



Global biogeographic synthesis and priority conservation regions of the relict tree family Juglandaceae

Yi-Gang Song^{1,2,3} | Yann Fragnière¹ | Hong-Hu Meng⁴ | Ying Li^{2,3} | Sébastien Bétrisey¹ | Adriana Corrales⁵ | Steven Manchester⁶ | Min Deng^{2,3} | Anna K. Jasińska⁷ | Hoàng Văn Sâm⁸ | Gregor Kozłowski^{1,9}

¹Department of Biology and Botanic Garden, University of Fribourg, Fribourg, Switzerland

²Shanghai Chenshan Plant Science Research Centre, Chinese Academy of Sciences / Shanghai Chenshan Botanical Garden, Shanghai, China

³Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, Shanghai, China

⁴Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, China

⁵Facultad de Ciencias Naturales y Matemáticas, Universidad del Rosario, Bogota, Colombia

⁶Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

⁷Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland

⁸Vietnam National University of Forestry, Ha Noi, Vietnam

⁹Natural History Museum Fribourg, Fribourg, Switzerland

Correspondence

Gregor Kozłowski, Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland.
Email: gregor.kozlowski@unifr.ch

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Abstract

Aim: To establish a complete database of Juglandaceae at a spatiotemporal scale and develop a phylogeographic framework with which to elucidate the distributional patterns, diversity patterns, origins, evolution, and conservation priority regions of this family.

Location: Worldwide.

Taxon: Walnut family (Juglandaceae).

Methods: Data on the distribution of all the extant and fossil species of Juglandaceae were collected, followed by analyses of its latitudinal distribution, elevational distribution, and species and generic diversity. Furthermore, based on all genera and 87% of the species, we reconstructed phylogenetic relationships, estimated divergence times, calculated phylogenetic diversity and inferred ancestral distributions.

Results: Extant Juglandaceae (10 genera and 60 species) are mainly distributed in eastern Asia and North America (principally between 20 and 40°N). Tropical Juglandaceae mainly inhabit mountainous areas higher than 1,000 m, especially in the New World. Southwest China and northern Vietnam are characterized by high species, generic and phylogenetic diversity. The United States of America has only high species diversity. The area of origin of Juglandaceae was North America and Europe in the early Eocene, and its widespread dispersal mainly occurred between 13 and 26 Ma.

Main conclusions: The members of Juglandaceae inhabit areas with temperate climatic conditions. The diversification centre has shifted intercontinentally from North America and Europe to Southwest China and northern Vietnam, which are identified as conservation priority regions. The high-latitude cooling during the Oligocene followed by a long-term stable warmer climate in the early and middle Miocene drove the southward translocation of the family.

KEYWORDS

diversity centre shifted, elevational and latitudinal distribution, phylogenetic diversity, relict trees, walnut family

1 | INTRODUCTION

Relict woody species offer a unique opportunity to study the evolutionary and biogeographical processes that shaped the diversity of our planet during past geological epochs (Milne, 2006; Milne & Abbott, 2002). Relict trees not only function as storehouses of information on the Earth's transformations over millions of years but also have the potential to enhance our understanding of how long-term environmental change affects world biomes and the services that ecosystems provide (Shiono, Kusumoto, Yasuhara, & Kubota, 2018; Silvertown, 1985; Woolbright, Whitham, Gehring, Allan, & Bailey, 2014). Information regarding spatial distributions and biodiversity is central to many fundamental questions in biogeography and macroecology (Collen et al., 2014; Guralnick, 2006; Mutke & Barthlott, 2005; Sax, 2001). Nevertheless, biodiversity maps and syntheses at continental to global scales are scarce (Fraginière, Bétrisey, Cardinaux, & Kozłowski, 2015; Pimm et al., 2014; Shrestha et al., 2018). Understanding global biogeography is also of great importance for the effective conservation of any group of organisms (Kozłowski & Gratzfeld, 2013).

Here, we investigate the global diversity and distribution pattern of the walnut family (Juglandaceae), one of the most emblematic tree groups. Although ranking among the smallest families in the plant kingdom in terms of the number of species, the family has extensive scientific and conservation value (Schaarschmidt, 2014). From a palaeobotanical perspective, all living Juglandaceae are relict trees (Manchester, 1987, 1989), thus meriting a number of in-depth research programmes and joint international protection efforts. Furthermore, the walnut family includes commercially significant timber and nut-producing trees, such as walnut, pecan and hickory (Kozłowski, Bétrisey, & Song, 2018; Lim, 2012; Schaarschmidt, 2014).

Juglandaceae has been the subject of numerous studies that involved anatomy, morphology, biogeography and taxonomy in the last 70 years. The most extensive anatomical, morphological source of information on Juglandaceae can be found in the publications of Wayne E. Manning (Manning, 1960, 1962, 1963, 1966) and Lu, Stone, and Grauke (1999). Followed by studies of Donald E. Stone, who produced numerous publications on species diversity, morphological and biogeographical affinities and phylogeny of Juglandaceae (e.g. Stone, 1972, 1997; Stone, Oh, Tripp, Rios, & Manos, 2009). Furthermore, his floristic studies of Juglandaceae in Costa Rica (Stone, 1977) and Mesoamerica (Stone, 2009, 2010) remain of great biogeographical and taxonomic importance. In contrast, his exhaustive global syntheses (Stone, 1989, 1993) are considered outdated in many respects.

Additional important information on Juglandaceae, mainly related to its rich fossil records and the historical biogeography of extant and extinct genera, can be found in the publications of Manchester (1987) and Manchester and Dilcher (1997). Moreover, several recent molecular approaches and new methods have clarified the species delimitation, phylogeny and phylogeography of many members of the family (Zhang et al., 2019; Zhao et al., 2018). At the global level, the main breakthrough in Juglandaceae systematics came from the

work of Manos and Stone (2001) and Manos et al. (2007). Moreover, valuable information can be found in floras available online, e.g., the Flora of North America (Stone, 1997) and Flora of China (Lu et al., 1999), as well as in family monographs authored by Schaarschmidt (2014) and Kozłowski et al. (2018).

Despite the long history of Juglandaceae research and the large number of related studies, a synthesis of the diversity and biogeography of this family that takes more recent publications and the current state of knowledge into account has yet to be produced. The aim of the present work is thus to provide such an up-to-date synthesis. Our main objectives are therefore to (a) produce a list of all the extant species, genera and subfamilies of Juglandaceae; (b) synthesise the global latitudinal and altitudinal distributions of Juglandaceae; (c) elucidate the centres of Juglandaceae diversity at the generic and species levels as well as the centres of its phylogenetic diversity; (d) designate conservation priority areas for the long-term global protection of Juglandaceae diversity; and (e) carry out historical biogeographical reconstructions of Juglandaceae.

2 | MATERIALS AND METHODS

2.1 | Taxonomic treatment

The current understanding of the taxonomic division of Juglandaceae into subfamilies and genera follows Manos and Stone (2001), Manos et al. (2007), APG III (2009) and APG IV (2016). The number of extant species per genus was assessed based on the most recently published floras, genetic studies and databases available online (for detailed information and a complete reference list, see Appendix S1; Jacobs, 1960; Lu et al., 1999; Stone, 1997, 2009, 2010; Zhang et al., 2019; Zhao et al., 2018). We did not include any subspecies, varieties or hybrids in our research.

