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Original Article

Genome-wide supermatrix analyses of maples (*Acer*, Sapindaceae) reveal recurring inter-continental migration, mass extinction, and rapid lineage divergence

Fabiola Areces-Berazain^{a,b}, Damien D. Hinsinger^{b,c}, Joeri S. Strijk^{d,b,*}

^a Biodiversity Genomics Team, Plant Ecophysiology & Evolution Group, Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, DaXueDongLu 100, Nanning, Guangxi 530005, China

^b Alliance for Conservation Tree Genomics, Pha Tad Ke Botanical Garden, PO Box 959, 06000 Luang Prabang, Laos

^c Génomique Métabolique, Genoscope, Institut de Biologie François Jacob, Commissariat à l'Énergie Atomique (CEA), CNRS, Université Évry, Université Paris-Saclay, 91057 Évry, France

^d Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan Tungku Link, BE1410, Brunei Darussalam



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ABSTRACT

Acer (Sapindaceae) is an exceptional study system for understanding the evolutionary history, divergence, and assembly of broad-leaved deciduous forests at higher latitudes. Maples stand out due to their high diversity, disjunct distribution pattern across the northern continents, and rich fossil record dating back to the Paleocene. Using a genome-wide supermatrix combining plastomes and nuclear sequences (~585 kb) for 110 *Acer* taxa, we built a robust time-calibrated hypothesis investigating the evolution of maples, inferring ancestral ranges, reconstructing diversification rates over time, and exploring the impact of mass-extinction on lineage accumulation. Contrary to fossil evidence, our results indicate *Acer* first originated in the (north)eastern Palearctic region, which acted as a source for recurring outward migration. Warm conditions favored rapid Eocene-onward divergence, but ranges and diversity declined extensively as a result of the Plio-Pleistocene glacial cycles. These signals in genome-wide sequence data corroborate paleobotanical evidence for other major woody north-temperate groups, highlighting the significant (disparate) impact of climatic changes on the evolution, composition, and distribution of the vegetation in the northern hemisphere.

1. Introduction

Eastern Asia is a core area of north temperate tree diversity. The region harbors at least 170 temperate woody genera (roughly four times more than Europe and two times more than North America), many of which reach their maximum in terms of species diversity there [1–3]. Many of these genera are relicts of the mesophytic vegetation that once occupied large areas throughout the northern hemisphere during the Cenozoic. These forests fragmented as a result of global cooling and the breakup of land connections during the second half of this era (Oligocene, Neogene, and Quaternary) [4]. The exceptional tree diversity at generic and species level in East Asia has been attributed to a larger refuge area with suitable climatic conditions during the Quaternary, a higher spatial heterogeneity promoting speciation, and to lower extinction rates than those prevalent in North America and Europe [1,5–8].

Acer L., the maple genus, is among the largest Cenozoic tree groups that best exemplifies this pattern. The genus includes approximately 155 species [9], all confined to the northern hemisphere except one, *Acer laurinum* Hassk., whose range includes the islands of Sulawesi and Java in Indonesia [10]. More than two-thirds of species occur in eastern Asia with a major center of diversity in China (over 100 species, 61 endemic) [9,11]. About 15 native species occur in Europe, northern Africa, and western Asia, and only 13 are found in North and Central America [12–14].

Maples are among the most prevalent trees in the broad-leaved deciduous forests of the northern hemisphere [15,16]. They are often the dominant element of the vegetation and can also act as keystone species maintaining fundamental ecosystem processes and the biodiversity of communities [17,18]. In addition to their ecological importance, maples are well-known and highly appreciated as ornamental trees for their attractive leaf shapes and autumn foliage colors [19]. A number of

* Corresponding author at: Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Jalan Tungku Link, BE1410, Brunei Darussalam
E-mail address: jstrijk@actg.science (J.S. Strijk).

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species are also valued as a source of timber and wood [20], sugar products [21], and medicinal or bioactive compounds [22].

Historically, the genus has been included either in the Sapindaceae [23,24] or in its own family Aceraceae together with the genus *Dipteronia* Oliv. consisting of two species endemic to China [11,25–28]. Molecular phylogenetic studies support the placement of *Acer* within the Sapindaceae, in the Hippocastanoideae clade together with *Dipteronia* (tribe Acereae), *Aesculus* L. (~13 spp.), *Billia* Peyritsch (two spp.), and *Handeliidendron* Rehder (one spp.) of tribe Hippocastaneae [29–33].

Given the global importance and distribution of the group, *Acer* has received substantial attention with regards to its biogeographic history and that of its role in the evolution of north temperate forests [34–37]. The genus has a remarkably rich fossil record that dates back to the late Paleocene (~60–56 Ma) and extends through most of the Cenozoic of the northern continents, most notably of western North America [15,34,38–40]. Because some of the earliest fossil occurrences and the greatest diversity (at both sectional and species level) have been recorded from this continent, it has been suggested that *Acer* originated in North America, where it experienced a major diversification by mid-Eocene (~49–47 Ma) followed by migrations to Asia and Europe [34,39]. The American origin is further supported by the fact that all reliable fossils of its sister genus, *Dipteronia*, are also from North America [41].

Phylogenetic analyses in *Acer* suggest a complex biogeographic history involving multiple migrations between the northern continents followed by waves of radiations and extinctions. For example, Renner et al. [37] found that the North American species diverged from their respective European and Asian relatives at widely different times between the late Eocene and late Miocene. These authors inferred a burst of diversification about 40 Ma followed by a decrease in the diversification rate between 30 and 20 Ma. This study, one of the largest in the genus in terms of species number and one of the few that have provided a time frame for some biogeographic events, however, was based on a few plastid loci and did not provide adequate resolution and support for the majority of major clades.

In a recent biogeographic analysis using a nuclear dataset of over 400,000 sites, [77] inferred eastern Asia as the most likely ancestral area for the genus, contradicting the American origin suggested by the fossil record. However, this study was limited by a reduced taxon sampling (30 taxa) and the fact that fossil data were not taken into account for the analysis. Here we use a supermatrix combining whole plastid genomes and nuclear data from 110 maple taxa to reconstruct the genus' evolutionary history. Our aim is to investigate the biogeographic history with an emphasis on the impact of climatic changes on its diversification and distribution. This is the first study that combines plastomes with a large nuclear dataset to generate a comprehensive phylogenomic evolutionary hypothesis for this diverse and economically important tree group.

2. Material and methods

2.1. Taxon sampling

We obtained leaf samples belonging to 87 species of *Acer* and four outgroup genera (*Aesculus*, *Dimocarpus* Lour., *Koelreuteria* Laxm. and *Litchi* Sonn) selected based on availability and results from previous phylogenetic studies [31,32,37]. Samples were collected from living plants in private and state institutions in Spain, France, and China (Supplementary Table S1) and kept frozen to generate whole plastomes and nuclear ribosomal cistron (NRC) sequences. Voucher specimens were deposited in the BGT herbarium (Guangxi University, China).

