Biological and geographic attributes of the EA–ENA disjuncts in 11 studied forest sites.

Region	Site	Species richness (total)	Area (km <sup>2</sup> )	Longitude (°) (centroid)	Latitude (°) (centroid)	SES-PD	SES-MPD	Mean DR (species/Myr)	Mean DT (Myr)
EA	–	263 (3666)	–	–	–	–1.12	0.05	0.18	9.33
ENA	–	128 (1850)	–	–	–	1.96	–0.67	0.14	11.04
EA	CBS	46 (1140)	1962.19	128.00	42.06	–1.84	–1.28	0.29	6.38
EA	DLS	34 (773)	301.73	115.50	39.93	–2.28	0.29	0.34	4.98
EA	SNJ	141 (1559)	732.4	110.31	31.49	–0.14	0.63	0.16	9.47
EA	TMS	108 (1188)	43.33	119.44	30.37	1.02	0.94	0.19	9.49
EA	GTS	99 (1209)	96.87	118.13	29.24	1.27	0.66	0.17	10.63
ENA	BART	21 (72)	15.72	–71.29	44.06	–1.16	4.79 <sup>b</sup>	0.10	9.46
ENA	HARV	59 (803)	11.08	–72.17	42.54	–0.26	0.71	0.11	8.26
ENA	MLBS	28 (153)	2.32	–80.52	37.38	1.27	1.75	0.09	12.35
ENA	CWHL	56 (588)	16.25	–83.45	35.05	1.81	–1.90	0.14	11.61
ENA	TALL	56 (352)	1330.64	–87.42	32.92	1.38	0.03	0.13	14.18
ENA	OSBS	31 (642)	37.89	–81.99	29.69	0.10	–2.04 <sup>a</sup>	0.17	11.59

The total species number of each forest site is reported in brackets; SES-PD: standardized effect size of phylogenetic diversity; SES-MPD: standardized effect size of mean phylogenetic distance; DR: diversification rate; DT: divergence time; Myr: million years.

CBS: Changbaishan; DLS: Donglingshan; SNJ: Shennongjia; TMS: Tianmushan; GTS: Gutianshan; BART: Bartlett Experimental Forest; HARV: Harvard Forest; MLBS: Mountain Lake Biological Station; CWHL: Coweeta Hydrologic Laboratory; TALL: Talladega National Forest; OSBS: Ordway-Swisher Biological Station.

<sup>a</sup> denotes significant phylogenetic clustering.

<sup>b</sup> denotes significant phylogenetic over-dispersion.

diversification rate, we employed the ‘DR statistic’ (Jetz et al., 2012), one of the most widely used semi-parametric approaches for diversification rate estimation (e.g., Harvey et al., 2017; Title and Rabosky, 2019; Sun et al., 2020). The ‘DR statistic’ quantifies the ‘splitting rate’ from each extant species to the tree root as a model-free estimate of the diversification rate. Specifically, it is the sum of the inverse of the branch lengths subtending a particular tip and reflects the number of splitting events subtending each tip on a phylogenetic tree. Our method and script followed those described in Jetz et al. (2012) and Harvey et al. (2017).

### 2.6. Correlations between SES-PD and its potential associated factors

Structural equation modeling has been applied to evaluate the factors that impact observed diversity patterns (Qian et al., 2015; Shrestha et al., 2018). Here, we generated a simple path model by assuming that climatic factors (approximated by the PC1 of the 19 bioclimatic variables), community structure (approximated by the SES-MPD), diversification rate (approximated by the mean DR statistic), and divergence time (approximated by mean divergence time) have potential associations with SES-PD. The structural equation modeling path analysis was performed using the R package ‘lavaan’ (Rosseel, 2012), and the path diagram plot was generated using the R package ‘semPlot’ (Epskamp, 2015). In addition, we calculated and plotted the pairwise Pearson’s *r* among these indexes using the R package ‘GGally’ (<https://ggobi.github.io/ggally/>). Values of each index were standardized (mean to 0 and standard deviation to 1) in R.