2.2 | Data collection on the distribution of extant and extinct species

For each extant species, we compiled data on its elevation, latitude and geographic distribution (see Appendix S2 for the complete table and list of references). The database used our field survey, open-access online resources, peer-reviewed publications, and local and global floras, taking only natural distribution areas into account (CVH, 2018; GBIF, 2017; Horikawa, 1972; Jacobs, 1960; Lu et al., 1999; Stone, 1997, 2009, 2010; Tropicos, 2017). In order to test the elevational pattern along the latitude, the elevational data included the minimum and maximum elevations documented for each species. Then the minimum and maximum latitudes of the species' geographical distributions are also listed. We assumed that the species had continuous ranges between their recorded minimum and maximum elevations and latitudes. Therefore, we calculated the mean elevation and mean latitude for each species. Mean latitude (°)–mean elevation (m a.s.l.) relationship for all the Juglandaceae species, the species in the Americas, and the species in



Eurasia were simulated. Each dot represents one species. We reviewed all of the Juglandaceae fossil records with high reliability (fossil fruits) based on the literature. For the fossil distribution areas, we use the following abbreviations: NA (North America), MA-SA (Mesoamerica to South America), Eu (Europe), WA (West Asia), EA (East Asia) and SEA (Southeast Asia).

2.3 | Phylogeny of Juglandaceae

DNA sequences of three chloroplast loci (*atpB-rbcL*, *matK* and *trnL-trnF*) and one nuclear locus (ITS) were downloaded from GenBank (Table S1) and aligned using MEGA 7.0.26. All 10 genera of Juglandaceae, as well as 52 (of the 60) species, were sampled. *Betula lenta* and *Carpinus laxiflora* were used as outgroups. A maximum likelihood (ML) tree was reconstructed with RAxML 8.2.4 (Stamatakis, 2014) with 1,000 rapid bootstrap replicates. General time reversible model of nucleotide substitution with the gamma model of rate heterogeneity (GTRGAMMA) was chosen as the substitution model. Thus, a phylogeny of Juglandaceae with selected extant species was built.

Divergence times were estimated using bayesian evolutionary analysis by sampling trees (BEAST) 2.4 under a Yule tree prior, a lognormal relaxed clock and a GTRGAMMA substitution model. The Markov chain Monte Carlo (MCMC) sampler was run for 100 million generations starting with a random tree. Trees were sampled every 1,000 generations, and the first 20% of trees were discarded burn-in. Convergence was monitored using tracer 1.5 (Rambaut & Drummond, 2009). The log files from two replicate runs were combined with logcombiner 1.8. A maximum clade credibility (MCC) tree was generated in treeannotator 1.8 (<http://beast.bio.ed.ac.uk/TreeAnnotator>). Three estimated ages were used to constrain the nodes of the tree: Juglandaceae stem age, Juglandaceae crown age, and the crown age of subfamilies Engelhardioideae and Juglandoideae (Xiang et al., 2014).

Fossilized birth-death (FBD) is a new model for calibrating divergence time estimates in a Bayesian framework. It allows for inclusion of all available fossils, and explicitly acknowledging that extant species and fossils are part of the same macroevolutionary process (Heath, Huelsenbeck, & Stadler, 2014). Based on the MCC tree and the compiled set of fossil ages from the literature (Appendix S3), we finally estimated divergence times under the FBD model for all the fossil species and built a resolved FBD tree with all the extant and extinct species (Herrera, Manchester, Koll, & Jaramillo, 2014; Manchester, 1987; Manchester & Dilcher, 1997; Meng, Su, Huang, Zhu, & Zhou, 2015; Wu, Wilf, Ding, An, & Dai, 2017).

2.4 | Species richness and phylogenetic diversity

We constructed a complete list of countries where Juglandaceae occur naturally. Moreover, to improve the geographical resolution, we divided countries that are larger than 200,000 km² into smaller units (e.g., into official administrative units of each country, such

as provinces or states). Although political boundaries do not correspond to natural limits of species distributions, they help highlight the regions that are of particular importance to the global conservation of Juglandaceae diversity. For each of these administrative units, we examined and recorded the number of Juglandaceae genera and species within them (see Appendix S2 for the complete table and list of references).

Phylogenetic diversity (PD) was calculated as the standardized diversity metric of Faith (1992), which is independent of species richness, using the R package 'PhyloMeasures' (Tsirogiannis & Sandel, 2016). The uniform null model was used to compute the standardized values of the measure. Based on the phylogenetic tree of extant species and the fine geographical resolution, PD was calculated for the current species. Furthermore, we calculated the current PD, Miocene PD and Eocene PD of Juglandaceae for each country based on FBD tree.

Since there is no correlation between the unit size and SD/PD (Figure S1), we have not applied a size correction to the SD and PD metrics, even though the biogeographic units have not the same sizes.

2.5 | Reconstruction of biogeographic history

Based on floristic regions delimited by Shrestha et al. (2018) and the extant distribution of Juglandaceae, six biogeographic regions were defined: (A) North America, (B) Europe, (C) North-West-East Asia, (D) South Asia, (E) the Malay Archipelago, and (F) Central and South America. Reconstructions of ancestral geographical ranges in Juglandaceae were implemented in RASP 4.0 (Yu, Harris, Blair, & He, 2015). First, a comparison of six models using BioGeoBEARS was employed to select the best model that based on the Akaike information criterion (AIC; Table S2). Ree and Sanmartín (2018) suggest that the biogeographic models with +J parameter (founder-event speciation) have conceptual and statistical problems. The Dispersal-Extinction-Cladogenesis (DEC) model is available to designate the time periods (dispersal constraints) and to define the most recent common ancestor (MRCA). The DEC model (Ree & Smith, 2008) was selected to reconstruct ancestral geographical ranges for Juglandaceae, even though the DEC model had a higher AIC. In the time-stratified reconstruction, the constraints on dispersal probabilities varied within five time periods (0–4.3, 4.3–8.5, 8.5–16.9, 16.9–33.7 and 33.7–67.5). Four pairs of taxa were used to define the MRCA (Appendix S4).

The historical general distribution and diversity centres, and the possible migration routes were reconstructed based on a summary of all the fossil data for Juglandaceae (Appendix S5).

2.6 | Data analyses

All the data analyses and graphs were completed using R (R Core Team, 2016). For the histograms, we used the LOESS nonparametric

local regression method (Cleveland & Devlin, 1988) with a smoothing parameter (span) fixed at 10% to obtain a smooth estimate of the species richness-latitude relationship. A linear regression was used to analyse the correlation between the mean latitude and elevation of the species and calculate the R-squared value and p-value. The maps were created using QGIS 3.0 (QGIS Development Team, 2018). The source data for the maps were obtained from GADM, a high-resolution global database of administrative areas (GADM, 2018).

3 | RESULTS

3.1 | Taxonomic issues of Juglandaceae

Juglandaceae is composed of three subfamilies (Table 1; Figure S2; Appendix S1): Rhoipteleoideae, with the monotypic genus *Rhoiptelea* and thus the single species *R. chiliantha*; Engelhardioideae, with 13 species distributed within the following four genera: *Engelhardia* (5 spp.), *Alfaropsis* (1 sp.), *Oreomunnea* (2 spp.) and *Alfaroa* (5 spp.); and Juglandoideae, with 46 species and five genera: *Carya* (18 spp.), *Platycarya* (1 sp.), *Cyclocarya* (1 sp.), *Pterocarya* (6 spp.) and *Juglans* (20 spp.). Collectively, the family is composed of 10 genera and 60 species.