Additional plastome sequences from five maple species, two species of *Dipteronia*, and *Spondias mombin* L. (Anacardiaceae) were obtained from GenBank (Table S1). The plastid and NRC datasets were combined with the dataset of [77] consisting of over 500 nuclear loci obtained with hybrid enrichment for 65 species of *Acer* (<https://doi.org/10.5061/dryad.g9j13fm>).

The total number of *Acer* taxa included in our supermatrix was 110 (about 71% of the genus) (Supplementary Table S1). Almost all American and Eurasian species were included, and all taxonomic sections were represented except for section *Wardiana*, whose only species, *Acer wardii* W.W. Sm., could not be sampled.

2.2. Library construction, sequencing, and assembly

DNA extraction, library construction, and sequencing were performed by Annoroad Gene Technology (Beijing, PR China) Co., Ltd. as described by [42]. The assembly and annotation of the chloroplast genomes also followed [42]. Newly generated sequences were deposited in Genbank under the accession numbers MW067026–MW067100 (Table S1).

The nuclear ribosomal cistron region was assembled and annotated using Geneious v. 11.0.4 (Biomatters, Auckland, New Zealand) as described by [43]. For most species, we obtained partial NRC sequences from GenBank, which were used as references for the extended assembly of our sequences as detailed elsewhere [44]. The paired reads were mapped to the reference sequence with medium-low sensitivity for 100 iterations.

To annotate the assemblies, we first transferred the annotations of the ITS1, ITS2, and 5.8S regions from a published partial NRC sequence of *Acer campestre* L. (DQ238434) to our sequence of this species. To establish the boundaries of the 18S and 26S regions we used the NRC sequence of *Spondias tuberosa* Arruda (KX522674). The boundary of the ETS region was identified searching for the transcription initiation site (TIS) sequence, which in *Acer* is TCTTTAGGGGGG. The resulting annotated NRC sequence of *A. campestre* was subsequently used as a reference to annotate the remaining species. NRC sequences were submitted to GenBank and deposited under the accession numbers MW070114–MW070204 (Table S1).

2.3. Phylogenomic reconstruction

Phylogenomic reconstruction was performed for the combined supermatrix consisting of the whole plastome sequences, the nuclear ribosomal cistrons, and the nuclear dataset of [77]. Alignments of the plastome and the NRC datasets were performed using MAFFT [45] with default settings in Geneious and then concatenated with the nuclear dataset of [77] for a total-evidence analysis. The plastome dataset was divided into three partitions, each corresponding to one of its regions (LSC, SSC, and one IR). We did not perform a finer-scale partitioning (e.g., into genes and introns) because in a previous study we found no effect of partitioning at this scale on tree inference [42]. The NRC sequences were divided into six partitions (ETS, 18S, ITS1, 5.8S, ITS2, and 26S), whereas the nuclear dataset was treated as a single partition. This supermatrix was deposited in the Dryad repository with doi: 10.5061/dryad.wm37pvmh.

A partitioned maximum likelihood (ML) analysis was conducted in RaxML-NG [46] using the best-fit substitution model selected with ModelTest-NG [47] for each partition (Supplementary Table S2). We performed an 'all-in-one' analysis (ML tree search + standard non-parametric bootstrap) [48] with 25 randomized parsimony starting trees and 1000 bootstrap replicates to assess branch support.

2.4. Dating analyses and fossil selection

Divergence times among *Acer* lineages were estimated in BEAST 2.6.1 [49–52]. Data partitions were unlinked and priors were set for the parameters of the corresponding evolutionary models. The Relaxed Clock Log Normal was selected as clock model [53], and the Birth-Death model [54] was selected as tree prior. The two clock model parameters were assigned an exponential distribution with a mean of 10 for the *uclMean*, and a mean of 0.333 for the *uclStdev*. The parameters of the Birth-Death model (birth rate and relative death rate) were assigned an

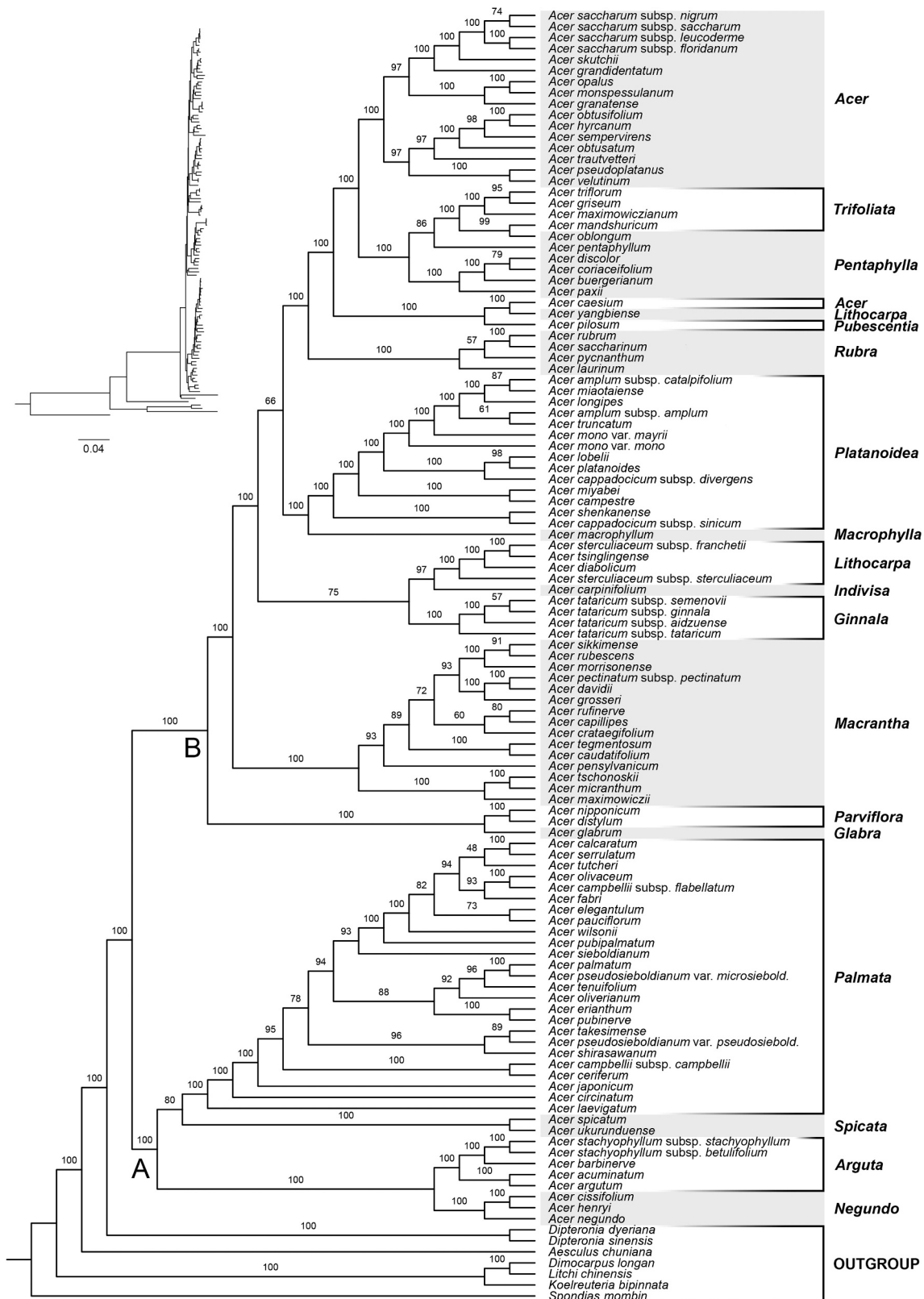


Fig. 1. Maximum likelihood tree of *Acer* based on the combined supermatrix (plastomes + nuclear loci) inferred with RaxML-NG. Names on the right indicate *Acer* sections. Letters A and B indicate the two major clades of *Acer* (see text for details).

