

RESEARCH ARTICLE

Waves of range dynamics and gene flow characterize the biogeographic history of *Litsea elongata*, a dominant tree in East Asian evergreen broadleaved forests

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Societal Impact Statement

Evergreen broadleaved forests (EBLFs) represent an iconic vegetation type in subtropical montane East Asia, but they are experiencing intensifying anthropogenic pressure and increasing habitat fragmentation. Here, using a dominant and widespread tree species characteristic of East Asian EBLFs, we examine its phylogeographic history and evaluate what it implies about connectivity via gene flow among subtropical montane forests. We found that the montane EBLFs of East Asia, presently disjunct, may have been extensively connected in the past. This work advances our understanding of the biogeography of East Asian EBLFs and provides evidence relevant to their conservation and management.

Summary

- Evergreen broadleaved forests (EBLFs) are widely distributed across montane regions of subtropical East Asia, but the evolutionary histories of their dominant species remain poorly understood.
- Here, we combine phylogenetic, population genetic, biogeographical, and fossil evidence to investigate the biogeographic history of *Litsea elongata*, a dominant and widespread tree in East Asian EBLFs.
- We identified distinct geographic clades of *L. elongata* and determined that present patterns of genetic diversity have been shaped by past waves of range expansion, gene flow, and range contraction. Two distinct clades co-occur sympatrically in the Himalaya-Hengduan Mountains, one of which experienced gene flow with a disjunct karst-specialized clade in southwest China. We also detected ancient gene flow between this karst clade and a clade in eastern China, presently separated by over 800 km.

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[Correction added on 13 April 2026, after first online publication: Figure 1 image panel D has been updated for accuracy.]

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- The geographic range of *L. elongata* has been historically dynamic and suggests that the dominant tree of EBLFs had more extensive ancient connections across distinct montane regions in subtropical East Asia than previously recognized.

KEYWORDS

climate change, evergreen broadleaved forests (EBLFs), gene flow, geogenomics, subtropical China

1 | INTRODUCTION

The subtropical latitudes of East Asia are dominated by an iconic vegetation type, evergreen broadleaved forests (EBLFs; Song & Da, 2016). Recent studies have suggested that East Asian EBLFs originated in the Eocene, or at the latest before the Early Oligocene (Hai et al., 2022; Qin et al., 2023; Zhang et al., 2024; Zhao et al., 2024), but their dominant extant species, such as those in Fagaceae and Lauraceae, started to occur after the Miocene (Hai et al., 2022; Ye & Li, 2022). During the Miocene to Pleistocene, drastic environmental changes, including global cooling, glacial periods, and intensification of the East Asian monsoon, led to habitat fragmentation and the formation of refugia, driving plant diversification (Kong et al., 2017; Qian & Ricklefs, 2000; Qin, Chen, et al., 2024; Wang et al., 2015) and shaping the current phylogeographic patterns of species in modern EBLFs (Hewitt, 2000; Liu et al., 2012; Lu et al., 2020; Ye et al., 2017; Ye & Li, 2021). Unlike species in Europe and North America, which largely followed a common pattern of southward retreat during glacial periods and northward expansion during interglacial periods (Hewitt, 2000; Hewitt, 2004; Shafer et al., 2010), species in East Asian EBLFs exhibited species-specific responses to Pleistocene climate cycles (Fan et al., 2016; Gong et al., 2015; Luo et al., 2021; Meng et al., 2025; Tang et al., 2022; Tian et al., 2015; Wang et al., 2015; Wei & Zhang, 2022; Ye et al., 2019). This difference was likely due to the limited extent of Pleistocene glaciation in subtropical East Asia (Jin et al., 2019). Recent megafossil evidence suggests that cold-tolerant EBLF species occupied a broader historical range during cold periods (Huang et al., 2024; Huang, Li, Huang, Jin, & Oskolski, 2023), whereas warm-adapted species underwent significant range contraction during these times (Huang, Li, Huang, Xiang, et al., 2023). These prior studies provided important insights into how EBLF species responded to Pleistocene climate oscillations, but most were based on fossil evidence or molecular data from limited genetic markers. Here, we combine genomic and fossil data to investigate the history of EBLFs with greater power.