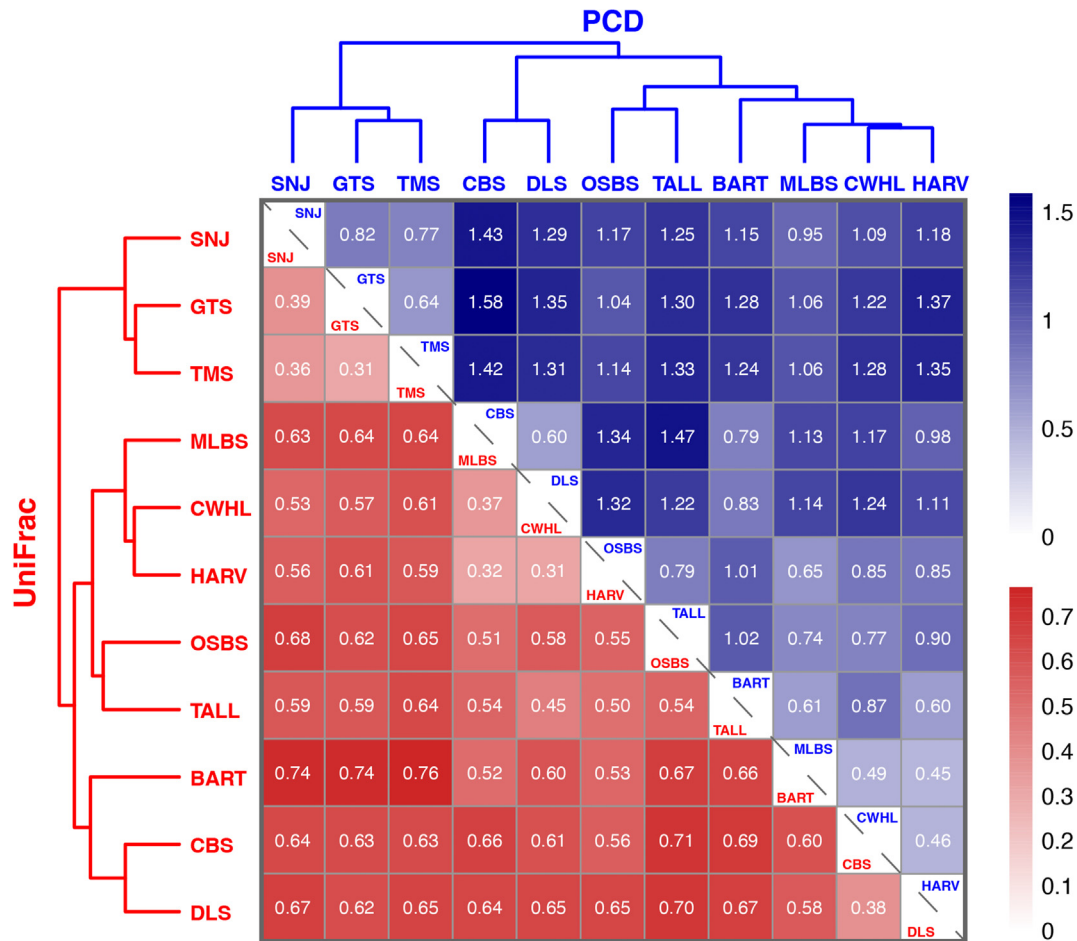
## 3. Results

### 3.1. A review of acronyms

To ensure the general readability of the Results and Discussion, we have listed the frequently-used acronyms here (Table 1).

### 3.2. SES-PD and PBD of the EA–ENA disjuncts

At the continental level, SES-PD of the EA–ENA disjuncts was greater in ENA than in EA, despite the fact that more disjunct species were documented in EA (SES-PD: 1.96 in ENA vs –1.12 in EA; species number: 128 in ENA vs 263 in EA; Table 2). Across the 11



**Fig. 2.** Phylogenetic beta diversity (PBD) of EA–ENA disjuncts among 11 forest sites based on the phylogenetic community dissimilarity (PCD; blue) and the unweighted UniFrac distance (red). GTS: Gutianshan; TMS: Tianmushan; SNJ: Shennongjia; DLS: Donglingshan; CBS: Changbaishan; OSBS: Ordway-Swisher Biological Station; TALL: Talladega National Forest; CWHL: Coweeta Hydrologic Laboratory; MLBS: Mountain Lake Biological Station; HARV: Harvard Forest; BART: Bartlett Experimental Forest. Warmer color in the heatmap indicates higher dissimilarity between sites.

sites, SES-PD of the EA–ENA disjuncts generally tended to decrease with increasing latitude (Fig. 1 and Table 2), showing an overall latitudinal diversity gradient (Pearson’s  $r = -0.640$ ,  $p$ -value < 0.05). In five EA sites, the latitudinal diversity gradient was clear, with SES-PD decreasing from the southern sites to the northern sites (Pearson’s  $r = -0.952$ ,  $p$ -value < 0.05); in contrast, such a pattern was not strongly supported in six ENA sites (Pearson’s  $r = -0.591$ ,  $p$ -value > 0.05). However, a significant latitudinal diversity gradient of SES-PD was observed in ENA with the exclusion of the OSBS site (Pearson’s  $r = -0.934$ ,  $p$ -value < 0.05) (Fig. 1).