exponential distribution with a mean of 1. Two independent runs of 1.2 billion generations each were performed in BEAST 2 on the CIPRES portal [55]. The convergence of both runs and ESS values were inspected with Tracer v1.7.1 [56]. Trees were sampled every 4000 generations

and combined with LogCombiner v2.6.0 (part of the BEAST 2 package, available at <https://www.beast2.org/>). The maximum clade credibility tree was constructed with TreeAnnotator v2.6.0 (also part of the BEAST 2 package) and edited in FigTree v1.4.3.

To calibrate our phylogenetic tree, we selected four fossil species of *Acer* and the oldest fossil record of *Dipteronia* as an external calibration point. *Dipteronia*, now consisting of two species endemic to China, is relatively well represented in the Paleogene of western North America but is absent from the fossil record of Asia. The age of the oldest known fruits is 63–60 Ma old [41]. This was used to set the minimum age of this genus.

The oldest *Acer*-like leaves and *Acer*-like fruits are from the late Paleocene of several high-latitude locations of the Palearctic region [40,57]. These fossils are often reported in the literature as ‘*Acer arcticum* Heer’, a variable taxon comprising a number of early morphospecies from the Paleocene and Eocene [34,40]. The oldest unequivocal fossil leaves of *Acer* from North America correspond to *A. alaskense* Wolfe & Tanai from the late Paleocene of Southern Alaska [34]. Samaras, leaves, and *Acer*-like pollen have also been recorded from late Paleocene locations of Canada and the US [58–60], indicating that the genus was already well established by the end of this epoch about 60 Ma. We used this age of 60 Ma to constrain the crown age of the genus *Acer*.

Despite a rich fossil record, it is very difficult to place extinct species of *Acer* in modern sections. Several authors [34,40] have assigned fossil leaves and detached samaras to currently recognized sections, but most of these assignments are not reliable because the fossils lack the diagnostic characteristics of the sections, and can match the morphology of more than one section [61]. For this reason, we did not include a high number of *Acer* fossils in our analysis but rather selected two fossil species that can be confidently assigned to extant clades and thus can provide internal calibration points.

The clade formed by members of section *Macrantha* was assigned a minimum age of 43 Ma based on fossil leaves of *Acer dettermani* Wolfe & Tanai from the middle Eocene of Alaska [34]. This species appears to be the oldest taxon assignable to this section. Its placement was confirmed by McClain (2000), who studied the venation pattern and the margin characters of the leaves. *Acer trifoliatum* Geng, described from the middle Miocene (16–13 Ma) of China [40], was assigned to the clade formed by three species of section *Trifoliata*: *Acer triflorum* Kom., *A. griseum* (Franch.) Pax, and *A. maximowiczianum* Miq. *Acer trifoliatum* was found to be closely related to *A. triflorum* based on a study of the leaf morphology that included many micromorphological features of the epidermal cells [62].

2.5. Ancestral range estimation

Ancestral ranges of *Acer* were inferred with the package BioGeoBEARS [63–65] in R [66]. We assigned *Acer* species to five biogeographic regions based on their native distribution: Western Nearctic (A), Eastern Nearctic (B), Western Palearctic (C), Eastern Palearctic (D), and Indomalaya (E). Geographic distribution was compiled from the literature [11,13] as well as online databases [67,68].

We performed non-stratified analyses, with and without fossil data, to test for several possible biogeographic scenarios. In the analysis incorporating fossil data, we constrained the ranges at three nodes based on the occurrence of the fossil species we used for calibration. *Acer alaskense*, *A. dettermani*, and *Dipteronia brownii* McClain & Manchester are from western North America and so the respective nodes were ‘fixed’ to include this information. In both types of analyses, we implemented the DEC, DIVALIKE, and BAYAREA models along with their +J versions and determined the one that best fits our data by using the AIC scores and Akaike weights. The probabilities of the ancestral states estimated with the best-fitting model were plotted as pie charts at the nodes of the chronogram inferred with BEAST.

2.6. Diversification analyses

We used the R package Phytools [69] to generate a lineage-through-time (LTT) plot for maples and to perform the Monte Carlo constant-rates (MCCR) test [70]. Rates of diversification through time were

estimated with the R package TESS [71]. We considered the following three models: a constant-rate birth-death (BD) process, an episodically variable-rate birth-death (EBD) model, and a birth-death process with one mass-extinction event (based on the high number of fossil species of maples) [71,72]. For the constant-rate BD process, we used an exponential prior distribution for both the speciation and extinction-rate parameters. For the EBD model, we assumed a single speciation-rate shift and a single extinction rate-shift. We used exponential prior distributions for the four model parameters (speciation and extinction rates before and after the shifts). For the BD process with one mass-extinction event, we assumed a survival probability of 30%. The speciation and extinction-rates parameters were assigned an exponential distribution, whereas the mass extinction time was assigned a uniform distribution. To account for incomplete taxon sampling, the parameter rho was set to 0.71 (the sampled fraction in *Acer*) in all models assuming a uniform (random) sampling. All analyses were run for 50,000 generations with a burnin of 20%. Stationarity was visually inspected using the trace plots. The relative fit of each model to the data was assessed via Bayes Factors comparison [71].

Additionally, we performed a compound Poisson process on Mass-Extinction Times (CoMET) analysis [73] in the package TESS to further explore the impact of mass-extinction events on the diversification of *Acer*. The CoMET method uses rjMCMC to estimate the parameter probabilities of an episodic BD model, including the number and timing of shifts in speciation and extinction rates, the speciation and extinction rates between the shifts, and the number, timing, and magnitude of mass-extinction events [73]. We assumed a survival probability of 30% and set the sampling fraction to 0.71, similar to previous models.

3. Results

3.1. Genomic data and evolutionary relationships

A total of 75 plastomes and 91 NRC sequences were generated in this study. Twenty-four previously published plastomes were incorporated from GenBank for a total of 99 plastid genomes, all representing different taxa (Table S1). The plastomes of *Acer* ranged in size from 155,212 (*A. carpinifolium* Siebold & Zucc.) to 157,046 bp (*A. tenuifolium* (Koidz.) Koidz.). The NRC sequences varied from 7264 (*A. micranthum* Siebold & Zucc.) to 7641 bp (*A. pycnanthum* K. Koch). The supermatrix combining these sequences with the nuclear dataset of Li et al. (2019) consisted of 117 taxa and 585,780 aligned sites, of which 155,166 were plastid, and 430,614 were nuclear (Table S2).