Across most of subtropical East Asia, EBLFs are primarily montane, in part because they face greater anthropogenic pressures with growing habitat loss and fragmentation (Tang, 2015). They occur as mid-elevation cloud forests in the Himalaya and Hengduan Mountains, in karst regions in southwest China, and in refugial montane areas of central and eastern China (Lu et al., 2018; Tang, 2015; Ye & Li, 2022; Yu et al., 2017). These diverse montane regions may have served as corridors for species dispersal (Fu & Wen, 2023; Perrigo

et al., 2020) and migration among regions (Li et al., 2024; Zhu et al., 2020), while simultaneously acting as geographical barriers, impeding local gene flow across mountain passes (Fu et al., 2024; Perrigo et al., 2020; Wang et al., 2024). However, the historical connections between mountain regions that have shaped the modern distribution of dominant trees of EBLFs in East Asia remain poorly understood. This underscores the need to elucidate how dominant species have come to form their present biogeographic distributions to protect this iconic vegetation and guide conservation efforts.

In this study, we investigate *Litsea elongata* (Wall. ex Nees) Benth. and Hook. f. (Lauraceae), a dominant EBLF tree (Song et al., 2015) that is widespread across subtropical East Asia. In the Himalayas-Hengduan Mountains, *L. elongata* occurs in cloud forests at elevations ranging from approximately 2000 to 2500 m. In this region, bark color is polymorphic, with reddish and gray-green individuals co-occurring within local populations. In southwest China, *L. elongata* var. *subverticillata* (Y.C. Yang) Yen C. Yang and P.H. Huang occurs at elevations from 1400 to 2500 m, particularly in karst areas, and has gray-green bark and subverticillate, thinner leaves. In Yunnan and Guizhou, *L. elongata* var. *faberi* (Hemsl.) Yen C. Yang and P.H. Huang has reddish bark and narrowly oblong-lanceolate leaves with caudate or long-caudate apices (Li et al., 2008). In central and eastern China, the species has reddish bark and occurs at elevations ranging from 500 to 1500 m; some individuals in eastern China have subverticillate leaves. The fossil record of *L. elongata* includes two well-preserved leaves, one from the Pliocene of Nepal (Paudyal, 2015), and the other from the Late Miocene Shengxian Formation in eastern China (He et al., 2023).

Our primary questions are: How is the widespread distribution of *L. elongata* genetically structured? How was its present range formed, and what does this reveal about historical connections between montane regions in subtropical East Asia? How does morphological variation, especially the bark color across regions, align with genetic structure, geography, and the fossil record?

2 | MATERIALS AND METHODS

2.1 | Sample collection and whole-genome resequencing

We sampled 224 individual *L. elongata* and 35 outgroup individuals, covering subtropical East Asia and representing the entire natural geographic range of *L. elongata* (Figure 1). Genomic DNA was