Of the 11 sites, the EA–ENA disjuncts showed the highest SES-PD at the CWHL site (SES-PD: 1.81, hereafter), while the lowest SES-PD was found in the DLS site (–2.28; Fig. 1). In EA, SES-PD of the EA–ENA disjuncts ranged from –2.28 (DLS, the second-most northern site) to 1.27 (GTS, the most southern site), whereas that in ENA ranged from –1.16 (BART, the most northern site) to 1.81 (CWHL; Fig. 1).

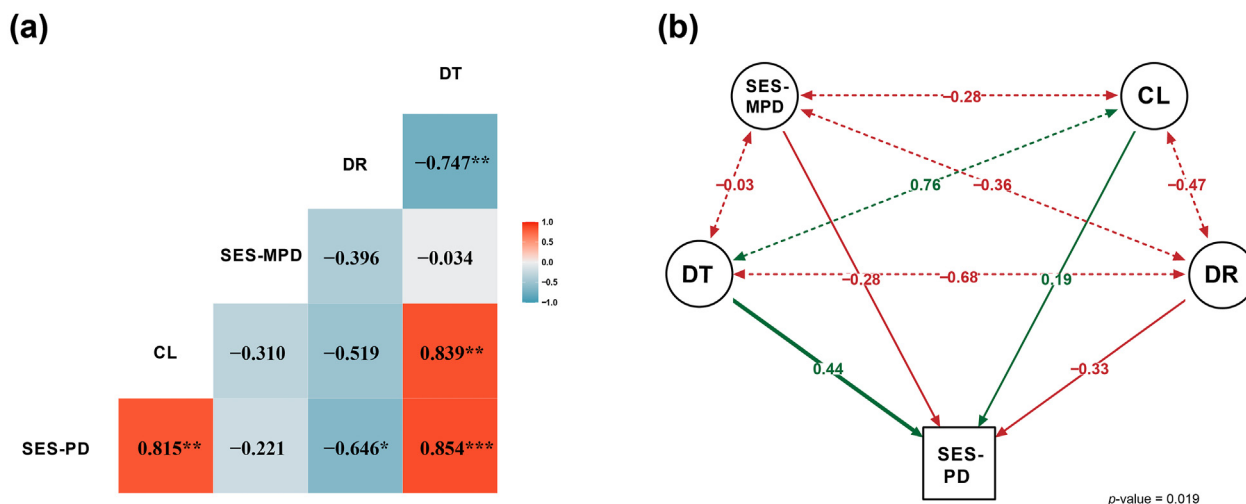
Overall, PBD in EA sites increased with increasing latitude span, but this pattern was not clearly observed in ENA sites (Fig. 2). For EA sites, the three southern sites (SNJ, TMS, and GTS) formed a group, while the two northern sites (CBS and DLS) formed another group. In ENA, the six sites formed a group in the distance-based dendrogram (Fig. 2). The ENA sites OSBS and TALL formed a cluster, as did MLBS, CWHL, and HARV. The results of both PCD and unweighted UniFrac analyses showed that the two northern sites (CBS and DLS) in EA

were much more similar to the six-site ENA group than to the remaining EA sites (SNJ, TMS, and GTS; Fig. 2). However, the arrangement of the groups in the ENA sites + (CBS + DLS) cluster differed between the two analyses (Fig. 2).

### 3.3. Divergence time, diversification rate, and community structure

We observed an older mean divergence time in ENA compared to that in EA at the continental level (mean: 11.04 vs 9.33 Myr;  $t = -1.0511$ ,  $df = 210.47$ ,  $p$ -value = 0.2944; Table 2). At the site level, the mean divergence time varied from 4.98 Myr (DLS) to 10.63 Myr (GTS) in EA and from 8.26 Myr (HARV) to 14.18 Myr (TALL) in ENA. The mean diversification rates of EA–ENA disjuncts were greater in EA than in ENA at the continental level (mean: 0.18 vs 0.14 species/Myr;  $t = 1.4882$ ,  $df = 324.83$ ,  $p$ -value = 0.1377; Table 2). At the site level, the mean diversification rate varied from 0.16 (SNJ) to 0.34 (DLS) species/Myr in EA and from 0.10 species/Myr (BART) to 0.17 species/Myr (OSBS) in ENA (Table 2).