The Maximum Likelihood analysis recovered two major clades of *Acer* with maximum support, one predominantly Asian and comprising species of sections *Negundo*, *Arguta*, *Spicata*, and *Palmata* (clade A in Fig. 1), and the other comprising the remaining sections which include Asian, European, and American species (clade B). Section *Negundo* was placed as sister to *Arguta* (BS = 100%), whereas *Spicata* was sister to *Palmata* (BS = 80%) (Fig. 1). Within the second major clade (B), species were grouped into five mutually exclusive clades with monotypic section *Glabra* plus section *Parviflora* sister to the clade including all other sections (BS = 100%). Most sections were recovered as monophyletic except for *Trifoliata*, *Pentaphylla*, *Acer*, and *Lithocarpa*. Sections *Trifoliata* and *Pentaphylla* were paraphyletic with *A. oblongum* Wall. ex DC. and *A. pentaphyllum* Diels more closely related to members of *Trifoliata* than *Pentaphylla*. Sections *Acer* and *Lithocarpa* were both biphyletic. *Acer caesium* Wall. ex Brandis (section *Acer*) and *A. yangbiense* Y.S. Chen & Q. E. Yang (section *Lithocarpa*) fell outside their respective clades, the two forming a sister pair with *A. pilosum* Maxim. of section *Pubescentia* (BS = 100%) (Fig. 1).

3.2. Divergence times

The maximum clade credibility tree resulting from the Bayesian analysis of the supermatrix in BEAST 2 was strongly supported and

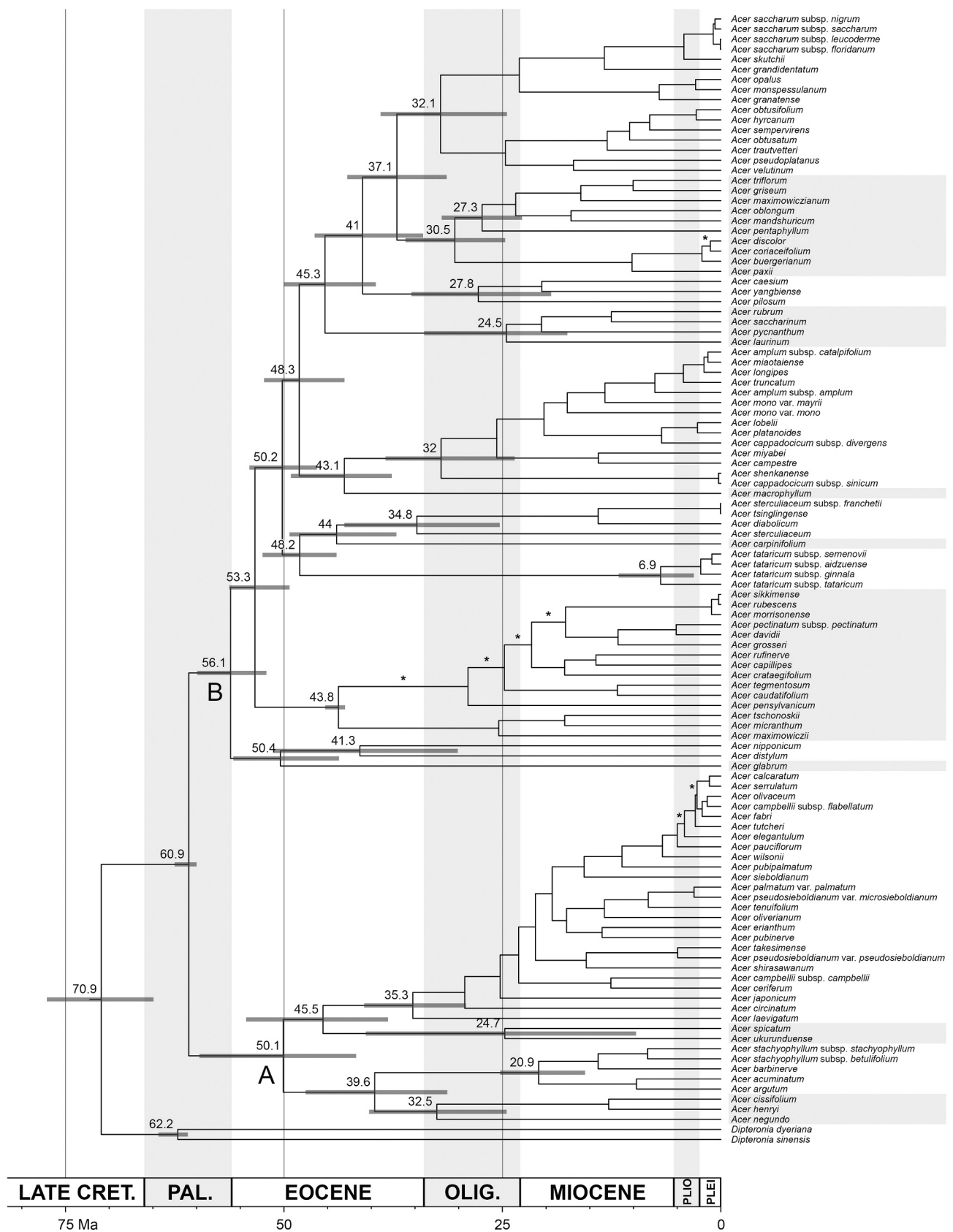


Fig. 2. Chronogram of *Acer* resulting from the analysis of the supermatrix (plastomes + nuclear loci) in BEAST 2. Numbers at the nodes are ages in million years (shown only for major clades and sections). All branches have posterior probabilities of 1.00 except for those with an asterisk, which have PP between 0.5 and 0.97.

Table 1Age estimates for the *Acer* genus and its sections inferred from the analysis in BEAST 2.