3.2 | Latitudinal distribution

The Juglandaceae family is distributed between 29°S and 50°N (Figure 1). The highest species diversity occurs at 34°N (28 spp.), which accounts for 46.7% of the total number of species. The number of species decreases more significantly at northern latitudes, with only three species distributed above 45°N. *Juglans regia* was observed at the highest latitude, 50°N. Only seven species cross the equator, including three species of *Engelhardia* (*E. apoensis*, *E. serrata* and *E. spicata*) and *Alfaropsis roxburghiana* in Southeast Asia as well

TABLE 1 Number of subfamilies, genera and species in Juglandaceae

Subfamily	Genus	Number of species
Rhoipteleoideae	<i>Rhoiptelea</i>	1
Engelhardioideae	<i>Engelhardia</i>	5
	<i>Alfaropsis</i>	1
	<i>Oreomunnea</i>	2
	<i>Alfaroa</i>	5
Juglandoideae	<i>Carya</i>	18
	<i>Platycarya</i>	1
	<i>Cyclocarya</i>	1
	<i>Pterocarya</i>	6
	<i>Juglans</i>	20
3	10	60

Note: The order of the genera follows the phylogenetic trees of Manos and Stone (2001) and Manos et al. (2007).

as three species of *Juglans* in South America (*J. neotropica*, *J. boliviana* and *J. australis*; Figure 1; Figure S3 and Appendix S2).

The generic diversity centre (with eight genera) of Juglandaceae lies at a 25°N latitude, slightly above the Tropic of Cancer, which is farther south than the latitudinal species diversity centre. Only three genera extend south of the equator (*Engelhardia*, *Alfaropsis*, and *Juglans*). *Juglans* is the only genus occurring below a 9°S latitude (Figure S3; Appendix S2).

For the majority of Juglandaceae genera, the species diversity centres occur in the northern temperate zone (*Carya*, *Platycarya*, *Cyclocarya*, *Pterocarya* and *Juglans*; Figure 1; Figure S3). The species diversity centres of *Engelhardia*, *Alfaropsis* and *Rhoiptelea* occur in the tropical zone. Only *Oreomunnea* and *Alfaroa* are exclusively tropical (in Mesoamerica and South America). The greatest latitudinal range is exhibited by *Juglans* (between 50°N and 29°S), followed by *Engelhardia* (19.5°N–9°S), *Carya* (45–11°N) and *Pterocarya* (43.5–17°N; Figure S2).

3.3 | Elevational distribution

Juglandaceae grow from sea level up to 3,500 m a.s.l. (Figures 2 and 3). Globally, a strong correlation can be observed between latitude and elevation: at locations closer to the equator, Juglandaceae species grow at higher mean elevations (Figure 2a). This correlation is particularly pronounced in the distribution patterns of New World Juglandaceae (Figure 2b). The vast majority of North American Juglandaceae are lowland species (14 species with a mean elevation between 0 and 500 m a. s. l. and a maximum altitude of 1,000 m a.s.l.). All the Central-South American Juglandaceae have a mean elevation between 900 and 2,125 m a. s. l. *Juglans neotropica* is particularly mountainous species, with an elevational mean of 2,125 m a.s.l., reaching its highest altitude at 3,200 m a.s.l. (Figure S4).

In contrast, there is no correlation between the latitude and altitude of Old World Juglandaceae (Figure 2c). The mean elevation of the northern species in this region, such as *Juglans regia*, and *Pterocarya macroptera*, is located between 1,800 and 2,300 m a. s. l. In comparison, several predominantly tropical Old World Juglandaceae (e.g., *Pterocarya tonkinensis*, *Alfaropsis roxburghiana* and *Carya sinensis*) have a mean elevation between 700 and 850 m a. s. l. Additionally, the absolute maximum altitude for Old World Juglandaceae (and for all walnut family members) was recorded for *Pterocarya macroptera* at 3,500 m a.s.l. (Figure S4).

On the whole, the largest number of Juglandaceae species can be observed in mountainous areas (between 800 and 1,600 m a.s.l.). However, only a small proportion of the species (5 spp.) are capable of growing at elevations higher than 2,600 m a.s.l. (Figure 3).

3.4 | Species diversity versus phylogenetic diversity

Juglandaceae species are distributed across 47 countries and are present in 583 political administrative units (small countries and

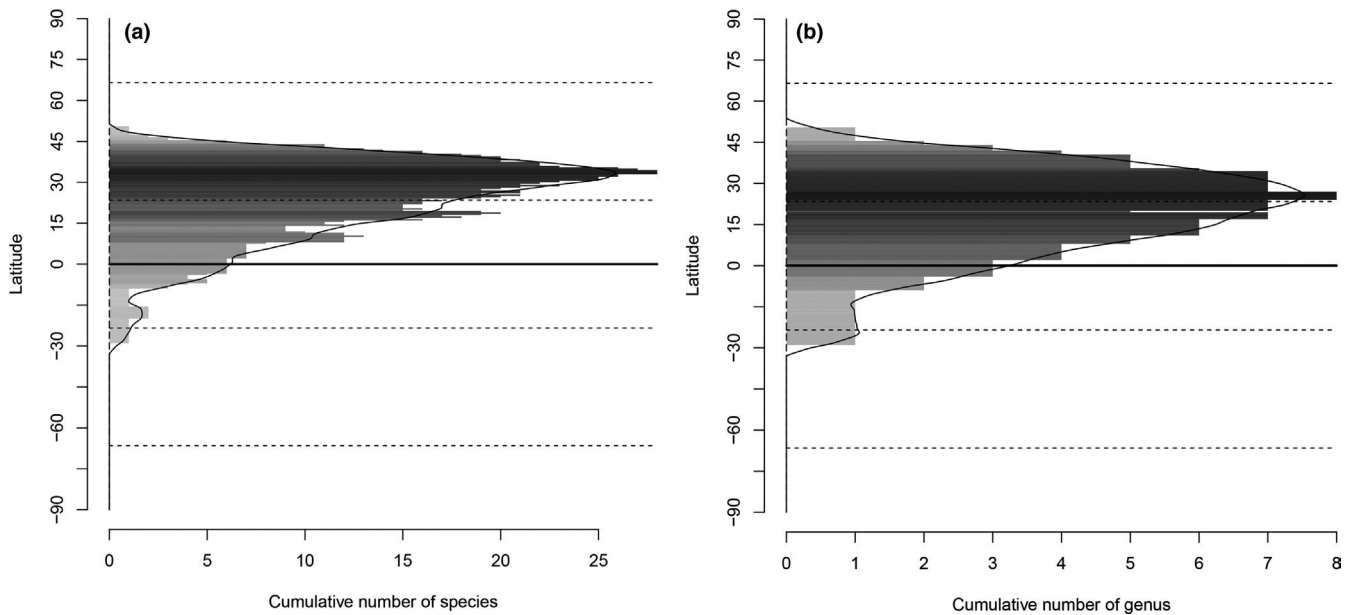


FIGURE 1 Global latitudinal distribution of the species (a) and genera (b) of Juglandaceae. The horizontal dashed lines represent the tropics and polar circles, and the solid line represents the equator. The histogram indicates the number of species/genera occurring in each 0.5° latitudinal span. The smooth line above the histogram was calculated with the LOESS procedure (smoothing parameter set at 0.1)