At the continental level, the mixed mesophytic forest sites analyzed here showed no significant trends toward either phylogenetic over-dispersion or clustering in EA or ENA based on SES-MPD (0.05 in EA; –0.67 in ENA; Table 2). At the site level, nine of the 11 studied sites showed neutral community structures ( $-1.96 \leq \text{SES-MPD} \leq 1.96$ ), similar to the results at the continental level (Table 2). However, two exceptions were observed: 1) the



**Fig. 3.** Pairwise Pearson correlations (a) and path diagrams (b) illustrating the associations among climatic factors (CL, approximated by the PC1 of 19 bioclimatic variables), mean diversification rate (DR), mean divergence time (DT), community structure (approximated by the standardized effect size of mean phylogenetic distance, SES-MPD), and the standardized effect size of phylogenetic diversity (SES-PD) of the EA–ENA disjuncts. (a) Pairwise Pearson correlation coefficients are reported with significance. \*:  $p$ -value < 0.05; \*\*:  $p$ -value < 0.01; \*\*\*:  $p$ -value < 0.001. (b) The numbers in lines are standardized path coefficients. Solid lines indicate associations between the dependent and independent variables, while dashed lines indicate those among independent variables. Green lines indicate positive path coefficients while red lines indicate negative path coefficients. Bold lines highlight the most predictive factors.

BART site showed significant phylogenetic over-dispersion (SES-MPD = 4.79), and 2) the OSBS site showed significant phylogenetic clustering (SES-MPD = -2.04).

### 3.4. Relative importance of factors associated with SES-PD patterns

The PCA results showed that 48.60% of the total variation could be explained by temperature-related bioclimatic variables of PC1, which included the following top five contributing variables: mean temperature of the coldest quarter (BIO11; 9.99%), mean temperature of the driest quarter (BIO9; 9.87%), minimum temperature of the coldest month (BIO6; 9.61%), annual mean temperature (BIO1; 9.36%), and temperature seasonality (BIO4; 8.81%) (Fig. S1).

Pearson's  $r$  and the results of the structural equation modeling analysis suggested identical relationships between SES-PD of the EA–ENA disjuncts and their associated factors (Fig. 3). Across 11 sites, SES-PD of the EA–ENA disjuncts was strongly and positively correlated with divergence time (Pearson's  $r = 0.854$ ,  $p$ -value < 0.001; standardized path coefficients = 0.44, model  $p$ -value = 0.019) and temperature-related climatic factors (Pearson's  $r = 0.815$ ,  $p$ -value < 0.01; standardized path coefficients = 0.19), but negatively correlated with diversification rate (Pearson's  $r = -0.646$ ,  $p$ -value < 0.05; standardized path coefficients = -0.33) and community structure (Pearson's  $r = -0.221$ , not significant; standardized path coefficients = -0.28) (Fig. 3). Of the four factors tested, divergence time was most strongly associated with SES-PD of the EA–ENA disjuncts as suggested by both Pearson's  $r$  and the standardized path coefficients of structural equation modeling, which is in accordance with a general observation that younger mean divergence time corresponds to lower values of SES-PD (Table 2). For example, with the lowest value of SES-PD among 11 sites (-2.28), the mean divergence time of the EA–ENA disjuncts in DLS was 4.98 Myr, which was also the lowest among sites, while the EA–ENA disjuncts had the greatest SES-PD in CWHL (1.81) with a mean divergence time of 11.61 Myr (Table 2 and Fig. 1).