	Stem		Crown	
	Age in My (95% HPD interval)	Geologic epoch	Age in My (95% HPD interval)	Geologic epoch
<i>Acer</i> genus	70.9 (64.9–77.1)	Late Cretaceous	60.9 (60–62.5)	Middle Paleocene
Clade A (sections <i>Negundo</i> , <i>Arguta</i> , <i>Spicata</i> and <i>Palmata</i>)	60.9 (60–62.5)	Middle Paleocene	50.1 (41.7–59.7)	Early Eocene
Clade B (all other sections)	60.9 (60–62.5)	Middle Paleocene	56.1 (52–59.9)	Late Paleocene–Early Eocene
Section <i>Macrantha</i>	53.3 (49.4–56.3)	Early Eocene	43.8 (43–45.3)	Middle Eocene
Section <i>Parviflora</i>	50.4 (43.7–55.8)	Early Eocene	41.3 (30.1–51.2)	Middle Eocene
Section <i>Glabra</i>	50.4 (43.7–55.8)	Early Eocene		
Section <i>Ginnala</i>	48.2 (44–52.5)	Early Eocene	6.9 (3.1–11.7)	Late Miocene
Section <i>Palmata</i>	45.5 (38.1–54.3)	Middle Eocene	35.3 (29.2–40.8)	Late Eocene
Section <i>Spicata</i>	45.5 (38.1–54.3)	Middle Eocene	24.7 (9.7–40.6)	Late Oligocene
Section <i>Rubra</i>	45.3 (39.5–50)	Middle Eocene	24.5 (17.6–34)	Late Oligocene
Section <i>Lithocarpa</i>	44 (37.1–49.4)	Middle Eocene	34.8 (25.3–43.1)	Late Eocene
Section <i>Indivisa</i>	44 (37.1–49.4)	Middle Eocene		
Section <i>Platanoidea</i>	43.1 (37.7–49.2)	Middle Eocene	32 (23.6–38.4)	Early Oligocene
Section <i>Macrophylla</i>	43.1 (37.7–49.2)	Middle Eocene		
Section <i>Negundo</i>	39.6 (31.3–47.5)	Middle Eocene	32.5 (24.5–40.3)	Early Oligocene
Section <i>Arguta</i>	39.6 (31.3–47.5)	Middle Eocene	20.9 (15.5–25.3)	Early Miocene
Section <i>Acer</i>	37.1 (31.4–42.8)	Late Eocene	32.1 (24.5–38.9)	Early Oligocene
Sections <i>Trifoliata</i> + <i>Pentaphylla</i>	37.1 (31.4–42.8)	Late Eocene	30.5 (24.7–36.1)	Early Oligocene

highly congruent with the ML tree (Fig. 2), with only minor differences in the placement of a few species within sections *Palmata* and *Platanoidea*, and among subspecies of *Acer tataricum* L. (section *Ginnala*). The analysis placed the split between *Acer* and *Dipteronia* in the late Cretaceous (~71 Ma), and the crown age of *Acer* in the middle Paleocene (~61 Ma). The two major lineages within the genus began to diversify in the late Paleocene–early Eocene, ca. 56 and 51 Ma, respectively (Fig. 2, Table 1).

The four sections of clade A (*Negundo*, *Arguta*, *Spicata*, and *Palmata*) differentiated in the middle Eocene (Fig. 2). Section *Palmata* separated from section *Spicata* 45.5 Ma, whereas *Arguta* and *Negundo* diverged from each other about 6 Ma later. Section *Palmata*, the largest and most diverse of the genus, began to diversify in the Late Eocene (~35 Ma). The other three much smaller sections diversified during the Oligocene and Miocene.

Within clade B, sections *Macrantha*, *Glabra*, and *Parviflora* diverged in the early Eocene (53–50 Ma), followed by section *Ginnala* (~48 Ma). Sections *Lithocarpa*, *Indivisa*, *Macrophylla*, *Platanoidea*, and *Rubra* differentiated around the same time in the middle Eocene (45–43 Ma). Sections *Acer* and *Trifoliata* + *Pentaphylla*, the most recently divergent groups, split in the late Eocene (~37 Ma). Diversification of these sections was estimated to have begun in the middle Eocene (43.8 Mya) and

continued throughout the Oligocene and Miocene. Several closely related species (and their subspecies) within sections *Acer*, *Trifoliata*, *Platanoidea*, *Lithocarpa*, *Ginnala*, and *Macrantha* appear to have originated more recently during the Plio-Pleistocene (Fig. 2).

3.3. Ancestral range estimation

Both, the unconstrained and the fossil-constrained analyses in Bio-GeoBEARS strongly favored the DEC + J model over the six models tested (Tables S3 and S4). However, the LnL value for this model was considerably lower ($\Delta\text{AIC} = 22.4$) in the fossil-constrained analysis, thus favoring the unconstrained analysis. This placed the origin of the genus in the Eastern Palearctic region, where it underwent its initial diversification to later spread to North America, Europe, and south into the Indomalayan region (Fig. 3).

Migrations from the Eastern Palearctic region to the Nearctic were inferred to have occurred at least seven times between the early Eocene (*A. glabrum* Torr. lineage) and early Miocene (*A. rubrum* L. + *A. saccharinum* L.). In all probability, this movement took place overland via the Bering Land Bridge, which allowed the floristic exchange between Eastern Asia and North America from the late Cretaceous to late Neogene [74].

Movement from the Eastern Palearctic region westwards to West Asia and Europe also occurred multiple times (Fig. 3). The earliest colonization to the west took place in the late Eocene (~37 Ma) with the separation of the lineage leading to section *Acer*. A second migration around 20 Ma gave rise to a group of European and West Asian species of section *Platanoidea* (*A. cappadocicum* Gled. subsp. *divergens* (Pax) A.E. Murray, *A. lobelii* Ten., and *A. platanooides* L.). *Acer campestre*, another widely distributed Eurasian species from section *Platanoidea*, diverged from its East Asian sister *A. miyabei* Maxim. around 15 Ma, whereas *Acer tataricum* subsp. *tataricum*, the westernmost subspecies of *A. tataricum* (Section *Ginnala*) appears to have originated as result of a recent migration ca. 7 Ma (Fig. 3).

Dispersal from Europe to eastern North America was inferred to have occurred only once, at the Oligocene/Miocene boundary (~23 Ma). This event led to the origin of the American series *Saccharodendron* of section *Acer* (represented in our study by *A. saccharum* Marshall, *A. grandidentatum* Nutt., and *A. skutchii* Rehder) (Fig. 3).

Southward spread from the Eastern Palearctic into the Indomalayan region appears to have occurred relatively recently, beginning in the middle Miocene (~15 Ma) and onward, except for the *A. laurinum* lineage, the southernmost species, which separated from the other species of section *Rubra* in the late Oligocene, ca. 25 Ma.

3.4. Diversification analyses

The LTT plot of *Acer* shows an initial period of constant accumulation of lineages followed by an increase between ~50 and ~40 Ma after which the lineage accumulation appears to slow slightly and remain nearly constant to the present (Fig. 4). The results of the MCCR test indicate that this pattern observed in *Acer* is not significantly different from the one expected under the null model of constant speciation and extinction rates ($\gamma = -0.8609$, $p = 0.92$).

Of the three branching-process models compared in TESS, we found positive but low support for the birth-death process with one mass-extinction event over the episodic BD model (BF = 3.12), but no support over the constant-rate BD process (Table S5). The CoMET analysis identified one significant extinction event (2 ln BF = 6) at ~3 Ma (Fig. 5 H, I). No shifts in the speciation or extinction rates were detected (Fig. 5 B, C, and E, F). The net-diversification rate was highest at 50 Ma in the early Eocene and then gradually decreased to remain relatively constant from the middle Eocene (~40 Ma) to the late Miocene (~10 Ma). It was lowest in the Plio-Pleistocene (last 4 Ma) due to increased extinction in this period (Fig. 5 A, D, G).