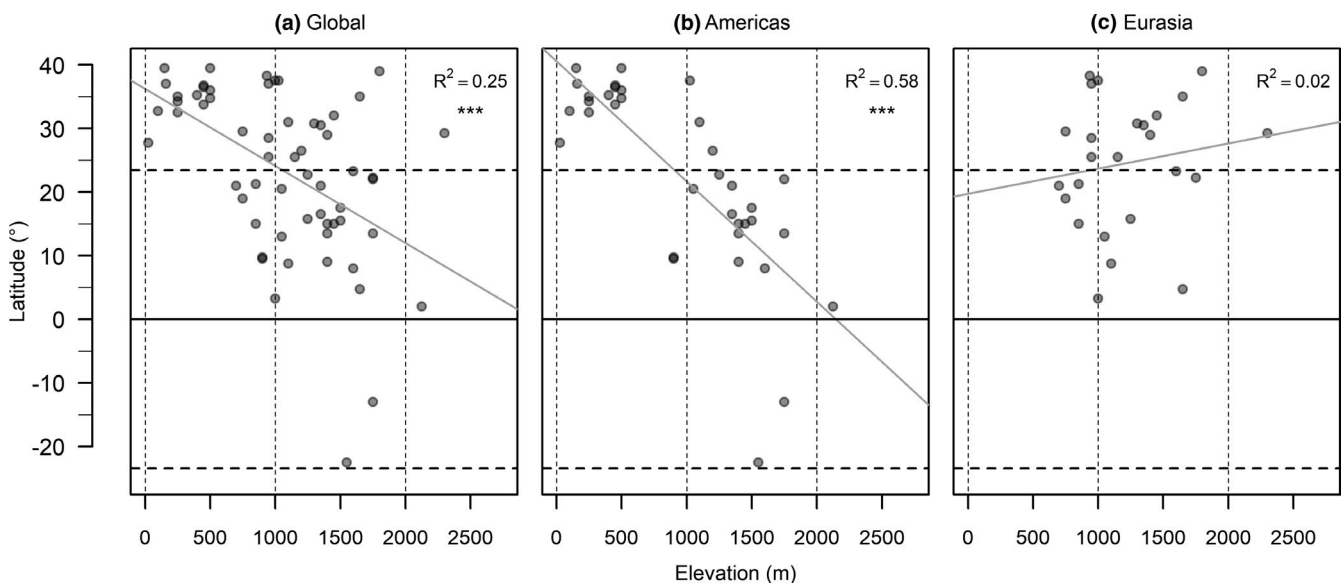


FIGURE 2 Mean latitude (°) - mean elevation (m a.s.l.) relationship for all the Juglandaceae species (a), for the species in the Americas (b), and for the species in Eurasia (c). Each dot represents one species. The two horizontal dashed lines represent the tropic circles, and the solid line represents the equator. The grey line shows the linear regression. Significant p -values ($p < .001$) are indicated by asterisks (***). The R-squared value (R^2) is given in each panel

provinces/states). The species diversity (SD) among assemblages ranged from 1 to 15. Overall, SD was highest in Southwest China, with secondary areas of diversity in the central and southern United States of America (USA). Northern Vietnam, the eastern USA, eastern China and Mexico also have a high SD (Figure 4; Table S3). In contrast, areas of high generic diversity occur only in Southwest China (Figure S5).

The analyses of the PD of Juglandaceae yielded different results. The PD was positive predominantly in Asia, clearly indicating

phylogenetic overdispersion in this region. In most of the Americas, PD was negative, indicating phylogenetic clustering in this region (Figure 5; Table S3). There was a strong positive correlation between SD and PD in China and Vietnam ($R^2 = .22$, $p < .01$), while the correlation was negative in the USA and Mexico ($R^2 = .72$, $p < .01$). Thus, Southwest China and northern Vietnam presented both high PD and high SD. In contrast, the central and southern USA presented low PD, despite high SD (Figures 4 and 5). In the Eocene, no areas with phylogenetic overdispersion could be detected. In the Miocene, the

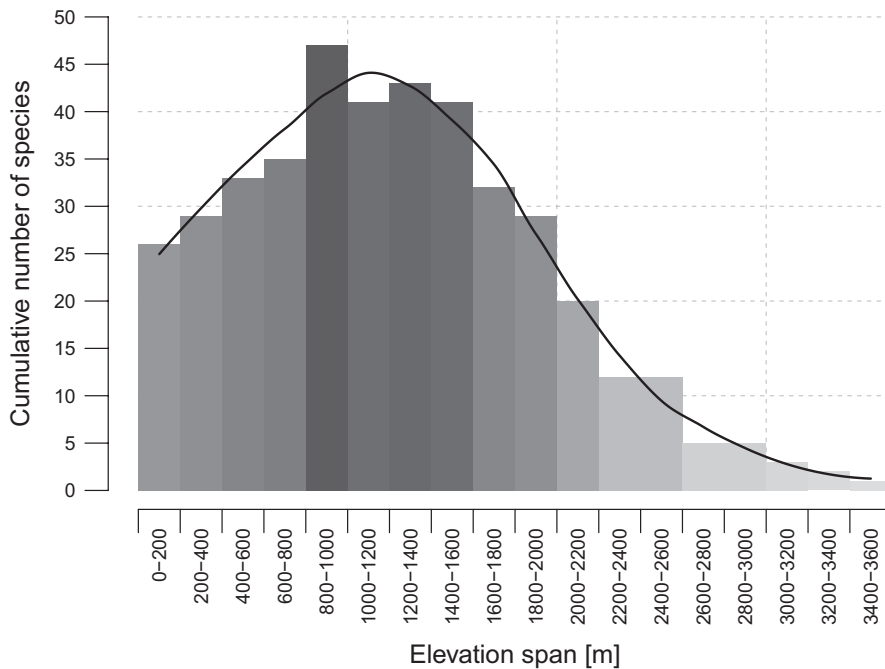


FIGURE 3 The global elevational distribution of Juglandaceae (m a.s.l.). Grey bars indicate the cumulative number of species in the corresponding 200 m elevation interval

areas with positive PD were geographically restricted to Europe (today's France and the Netherlands) as well as to South Korea (Figure S6).

3.5 | Reconstruction of the historic biogeography of Juglandaceae

The phylogenetic reconstructions provided improved resolution and well-resolved nodes. Three clades corresponding to the three subfamilies and 10 genera in Juglandaceae were resolved. All the genera were monophyletic insofar as we sampled them. The stem age of the subfamilies Engelhardioideae and Juglandoideae (the main clade of Juglandaceae) was dated to the end of the Paleocene and the early Eocene (c. 56.64 Ma; Figure 6; Figures S7 and S8). The ancestral distribution areas for the stem nodes of the main clade of Juglandaceae were estimated to be North America and Europe, based on the DEC model (Figure 6). Dispersal from the ancestral area to North-West-East Asia (NWEA), South Asia (SA), the Malay Archipelago (MA) and Central-South America (CSA) is inferred to have occurred between 13 and 26 Ma in different clades (Figure 6).

The earliest confirmed record of Juglandaceae (based on fruits and not on questionable fossils of pollen or leaves) is of the extinct genus *Polyptera* from the Paleocene (Torrejonian-Tiffanian) in North America. However, probable records of the family extend to the late Cretaceous in Europe and North America, including the fruits and flowers of *Caryanthus* and *Zlivifructus*, with similarities to extant *Rhoiptelea* (Figure 7; Appendix S4). The richest fossil records and generic diversity were reported from the Paleogene in Europe and North America. Therefore, these two regions seem to be the most plausible centres of origin of virtually all the extant genera of Juglandaceae.

From the Late Eocene to Oligocene, several genera of Juglandaceae began to appear in eastern Asia; the disappearance of *Cyclocarya* and *Platycarya* in North America also occurred during this period. Engelhardioideae persisted until the Miocene in Europe, North America, and East Asia. Engelhardioideae and *Juglans* are known to have occurred in Central and South America in the early Miocene. The fossil records indicate that Juglandaceae reached its widest distribution in the Northern Hemisphere and highest generic diversity on each continent during the Miocene (Figure 7). At this time, the generic distribution pattern began to change, with the disappearance and appearance of genera in local regions. Only *Carya* and *Juglans* persisted in North America from the Pliocene to the present day. The generic diversity in Europe decreased significantly in the late Pliocene (only *Pterocarya* persists in a small refugium in Transcaucasia). The high generic diversity in East Asia has been stable since the Miocene (Figure 7).