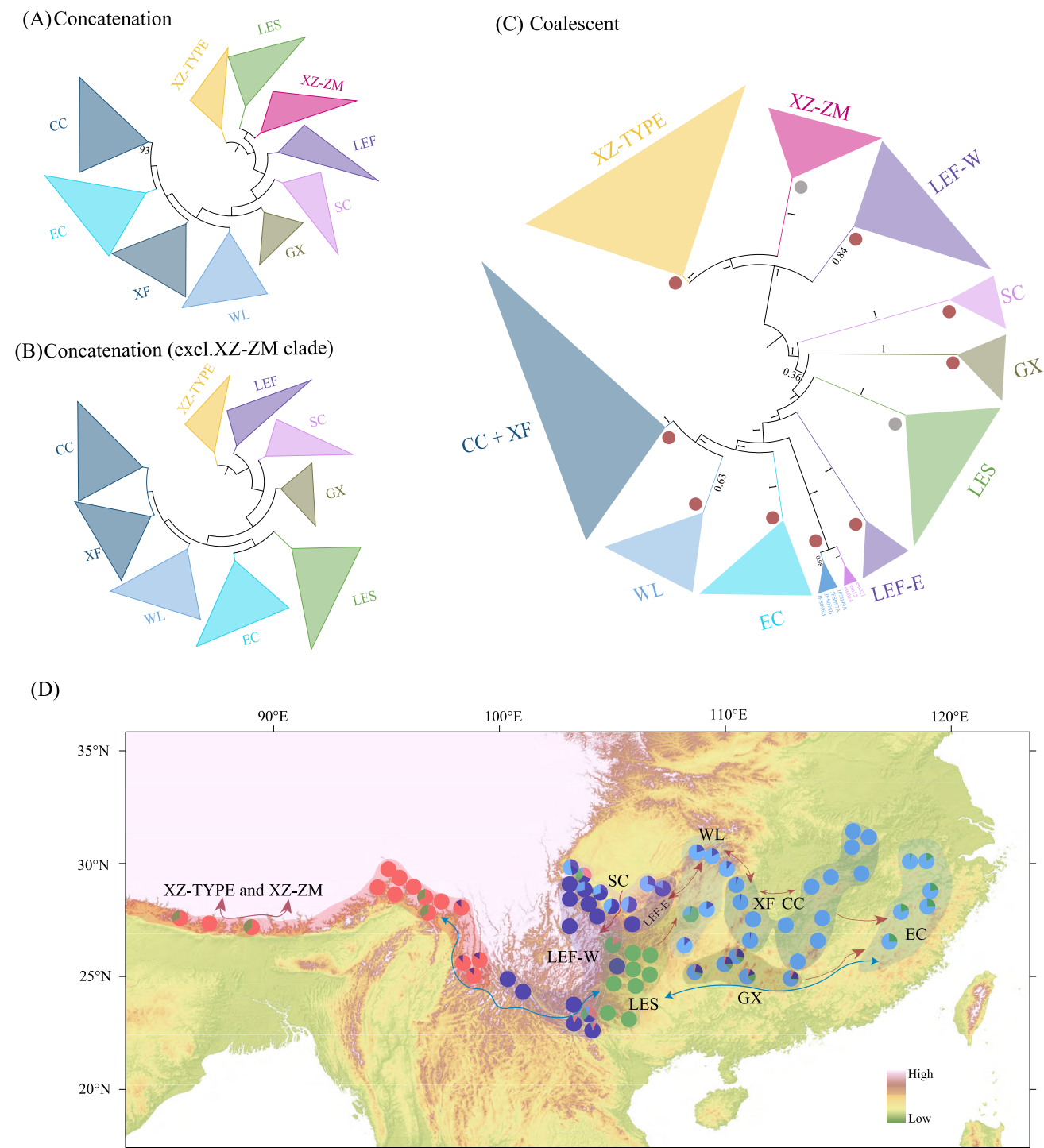


FIGURE 1 Phylogeny of *Litsea elongata* based on maximum likelihood (ML) analysis of concatenated SNVs. (a) Topologies inferred by Strategies 1–3. (b) Topologies from Strategies 4–6, with the XZ-ZM clade removed. Bootstrap percentages less than 100 are displayed. (c) Topology inferred with ASTRAL using 1,168 SNV sliding windows, with the bark color of each clade indicated by a circle. (d) Geographic distribution and genetic structure inferred from ADMIXTURE based on $K = 4$; the blue arrows indicate gene flow between disjunct clades, and the red arrows represent gene flow detected among adjacent clades. Abbreviations: CC, Subtropical Central China clade; EC, Subtropical Eastern China clade; GX, Guangxi clade; LEF, *Litsea elongata* var. *faberii*; LES, *Litsea elongata* var. *subverticillata*; SC, Sichuan clade; WL, Wuling Mountains clade; XF, Xuefeng Mountains clade; XZ-TYPE, Xi-Zang (Tibet) type-bearing clade; XZ-ZM, Xi-Zang–Zhangmu clade.

extracted from fresh leaves and sequenced on the BGISEQ-500 platform, yielding an average of 10- to 12-Gb raw data and depth of up to 5.8-fold for each individual. The genome of *Litsea cubeba* (Lour.)