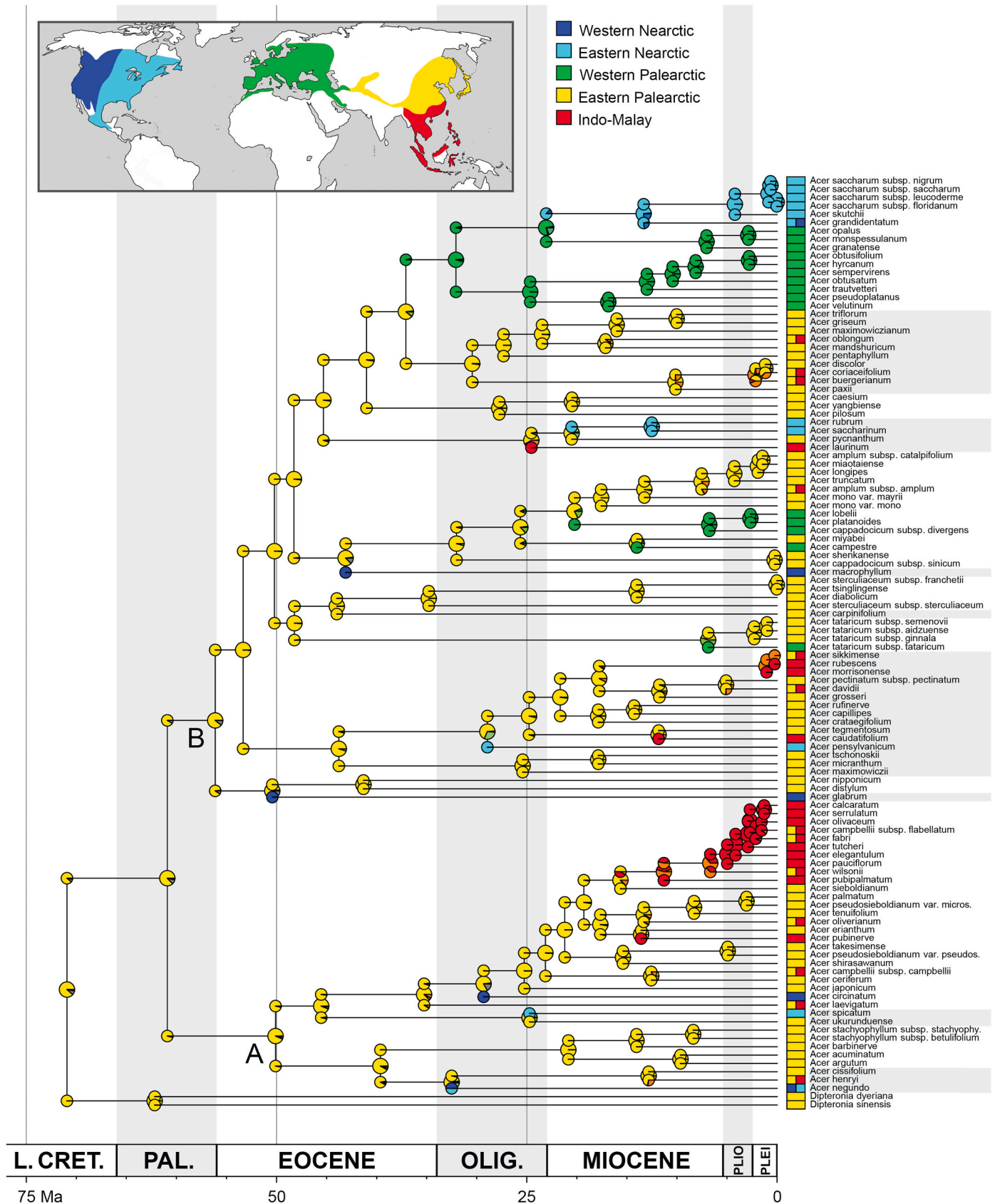


Fig. 3. Ancestral geographic ranges of *Acer* inferred with BioGeoBEARS using the DEC + J model in the unconstrained analysis (ancstates: global optim, 2 areas max. $d = 0.0022$; $e = 0$; $j = 0.0174$; $\text{LnL} = -152.92$). The inset map shows the present distribution of the genus.

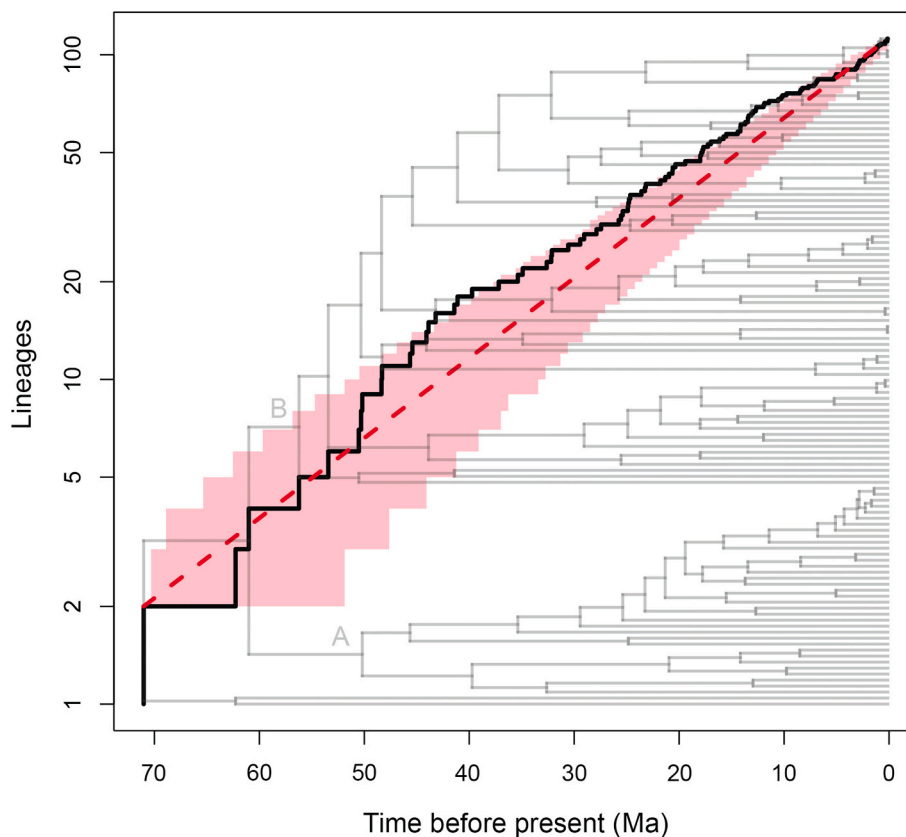


Fig. 4. Lineage-through-time (LTT) plot for *Acer* (black line). The dashed red line is the expected LTT plot under a pure-birth (no extinction) process. The pink area represents the 95% confidence interval based on 1000 simulated trees assuming a pure-birth process. The tree in the background is the maximum clade credibility tree. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Phylogenomic relationships

Our ML and Bayesian trees obtained with the combined plastid and nuclear datasets largely agree with the infrageneric classification of maples. Of the 18 currently accepted sections [9,75], 13 are well-supported in our study (BS = 100%, PP = 1.00) and only four, *Trifoliata*, *Pentaphylla*, *Acer*, and *Lithocarpa*, are non-monophyletic due to the placement of four species: *A. oblongum*, *A. pentaphyllum*, *A. caesium*, and *A. yangbiense* (Fig. 1). Only the monotypic section *Wardiana* was not included in this study.