4 | DISCUSSION

4.1 | Taxonomic issues of Juglandaceae

Juglandaceae has fascinated naturalists and researchers around the world for centuries. Nevertheless, many aspects of their taxonomy still require thorough revision, especially at the species level. Undoubtedly, Juglandaceae is monophyletic and consists of three subfamilies (Rhoipteleoideae, Engelhardioideae and Juglandoideae) and 10 genera (APG III, 2009; APG IV, 2016; Manos et al., 2007; Manos & Stone, 2001; Figure 6; Appendix S1 and S2). The recent significant changes within genera of Juglandaceae are now widely accepted within the scientific literature, such as (a)

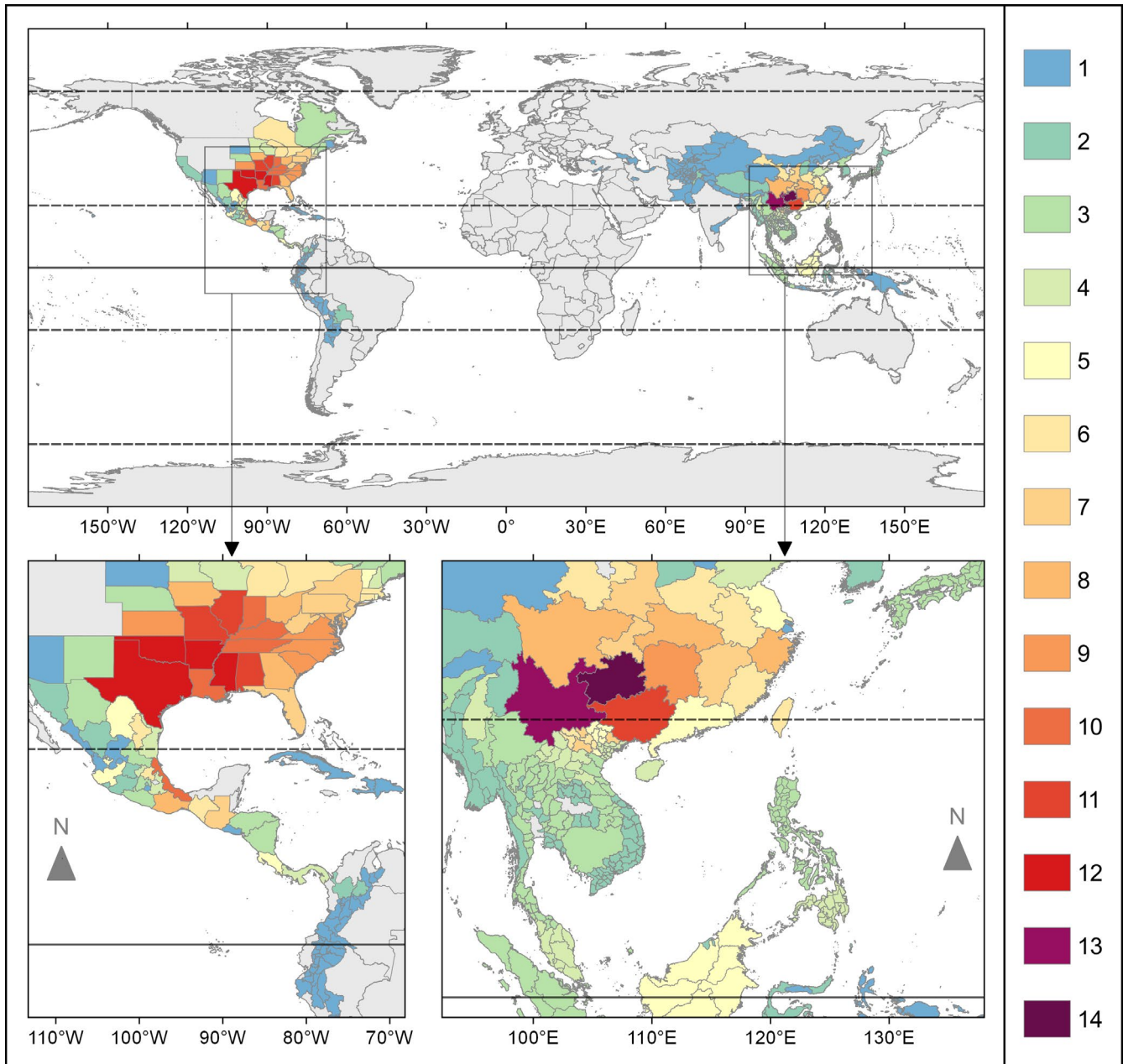


FIGURE 4 Species diversity (SD) hotspots of Juglandaceae: administrative units with a high international conservation responsibility. The right colour scale indicates the number of species in each administrative unit: blue and dark green colours indicate low richness; and light-green, yellow, red and violet colours indicate high richness

the inclusion of the genus *Rhoiptelea* (APG IV, 2016; Figure S2a), (b) the recognition of a new genus *Alfaropsis* (Figure S2c, formerly *Engelhardia roxburghiana*), and (c) the formerly recognized genus *Annamocarya* (= *Rhamphocarya*) is now considered to be within *Carya*.

The phylogenomics studies of *Juglans* have clearly elucidated its species delimitation and 20 species were identified in this genus (Zhang et al., 2019; Zhao et al., 2018). In contrast, the species delimitations in *Engelhardia*, *Alfaroa*, *Carya* and *Pterocarya* remain a subject of debate. Thus, genome-scale datasets should be used to address phylogenetic relationships among closely related species in these genera.

4.2 | Global patterns of Juglandaceae diversity

Global patterns of biodiversity result from processes that operate over both space and time and thus require an integrated macroecological and macroevolutionary perspective (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Our results show high abundance of Juglandaceae in the humid subtropical and warm-temperate forest regions, which are located in the East Asia and North America between 15° and 35° N (Figures 1, 4 and 5; Figure S5). These regions belong to four of the five main refugia of relict trees worldwide (Kozłowski & Gratzfeld, 2013; Milne & Abbott, 2002). Comparing with the fossil data, we found higher diversity at lower latitudes in