## 4. Discussion

Our study sites and sampling scheme constitute a study system that is well-suited to answering fundamental questions about the

underlying patterns and associated factors of SES-PD and PBD of the EA–ENA disjuncts. In contrast to the well-documented species diversity anomaly in the EA–ENA disjuncts (e.g., Qian and Ricklefs, 2000), which is reflected in the species numbers across our sampled sites (263 species in EA vs 128 in ENA), this anomaly did not extend to SES-PD. Higher species richness in EA for EA–ENA disjuncts has been attributed to higher rates of speciation in EA (Xiang et al., 2004), which would result in shorter branches. In accordance with this hypothesis, we found a higher mean diversification rate in EA, which may account for the lower SES-PD of the EA–ENA disjuncts in EA sites (Table 2). On the other hand, divergence time can be important in shaping patterns of PD, given that recent divergences are reflected in short branch lengths, which will lead to low values of PD. A previous study indicated that eastern China represents a floristic museum, where angiosperm lineages are older than those in other regions of China, and divergence times for angiosperm lineages in China decrease from southeastern to northwestern (Lu et al., 2018); this pattern is consistent with our observations (Table 2). Here, we had a novel finding, i.e., SES-PD of the EA–ENA disjuncts across 11 studied sites was strongly positively correlated with divergence time (Fig. 3). Given that the phylogenetic tree was dated and that branch length is proportional to divergence time, we interpret the higher SES-PD value for ENA than for EA to result from the longer branches (which means lineages underwent longer evolutionary time with lower diversification rate) of ENA species compared to EA in the tree (Fig. 3).

In addition to divergence time and divergent rate, community structure and climatic factors also showed certain correlations with the SES-PD of EA–ENA disjuncts (Fig. 3). Based on SES-MPD (and interpretations outlined in Webb et al. (2002)), all of the mixed forest sites examined in EA and four of the six sites from ENA have undergone nearly neutral community assembly; and a neutral community structure was also found at the continental level (Table 2). This finding implies that the seed plants were randomly recruited from local species pools in those natural ecosystems, which is also coincident with the weak correlation between community structure and the SES-PD (Pearson's  $r = -0.221$ , not significant). Moreover, temperature-related climatic factors were strongly correlated with SES-PD (Pearson's  $r = 0.815$ ,  $p$ -value < 0.01), suggesting that SES-PD of the EA–ENA disjuncts may have

been constrained by certain climatic conditions. A recent study revealed a negative correlation between climatic niche overlap and divergence times within the EA–ENA disjuncts, which also supports niche conservatism among those congeneric species pairs (Yin et al., 2021).

Our finding that EA–ENA disjuncts exhibit a general phylogenetic latitudinal diversity gradient, with SES–PD decreasing along an increasing latitude, agrees with large-scale PD studies in EA, but not in ENA (Fig. 1; Qian et al., 2017; Hu et al., 2022). Mishler et al. (2020) examined spatial phylogenetic patterns in seed plants across North America and reported significantly low PD across the continent. All previous studies (Qian et al., 2017; Mishler et al., 2020; Hu et al., 2022) rejected a clear phylogenetic latitudinal diversity gradient in ENA. However, none of these studies considered the EA–ENA disjuncts separately from the total plant species in studied sites or grids. Our results, compared with those of Qian et al. (2017), Mishler et al. (2020) and Hu et al. (2022), suggest that the EA–ENA disjuncts have their unique signatures in PD patterns of EA–ENA disjuncts, even though the phylogenetic latitudinal diversity gradient of SES–PD in ENA was not as strong as in EA (Fig. 1). With the exclusion of the OSBS site, a significant latitudinal diversity gradient of SES–PD emerged in ENA (Pearson's  $r = -0.934$ ,  $p$ -value  $< 0.05$ ). The unusual low SES–PD (0.10) of the EA–ENA disjuncts at the OSBS (Ordway-Swisher Biological Station) site may be related to its vegetation type. Compared to three sites further north in ENA, i.e., TALL (Talladega National Forest), CWHL (Coweeta Hydrologic Laboratory), and MLBS (Mountain Lake Biological Station), the floristic elements are simpler in OSBS. OSBS is dominated by pines (*Pinus palustris* and *Pinus taeda*) and turkey oak (*Quercus laevis*), vegetation with a grass and forb groundcover (<https://www.neonscience.org/field-sites/osbs>); in contrast, TALL is dominated by conifers with mixed species of oaks (including *Quercus alba*, *Q. coccinea*, *Q. falcata*, *Q. incana*, *Q. laevis*, *Q. marilandica* and others) in the understory, and some areas are covered with intermixed conifers, hardwoods, bottomland hardwoods, and wetlands (<https://www.neonscience.org/field-sites/tall>). The vegetation at MLBS is typical of Southern Appalachian forests and is composed of mosaics of deciduous species. With Red maple (*Acer rubrum*) and white oak (*Q. alba*) dominating the canopy, Witch-hazel (*Hamamelis virginiana*) and shadbush (*Amelanchier laevis*) are common throughout the understory, and pockets of eastern white pine (*Pinus strobus*) are found along the creeks (<https://www.neonscience.org/field-sites/mlbs>). The dominant vegetation type in CWHL is southern mixed deciduous forests with the overstory co-dominated by oaks (*Quercus* spp.), maples (*Acer* spp.), hickories (*Carya* spp.), and tulip poplar (*Liriodendron tulipifera*) and an evergreen understory of woody shrubs (Miniat et al., 2021).