Our results confirm previous analyses showing the close relationship between sections *Trifoliata* and *Pentaphylla* [37,42,76,77] and provide further evidence for merging of the two groups (Fig. 1). Shared morphological features, including the presence of compound leaves, corymbiform inflorescences, extrastaminal floral disk, and convex or inflated seed locules [11,14] also point to the strong association between the two sections.

Sections *Acer* and *Lithocarpa* are both biphyletic due to the exclusion of *A. caesium* and *A. yangbiense*, respectively (Fig. 1). *Acer caesium*, the only extant East Asian member of section *Acer*, appears to be a distinct, genetically isolated taxon that has been previously recovered outside the *Acer* core clade both in the ITS [76,78] and plastid trees [37,79]. This species was placed in our trees sister to the Chinese endemic *A. yangbiense* and forming a strongly supported (BS = 100%, PP = 1.00) clade together with *A. pilosum* of section *Pubescentia* (Fig. 1). However, in the nuclear tree of Li et al. (2019) *A. caesium* and *A. yangbiense* were grouped together within section *Acer*, suggesting that the dissimilar placement in our trees is given by the signal contained in the plastid genome. A plausible explanation might be chloroplast capture via ancient

hybridization between *A. caesium*-*A. yangbiense* and *A. pilosum* lineages. The latter species was not included in the study of Li et al. (2019) and is represented in our analyses only by the plastid genome and the NRC cistron. It was recovered in the plastid tree of Renner (2008) forming a sister pair with *A. caesium* as in our study, but it was placed sister to the *Pentaphylla-Trifoliata* clade in the ITS tree of Grimm et al. (2006).

Aside from the different placement of the *A. caesium* -*A. yangbiense* lineage, relationships among sections are consistent with the nuclear tree of [77]. The only exception concerns section *Spicata*, which was recovered in our analyses as sister to section *Palmata* (Fig. 1). By contrast, it was placed as sister to a clade formed by sections *Negundo*, *Arguta*, and *Palmata* [77].

4.2. Historical biogeography

Our analyses placed the origin of *Acer* in the Eastern Palearctic region, and a crown age of 61 Ma, similar to previous estimates [77], but 15 Ma older than the age inferred by [37]. Estimates for the divergence times between the New World and Old World lineages are, in general, older than the ones inferred by these authors (Table 1, Figs. 2 and 3).

Wolfe and Tanai [34] proposed an American origin for *Acer* based on a detailed revision of North American megafossils. Around 100 fossil species have been described from this continent [34,80] compared to approximately 45 and 50 from Eurasia and East Asia, respectively [40,81–83]. This greatest diversity led to suggest an initial radiation in North America with subsequent dispersals to East Asia and Europe [34,39,40]. However, no migrations from North America to Asia or Europe were inferred in the most likely biogeographic scenario. When the deepest nodes of our tree were constrained to include Western North America within the ancestral distribution range, the resulting LnL values were significantly lower ($\Delta\text{AIC} > 10$) than the ones obtained in the

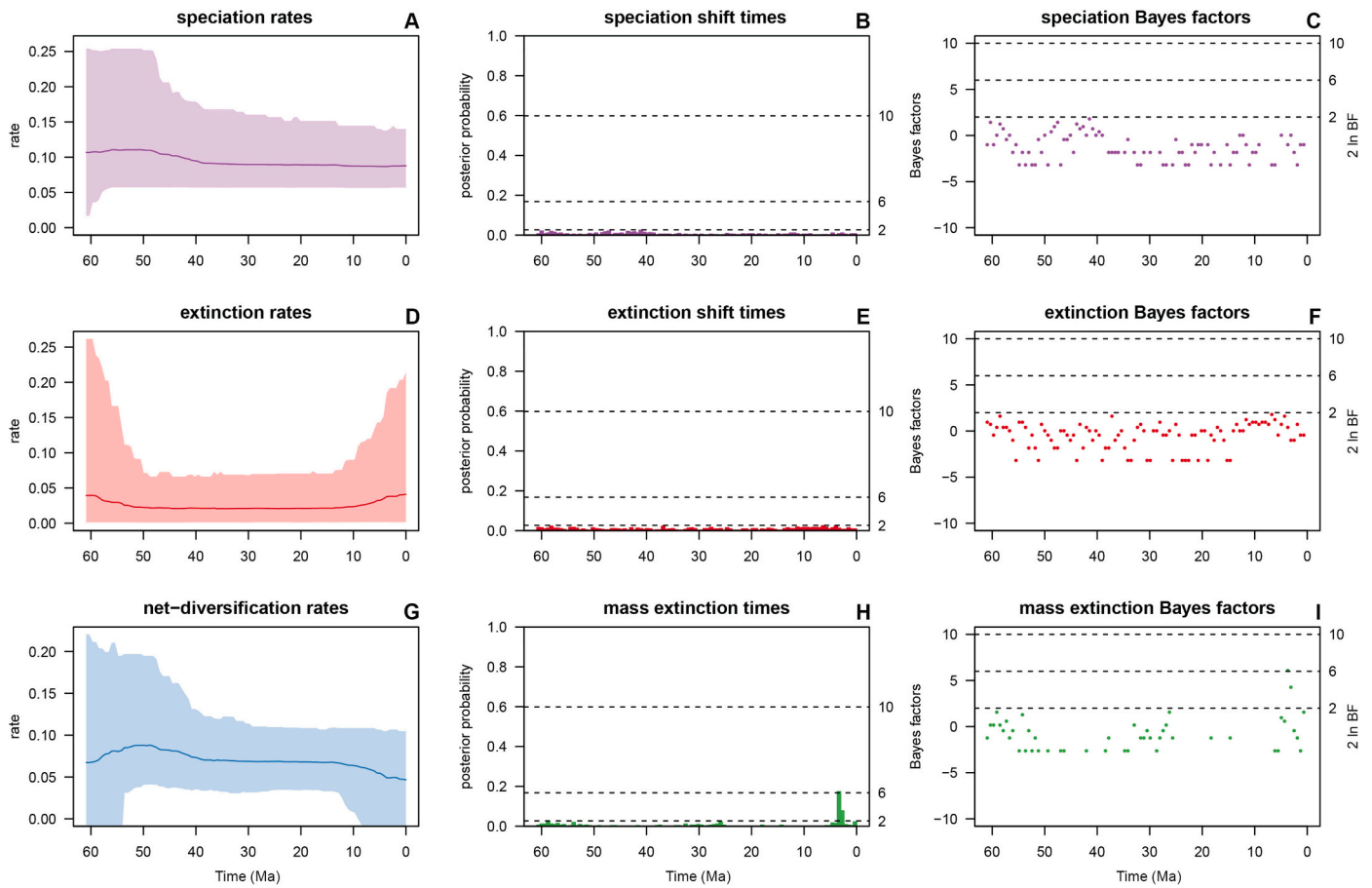


Fig. 5. Results of the CoMET analysis. A, D, G: Plots of speciation, extinction, and diversification rates over time. Shaded areas indicate the 95% credible interval. B, E: Posterior probabilities for speciation and extinction-rate shifts. No significant shifts were detected (all bars are below the significance thresholds). H: Posterior probabilities for the mass-extinction events. A significant mass extinction event ($2 \ln BF \sim 6$) that occurred ca. 3 Ma was identified. C, F: Bayes Factor values for the speciation and extinction-rate shifts. I: Bayes Factor values for the mass extinction events.

unconstrained analysis (Tables S3 and S4).