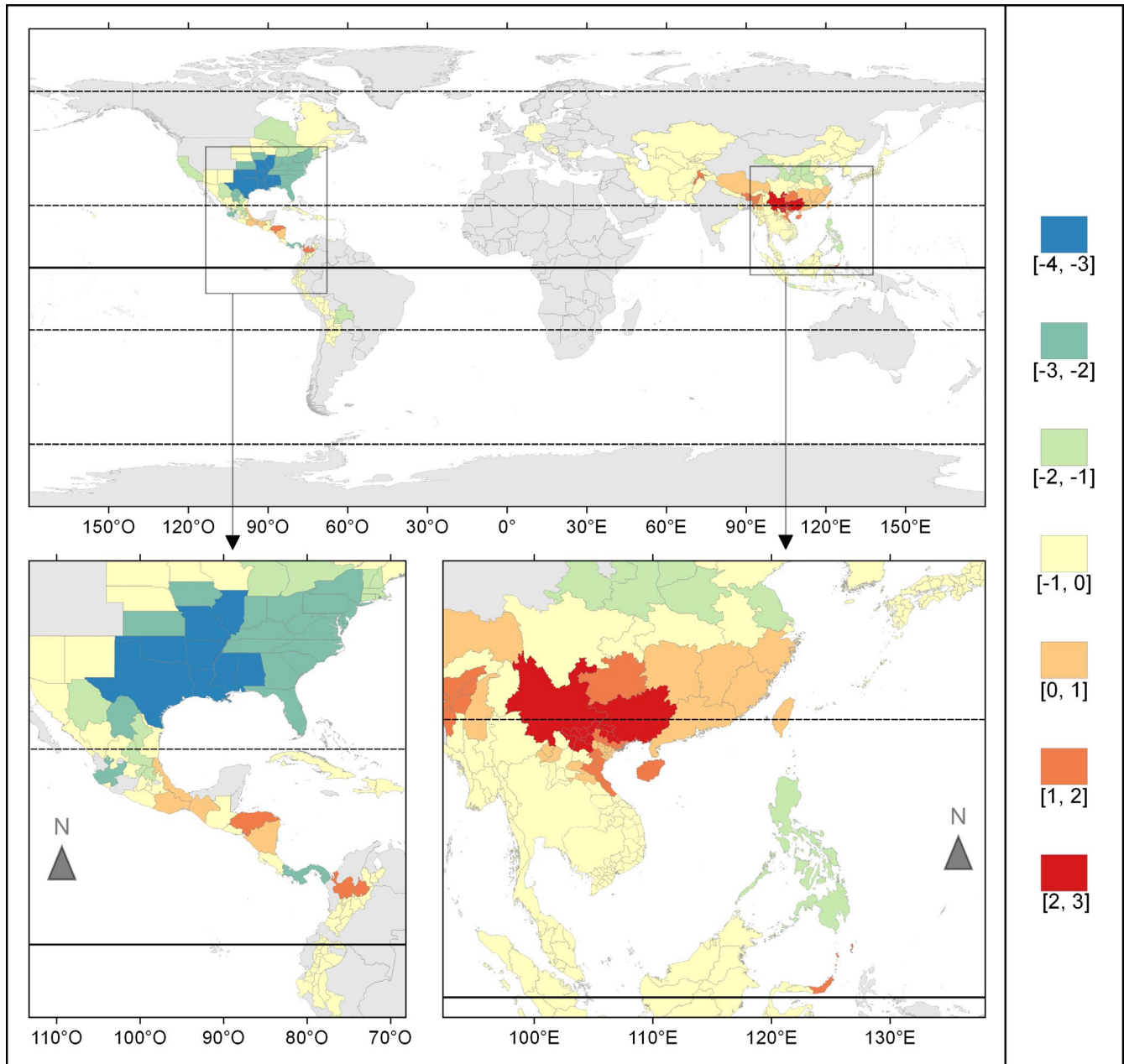


FIGURE 5 Phylogenetic diversity (PD) of Juglandaceae: administrative units with a high international conservation responsibility. The right colour scale indicates the PD in each administrative unit: blue and green colours indicate negative values; orange and red colours indicate positive values

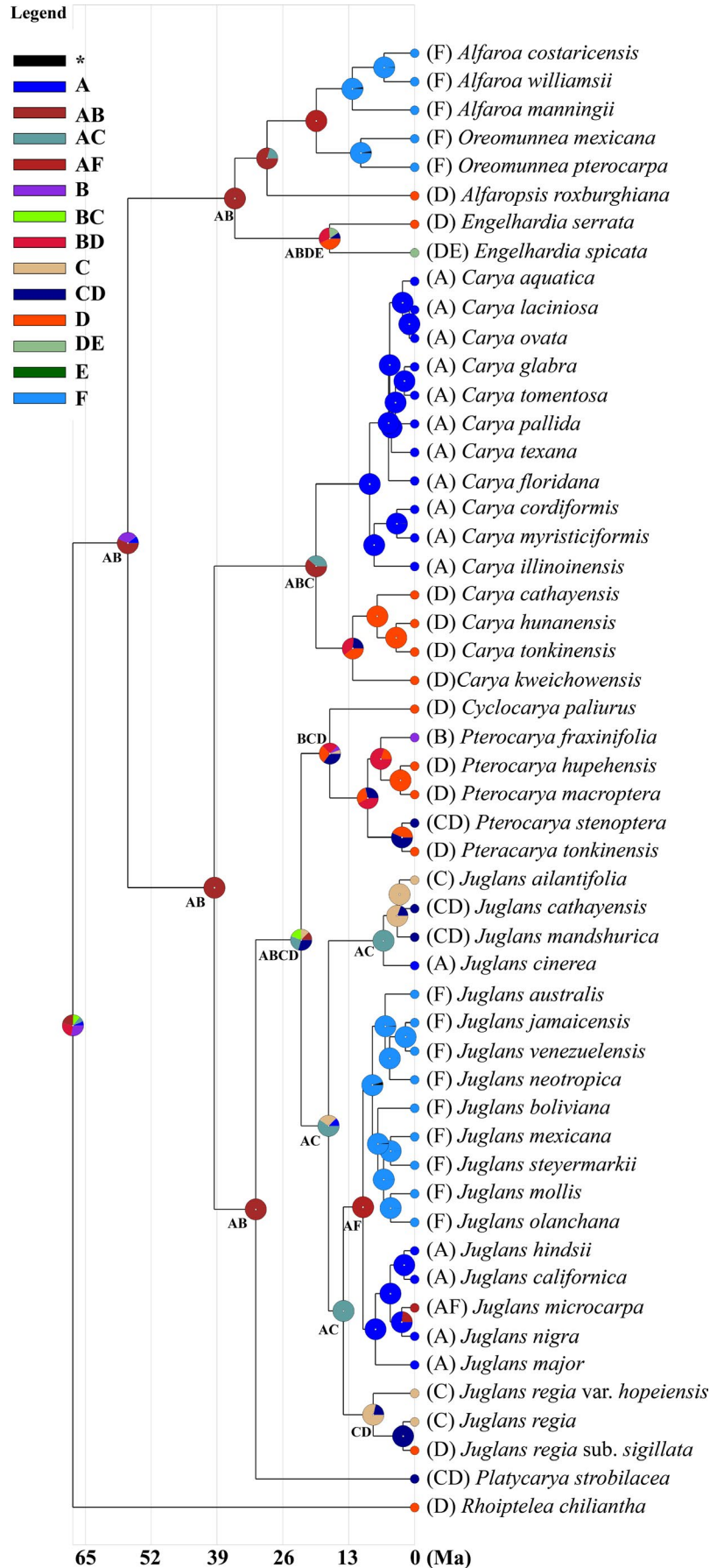
the extant Juglandaceae. These findings demonstrate the role of selective extinction and retreat of warm-adapted genera from mid and high latitudes.

The long-term stability of favourable climate and topographically diverse landscapes in the mountains of Eastern Asia, provided advantageous conditions for relict species survival (Shiono et al., 2018; Tang et al., 2018). In this region, the highest species and generic diversity of Juglandaceae are located in Southwest China (Figure 4; Figure S5); where the species prefer to occupy high elevations (Figure 2). In North America, our results suggest that the elevated species diversity in southern USA and Mexico

are due to higher rates of speciation in *Carya* and *Juglans* from the Pliocene (Figure 6).

Taking into account the latitudinal and elevational distribution, Juglandaceae species are concentrated in areas with temperate climatic conditions. The main exceptions are the members of the Engelhardioideae subfamily, with evident tropical affinity, such as *Oreomunnea* and *Alfaroa* from Mesoamerica, and *Engelhardia* in Southeast Asia. However, most of engelhardioids (eight of 13 species) still prefer cool habitats at high altitude (Figure S4). Similarly, the small number of *Juglans* species occurring in tropical areas, is also located in the high mountains (Figure S4).