Even though it is hard to perfectly test the underlying mechanisms of the observed phylogenetic latitudinal diversity gradient of the EA–ENA disjuncts in the present study, we can still infer some plausible causes here. Pontarp et al. (2019) reviewed the main hypotheses proposed for the latitudinal diversity gradient and classified them into three categories: ecological limits, diversification rates, and time for species accumulation. Based on our data and results, we deduce that niche conservatism is the most likely evolutionary process that explains the phylogenetic latitudinal diversity gradient of the EA–ENA disjuncts (see Pontarp et al. (2019)). It holds the rationale that climatic preferences and phylogenetic niche conservatism limit the migration or trait evolution of certain groups of organisms (Wiens et al., 2010). As modern relicts of a once widespread flora across the Northern Hemisphere, the EA–ENA disjuncts are believed to be subject to niche conservatism, which is further interpreted as evolutionary stasis (Wen, 1999; Qian and Ricklefs, 2004; Wen et al., 2010; Zhang et al., 2015; Yin et al., 2021). Apart from the evolutionary stasis in terms of morphology

and geographical distribution, the present study provides insights into the niche conservatism of the EA–ENA disjuncts from a phylogenetic diversity perspective.

On the other hand, PBD among sites suggested that the two northern sites (CBS and DLS) in EA were more similar to the six ENA sites than to the remaining EA sites (Fig. 2), which is consistent with the Bering Land Bridge having played a crucial role in the long-term exchange of floristic elements between EA and ENA (Wen et al., 2010). The Bering Land Bridge provided a migration corridor for plants and animals across the Beringian region from the middle Cretaceous (ca. 100 million years ago) until the late Pliocene (3.5 million years ago) (Sanmartín et al., 2001). The mean divergence time of the EA–ENA disjuncts in CBS was estimated to be 6.38 Myr and that in DLS was estimated to be 4.98 Myr, which perfectly fit the chronology of the Bering Land Bridge.

Overall, this study represents a novel approach to understanding patterns of biodiversity through a comparative analysis of phylogenetic diversity and the factors associated with it, across both latitudinal and intercontinental scales. Future research that expands the number of study sites would provide a more comprehensive view of the latitudinal variation in phylogenetic diversity and its distribution across the EA–ENA floristic disjunction. Phylogenetic diversity may be impacted by several factors, only a few of which were examined here. For example, other potential drivers may be soil- or microbe-related (e.g., Yang et al., 2019), and these factors should be incorporated into the design of future investigations.

## 5. Conclusion

Across 11 natural forest sites sampled in EA and ENA, we observed a higher SES–PD of the EA–ENA disjuncts in ENA than in EA at the continental level. SES–PD of the EA–ENA disjuncts generally decreased with increasing latitude at the site level. PBD showed a clear latitudinal pattern, with the six ENA sites clustering as a group and the two northern sites in EA more similar to the ENA group than to other sites in EA. Compared to mean diversification rate, temperature-related climatic factors and community structure, mean divergence time showed the strongest correlation with SES–PD of the EA–ENA disjuncts. By taking more evolutionary factors (e.g., diversification rate, divergence time) and/or increasing more sites from both EA and ENA, the present study provides insights into future, more detailed research regarding the biodiversity anomaly of the EA–ENA disjunction, one of the most famous biogeographic patterns known and one recognized since the time of Linnaeus.

## Data accessibility statement

All the data are available from Science Data Bank (<https://doi.org/10.57760/sciencedb.j00143.00029>).

## Author contributions

P.S.S. D.E.S. C.X.F. and Y.P.Z. conceived the project. P.S.S. D.E.S. and Y.P.Z. supervised the work. M.S. H.Y.L. and Y.J.H. gathered and analyzed data. D.J.L. contributed to data interpretation. H.Y.L. M.S. Y.P.Z. D.E.S. and P.S.S. wrote the manuscript with help from all co-authors.

## Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2022.09.008>.

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