Pers. (Y. C. Chen, Li, et al., 2020) was used as the reference. We performed SNV calling on deduplicated reads using BWA-MEM v.0.7.17 (Li & Durbin, 2009), SAMtools (Li et al., 2009), and Picard v.1.118

(<http://picard.sourceforge.net>). Population genotyping was conducted with GATK (DePristo et al., 2011). Detailed parameters are provided in Method S1.

2.2 | Phylogenomic and population structure inference

To elucidate the phylogenetic history and characterize the spatial genetic structure of *L. elongata* across its broad range, we implemented several different strategies. For analyses of concatenated SNVs, we generated subsets of the data by removing neighboring SNVs separated by varying distances across the genome: 1000, 2000, and 5000 bp, which we refer to as Strategies 1–3, respectively. We estimated maximum likelihood (ML) trees using IQTREE v1.6.10 (Nguyen et al., 2015), with 1000 ultrafast bootstrap replicates and the general time reversible substitution model with ascertainment bias correction (–m GTR + ASC). Because excluding hybrids prior to analysis can improve the accuracy of phylogenetic inference (Gauthier & Lapointe, 2007), we repeated these analyses with members of one clade (the XZ-ZM clade; see Section 3 and Table 1) removed from the data sets to investigate a hypothesis of hybrid origins. We refer to these analyses as Strategies 4–6.

To generate data sets of putatively unlinked recombinational units (“genes”) for coalescent-based species tree inference, we extracted

windows of 1000 adjacent SNVs, with windows separated by a minimum of 5000 SNVs. This process generated 1168 windows, for which ML trees were estimated using IQTREE under the GTR model and subsequently used to infer the species tree using ASTRAL III (Zhang et al., 2018). We calculated the weights of alternative tree topologies across the genome using TWISST (Martin & Van Belleghem, 2017). For this, we estimated ML trees as above for nonoverlapping windows of 1000 SNVs and summarized the frequencies of topological relationships among five key clades and the outgroup (XZ-TYPE, XZ-ZM, LES, EC, and CC + XF; see acronym definitions in Section 3 and Table 1), resulting in a total of 105 possible rooted tree topologies. We also used SVDquartets (Vachaspati & Warnow, 2018) to estimate the species tree in PAUP v4.0 (Wilgenbusch & Swofford, 2003).

For the major clades identified by the preceding analyses, we estimated nucleotide diversity (π) and inbreeding coefficient. We estimated population structure and genetic admixture using ADMIXTURE v1.3.0 (Alexander et al., 2009), using five replicates and a ten-fold cross-validation error with K ranging from 2 to 10, following Qin, Zuo, et al. (2024).

2.3 | Estimation of gene flow and migration rates

In order to investigate the potential historical connections between different montane regions in subtropical East Asia, we used TREEMIX

TABLE 1 Information of ten clades of *Litsea elongata*.