FIGURE 6 Biogeographic history reconstruction of Juglandaceae based on the Dispersal-Extinction-Cladogenesis (DEC) model. Inferred ancestral distribution areas prior to speciation are indicated at the nodes. Pie charts at the nodes represent the relative probability (proportional likelihood) of alternative ancestral areas: A: North America; B: Europe; C: North-West-East Asia; D: South Asia; E: the Malay Archipelago; and F: Central-South America



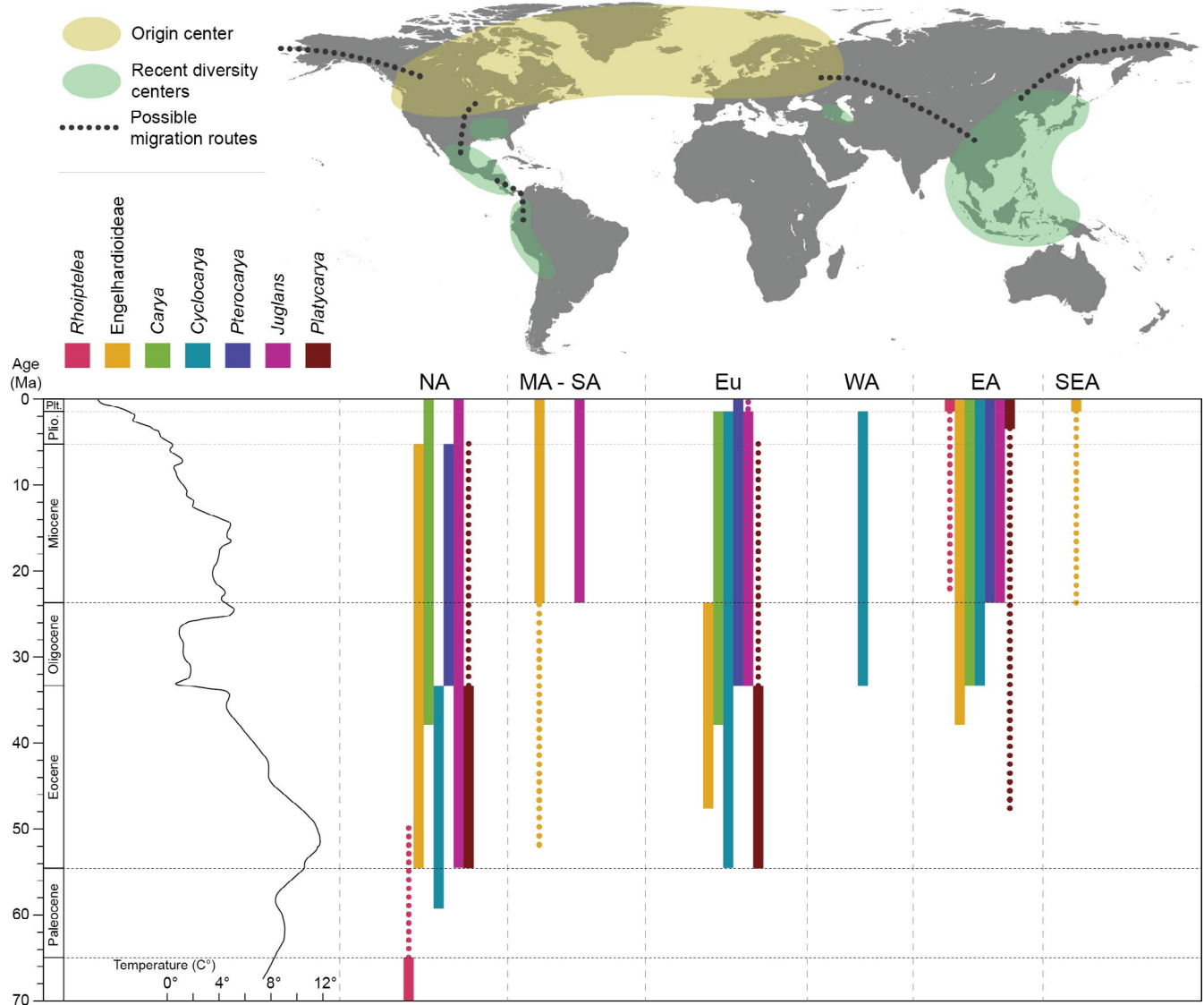


FIGURE 7 Past and present distribution centres: palaeogeographic displacement of the Juglandaceae genera. Climatic sequence of events based on Zachos et al. (2001). Geological time abbreviations: Plio. = Pliocene and Plt. = Pleistocene. Engelhardioideae includes four extant genera (*Engelhardia* and *Alfaropsis* in Asia and *Oreomunnea* and *Alfaroa* in Mesoamerica) and one fossil genus (*Palaeocarya*). NA: North America, MA: Mesoamerica, SA: South America, Eu: Europe, WA: West Asia, EA: East Asia, and SEA: Southeast Asia. The dashed straight line represents the possible distribution along the age axis. The black dashed curve traces the spread of Juglandaceae from its origin centre to its recent diversity centres.

From an elevational pattern perspective (McCain & Grytnes, 2010), Juglandaceae globally show a low plateau pattern with a mid-elevational peak (Figure 3). The vast majority of lowland North American species and Juglandaceae species occurring between 30°N and 25°S, are located at relatively high elevations, making the main contribution to this elevational richness pattern (Figure 2a). Furthermore, the elevational pattern of the New World Juglandaceae is quite different from that of the Eurasian taxa. Some Asiatic *Engelhardia*, *Pterocarya* and *Juglans* species have an elevational range of 2,000–2,400 m, whereas North American *Juglans* and *Carya* species rarely have ranges exceeding 1,000 m (Figure S4). This distributional trend might be explained by differences in orography, given the presence of

the Himalayas in Asia and the absence of high mountains in the eastern USA, where the majority of North American taxa grow, and thus simply be due to the absence of high-mountain habitats in this area.

4.3 | Recommended conservation priority regions

Practical conservation management requires the identification of least-cost approaches for maximizing conservation outcomes (Jetz et al., 2014). Possessing information on multiple diversity indices, conservation efforts need to adopt an integrative approach (Davies & Buckley, 2011; Devictor et al., 2010).

The PD-based priority regions for conservation were quite different from those based on SD. Taking SD into account, the following regions possess very high conservation priority: (a) Southwest China; (b) southern USA; (c) Veracruz and Oaxaca in Mexico; and (d) northern provinces of Vietnam (Table S3). In contrast, from the PD perspective, only southwest China and northern Vietnam, and to a lesser extent that several regions in Mesoamerica and South America, are the main priority regions for Juglandaceae conservation. The species of Juglandaceae in East Asia are members of eight different genera, six of them (*Rhoiptelea*, *Engelhardia*, *Alfaropsis*, *Platycarya*, *Cyclocarya*, *Pterocarya*) are belonging to lineages that disappeared from North America. In contrast, species in *Carya* and *Juglans* are closely related, being probably a result of recent speciation (Figure 6).

Taken together, our results indicate that Southwest China (especially in Guizhou and Yunnan province) is undoubtedly the primary centre for extant Juglandaceae and this region is thus the most important priority area for global conservation of this relict tree family. All but two genera of the walnut family are represented by at least one species within this region, as only the Mesoamerican Engelhardioideae genera, namely, *Alfaroa* and *Oreomunnea*, are absent there. Additionally, China includes more than 20 Juglandaceae species (approx. 30% of all Juglandaceae), with nearly half of them being endemic. Northern Vietnam is the second-most important conservation priority region, possessing 6 genera and 10 species of Juglandaceae (Appendix S2).

Nevertheless, the central and southern USA have a high SD (e.g. Mississippi, Arkansas, Oklahoma, and Texas, each with 12 species). This region is also clearly the global centre of *Carya*, harbouring 11 of the 18 species found worldwide. However, due to a low PD and low generic diversity, conservation efforts should be concentrated only on the endangered species of this region.