Acer first emerged in the fossil record of the Russian Far East and Alaska almost simultaneously [34,40,57]. The genus most likely originated in the north-eastern Palearctic from where it dispersed to North America soon after its appearance. Based on fossil evidence, it appears to have diversified rapidly in western North America to later undergo significant extinction in this continent. More than 50 fossil species from at least 15 sections are recorded just from the Eocene of North America compared to six in Asia [34,40], but only 12–13 American species exist today. Most of these, e.g., *Acer macrophyllum* Pursh, *A. glabrum*, and *A. negundo* L. are placed in our time-calibrated tree on long branches that go back to the Eocene and Oligocene (Figs. 2 and 3), reflecting the past extinctions along these old lineages.

The several migrations to the Nearctic occurred across widely different time periods (Fig. 3), meaning that *Acer* spread (and diversified) under a broad range of climatic conditions. The Beringia corridor would have allowed the eastward movement, first during the warm and wet climate of the late Paleocene-early Eocene (e.g., *A. glabrum* lineage), and later during the cooler and drier regimes of the Oligocene and early Miocene (Fig. 3) [74,84]. According to the fossil record, *Acer* became a common component of the broad-leaved deciduous forests of North America by the late Eocene [34].

The migration from East Asia into Europe was inferred to have begun in the late Eocene with the separation of section *Acer* from the Asian *Pentaphylla-Trifoliata* lineage (Fig. 3). This estimate is consistent with the fossil evidence. The oldest records of *Acer* in Europe are from the late Eocene (Priabonian) of Spitsbergen [85], and the oldest records assignable to section *Acer* (*A. haselbachense* Walther and *A. engelhardtii* Walther), are from the early Oligocene of Central Europe [86,87]. The presence of *Acer* fossils in Svalbard points to early movement from the north through the arctic islands and across Greenland to Western Europe. Subsequent migrations from the east would have been possible after the closure of the Turgai Seaway in the early Oligocene (~30 Ma), a time during which temperate broad-leaved deciduous forests were expanding in response to a cooler, dryer, and more seasonal climate [4,86].

The ancestor of the sugar maple group (series *Saccharodendron* of Section *Acer*) would have reached Eastern North America from Europe by the beginning of the Miocene (Fig. 3) through long-distance dispersal, likely via Iceland-Greenland. The earliest fossils assignable to this series are from several early Miocene localities of western North America (British Columbia, Oregon, Nevada) [34], indicating rapid colonization and broader distribution in North America than the present. Fossils of *Saccharodendron* are absent from Alaska and high latitude locations of Eastern Asia [34], but they have been reported from the middle-late Miocene (12 Ma) of Iceland [88], lending support to the transatlantic migration of the *Saccharodendron* lineage inferred in our study.

The southward movement of *Acer* into the Indomalayan tropics (Fig. 3) was likely driven by the climatic cooling during the Oligocene and Miocene. Given the strong floristic affinities with several Eocene plant assemblages from the northern hemisphere, the Indomalayan region has been viewed as a refugium for the once widespread Eocene ‘boreotropical’ flora of which *Acer* was a part [89,90].

4.3. Diversification of *Acer*

Acer diversified most rapidly in the early to middle Eocene (55–45 Ma). Diversification remained relatively constant afterward with no appreciable changes in the speciation and extinction rates until the late Miocene. It declined in the last five million years as extinction increased, presumably with the Plio-Pleistocene glaciations (Fig. 5).

Dating analysis shows that *Acer* sections differentiated over a period of ~15 Ma, between the early and mid-Eocene, except for *Acer* and *Pentaphylla + Trifoliata*, which split at the end of the Eocene (Table 1, Figs. 2 and 3). A similar inference was drawn by Wolfe and Tanai (1987) based on the fossil record. These authors noted that the “simultaneous

occurrences in the early middle Eocene of species that represent divergences leading to major groups indicate that evolution was proceeding at a very rapid pace” [34]. The rapid differentiation of major lineages may have been favored by the warm climate of the early Eocene. *Acer* fossils from this period belong to megathermal and mesothermal plant assemblages despite the genus being now primarily found in mesothermal to microthermal vegetation [34]. The cool tolerance likely evolved progressively from the late Eocene as microthermal climates extended through the northern hemisphere.

Our findings show that *Acer* diversified at a constant rate during the Oligocene and Miocene and that diversification does not appear to have been affected by the climatic cooling of the Eocene-Oligocene transition. However, the CoMET analysis detected one extinction event at ~3.5–3 Ma that coincides with the start of the Plio-Pleistocene glacial cycles in the northern hemisphere (Fig. 5). As in many north temperate groups, the evolutionary history and distribution of *Acer* were shaped by the climatic fluctuations of the last 3.5 Ma [91]. In particular, the climatic changes associated with the advance (and retreat) of ice sheets over extensive areas of North America and Europe would lead to the extinction of a large fraction of the *Acer* diversity in these continents [92]. In East Asia, extinction was less severe due to much larger ice-free refugia that harbored the flora during the glacial peaks [93,94].

Several of the North American and Eurasian lineages of *Acer* appear to have experienced some but limited diversification during the last 5–4 Ma; for example, series *Saccharodendron*, and various groups of Eurasian species within sections *Acer* and *Platanoides* (Fig. 3.). This is likely to have been generated through allopatric speciation driven by isolation in glacial refugia [94].

5. Conclusions

Using a genome-wide supermatrix combining both plastomes and nuclear loci we reconstructed the most complete phylogenomic evolutionary hypothesis of maples to date. The results of our analyses do not support the American origin suggested by earlier paleobotanists [34], but instead indicate an East Asian origin for the group. We argue that the greater abundance of maple fossils in North America is due to a higher sampling intensity in this continent, given by a long history of geological exploration and paleobotanical research [95].

The biogeographic patterns inferred from our genomic data are very similar to those of other woody north-temperate genera (e.g., *Aesculus* [96], *Prunus* [97], *Fagus* [98,99]), and agree with the paleobotanical evidence for the origin and migration of the north-temperate flora [100]. Our results highlight the significance of the (north-)eastern Palearctic region as the center of origin and early development for many north-temperate groups, as well as the impact of climatic changes, in particular of the climatic deterioration of the last five million years, on the evolution and distribution of the vegetation in the northern hemisphere.

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Declaration of Competing Interest

We declare that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ygeno.2021.01.014>.

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