Moreover, the mountain chains (Cordillera) of Mexico and Central America are also one of the main conservation regions for Juglandaceae. First, this area is a diversity centre for the two exclusively Neotropical engelhardioid genera, since all five species of *Alfaroa* and the two species of *Oreomunnea* are endemic to this region (Appendix S2). Second, this area supports not only several widespread *Carya* and *Juglans* species with a northern distribution (e.g., *C. illinoensis*), but also other endemic taxa of the region (e.g., *C. palmeri*, *J. mollis*). Furthermore, most of the Juglandaceae species in this region were assessed as Vulnerable (VU) or Endangered (EN; IUCN, 2019).

4.4 | Palaeogeographic diversity displacement of Juglandaceae

A critical review of the fossil record, providing a framework for interpreting the evolutionary and biogeographic history of the walnut family, was presented 30 years ago (Manchester, 1987). Since then, a large number of new fossils have been recovered that expand the geographic coverage (Herrera et al., 2014; Meng et al., 2015; Wu et al.,

2017). Our study offers new perspectives on global biogeographic history of Juglandaceae based on synthesis of fossil occurrences and modern distributions.

The centre of origin for a given taxonomic group is often hypothesized to be in the regions with the highest extant diversity, both in terms of the number of closely related species and the genetic variability within these species (Hummer & Hancock, 2015). According to our results, the diversity centre of Juglandaceae has moved three times among different areas during the last epochs (Figures 6 and 7). Our synthesis, and especially the ancestral area reconstruction, clearly favour a North American-European origin of the family, with high-latitude intercontinental migration early in the radiation of the family (Eocene and Oligocene). Later, during the Miocene and Pliocene, the diversity centre shifted to Eurasia. Finally, the diversity centre has been shrunk to East Asia (and to a lesser extent to Central America).

Similar patterns of historical diversity displacement was detected in other taxa, such as selected coniferous genera (*Pinus* and *Abies*), and other relict tree families of Cercidiphyllaceae, Eupteleaceae and Hamamelidaceae (Farjon, 1996; Manchester, Chen, Lu, & Uemura, 2009; Millar, 1993; Semerikova, Khrunyk, Lascoux, & Semerikov, 2018). Many of these taxa have originated in North America or Europe, and expanded their ranges when tectonic and climatic conditions allowed.

The fossil synthesis indicates three main milestones in the historical biogeography of Juglandaceae. First, in the Eocene, the main diversification of Juglandaceae occurred in North America and Europe (Manchester, 1987). This scenario is supported by the multiple fossils in these regions and by the ancestral area reconstructions (Manchester, 1987; Meng et al., 2015; Wu et al., 2017; Figures 6 and 7). We deduce that the relatively warm global climates of the Paleocene to Mid-Eocene contributed to the diversification and range expansion into high northern latitudes. Similar expansion pattern from Paleocene to Mid-Eocene can be found in other angiosperms, for example, in *Magnolia*, *Meliosma*, *Hypserpa*, Icacinaceae and Cornaceae (Wolfe, 1975).

Second, global cooling and climate fluctuations from the Oligocene to the Early Miocene were important for the migration of Juglandaceae (Figures 6 and 7). The family had a widespread distribution in the Northern Hemisphere during the Miocene and reached its largest geographic extension at that time (Figure 7; Appendix 5). In this epoch the range of Juglandaceae expanded significantly from the high latitudes towards the south (Central-South America, West Asia and East Asia), attaining new suitable environments due to the influence of a cooling climate. The local disappearance of *Cyclocarya* in North America and the accompanied appearance of *Pterocarya* can also be attributed to this event. The genera of Engelhardioideae typically prefer tropical to subtropical areas and thus no longer survive at middle latitudes, where they were common in the Paleogene (Meng et al., 2015).

Finally, global climate fluctuations were followed by a gradual cooling from the late middle Miocene to the Pliocene and

progressed stepwise to the Pleistocene ice ages (Tiffney & Manchester, 2001; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The fossil record indicates that Engelhardioideae and *Pterocarya* went extinct in mid-latitude North America due to gradual cooling from the late middle Miocene to the Pliocene. During the Pleistocene ice ages, the majority of Juglandaceae genera went extinct in Europe. Some authors have hypothesized that the climatic oscillations during the Quaternary were the major contributing factor to the contracted geographic distribution of the taxa within Juglandaceae (Bai, Liao, & Zhang, 2010; Chen et al., 2012; Meng et al., 2015). From a broader perspective, this outcome can be considered as the culmination of the earlier events during the past 60 million years, which together shaped the current distribution pattern of the family.

4.5 | Methodological challenges and limitations

There are numerous methodological and conceptual difficulties enclosed in each of the steps required to elaborate molecular phylogenies as well as in biogeographical reconstructions (Suarez-Diaz & Anaya-Munoz, 2008). At least two of such difficulties were directly relevant to the present study.

First, a single dated phylogenetic tree was applied for calculations of the phylogenetic diversity and to infer the ancestral distribution areas. However, since the genomic data available on Juglandaceae are finite, the phylogenetic tree presented in this study was constructed based on only few genes. Even though a large proportion of recent molecular systematic literature follows similar methodology, such comparative methods are often underpowered, biased and suffer from non-independence (Ho & Ane, 2014; Pyron, 2015). The coming of a new era of phylogenomics can increase the confidence and robustness of phylogenetic comparative methods (Pyron, 2015; Zhang et al., 2019).

Second, methods in historical biogeography based on phylogeny of extant taxa are likely to provide limited and potentially biased information about past biogeographic processes (Silvestro et al., 2016). Fossil data hold considerable information about past distribution of lineages, but suffer from largely incomplete sampling in DEC model. Methodological concerns have also been raised on how to choose among variants of the DEC model, especially between the DEC and DEC +J models, a variant that emphasizes “jump dispersal” or founder-event speciation (Ree & Sanmartin, 2018). In order to reduce these biases, we selected the DEC model, according to the recommendations of Ree and Sanmartin (2018) and summarized all the fossil data of Juglandaceae.

5 | CONCLUSIONS

Juglandaceae originated in temperate deciduous broad-leaved forests of the Paleocene at high northern latitudes what is today North

America and Europe, where its members formed a diversity centre in the Eocene. Whereas, the present diversity centre is located in subtropical and tropical mountains of southern China, northern Vietnam and to a lesser extent of Central America. Juglandaceae is thus one of the best-documented cases that the diversification centre has shifted intercontinentally from North America and Europe to Southwest China and northern Vietnam. It could serve as a textbook example for the displacement of the diversity centre far away from the area of origin. These shifts were driven by the high-latitude cooling in the Oligocene and Quaternary through extinction at higher latitudes of less-diversified tropical genera and an equatorward distributional shift of temperate genera.

Southwest China and northern Vietnam are undoubtedly the main diversity hotspots and conservation priority areas of the walnut family. Furthermore, Mexico and Central America, due to a high proportion of endemic and endangered species, also merit enhanced and coordinated conservation efforts.

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ORCID

Yi-Gang Song  <https://orcid.org/0000-0003-2584-2338>

Hong-Hu Meng  <https://orcid.org/0000-0002-4504-0001>

Min Deng  <https://orcid.org/0000-0001-7041-4418>

Gregor Kozłowski  <https://orcid.org/0000-0003-4856-2005>

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**BIOSKETCH**

Yi-Gang Song is studying for a PhD at the University of Fribourg (Switzerland) in collaboration with the Shanghai Chenshan Plant Science Research Centre (SCPSRC) of the Chinese Academy of Sciences in Shanghai, China. His main research interests are seed physiology, phylogeny, phylogeography and conservation biology of *Pterocarya* (Juglandaceae) and *Quercus* (Fagaceae). The publication is a result of an international cooperation in the framework of the interdisciplinary Project *Pterocarya*.

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SUPPORTING INFORMATION

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

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