Clade	Definitions of acronyms	Geographic range and notes	Nucleotide diversity (π)	Inbreeding coefficient (F)	Distinguishing features
XZ-TYPE	Xi-Zang (Tibet) type-bearing clade	Includes the species' nomenclatural type, mainly in Himalayas and Hengduan Mountains, Tibet, China.	0.00272	0.4816	Reddish bark and leaves alternate, narrowly lanceolate; vein angle <50°
XZ-ZM	Xi-Zang–Zhangmu clade (first identified near Zhangmu, Tibet)	Himalayas, mainly in Tibet	0.00148	0.5424	Bark gray-green; leaves subverticillate, variable in size and shape; root suckers often present (Figure S12); vein angle mostly < 50°.
GX	Guangxi clade	Guangxi, China	0.00228	0.4160	Reddish bark and elliptic leaves. Vein angle mostly >50°
SC	Sichuan clade	Southern Sichuan Basin	0.00138	0.4751	Bark reddish; leaves alternate, narrowly lanceolate; vein angle mostly >50°
LEF	<i>Litsea elongata</i> var. <i>faberi</i>	Yunnan-Guizhou Plateau	0.000891	0.5478	Reddish bark and narrowly oblong-lanceolate leaves with caudate or long-caudate apices; vein angle mostly >50°
LES	<i>Litsea elongata</i> var. <i>subverticillata</i>	Karst regions of Southwest China	0.000683	0.6228	Bark gray-green; leaves subverticillate and relatively thin; root suckers often present (Figure S12); vein angle mostly >50°
EC	Subtropical Eastern China clade	Wuyi Mountains, Fujian, China.	0.000564	0.6826	Reddish bark and leaves alternate; vein angle mostly >50°
WL	Wuling Mountains clade	Chongqing and Hubei, China	0.00055	0.6922	Reddish bark and leaves alternate; vein angle mostly >50°
XF	Xuefeng Mountains clade	Hunan, China	0.000538	0.6880	Reddish bark and leaves alternate; vein angle mostly >50°
CC	Central China mountains clade;	Mountains of subtropical Central China	0.000525	0.6917	Reddish bark and leaves alternate; vein angle mostly >50°

v1.13 (Pickrell & Pritchard, 2012) to estimate ancestral gene flow between clades of *L. elongata*. We did not constrain the topology, set the number of admixture events to range from 0 to 5, and ran each analysis 10 times. For each run, a total of 1000 bootstrap replicates were performed and the optimal number of migration events was estimated. We also calculated gene flow using the *Dtrios* command in *Dsuite* (Malinsky et al., 2021) for all possible trios of clades, based on the 10 and 11 clades identified from the concatenated and ASTRAL topologies, respectively, with significance thresholds $Z > 3$ and $p < .002$ (Dong et al., 2022). The lowest absolute value of the *D* statistic (*D*_{min}) was used to test for hybridization among clades. We also performed the *F*-statistic analysis implemented in *Dsuite* *Dinvestigate* (Malinsky et al., 2021) to identify the genomic sites most likely affected by gene flow (top 5% of *D* values) and those least affected by gene flow (absolute *D* values < 0.01). We inferred phylogenetic relationships using these two data sets (details in Method S1).

To investigate ongoing gene flow among clades, we used the multispecies coalescent with migration (MSC-M) model (Flouri et al., 2023) implemented in BPP v4.6.2 (Flouri et al., 2018). To ensure computational feasibility, we used the ASTRAL topology as a guide tree, limited the taxon sampling to 21 individuals representing all major clades and an outgroup (*Litsea acutivena*), and limited the input data to 100 randomly selected loci (SNV windows) out of the 1168 assembled earlier. A gamma distribution $G(0.1, 10)$ with a mean of 0.01 was used as the prior distribution for migration rates (Leaché et al., 2024). The MCMC was run for 1 million generations, with sampling every two generations and a burn-in of 5000 generations (see details in Method S1).

To infer the timing and extent of historical gene flow across clades and specifically to investigate the XZ-ZM clade, we used the multispecies coalescent-with-introgression model (MSC-I; Flouri et al., 2020) implemented in BPP v4.6.2 (A00 analysis). We did not remove sites with ambiguity codes (cleandata = 0), and the inverse gamma prior (invG) was parameterized, $a = 3$, $b = 0.2$ for the root age (τ_0) and invG ($a = 3$, $b = 0.04$) for all populations' effective population sizes (θ). The probability was assigned a beta prior with parameters $a = 1$, $b = 1$. The MCMC was run for 1,000,000 iterations after 5000 iterations of burn-in, sampling every two iterations. To convert the τ_0 value to the divergence time, we assigned 8.75 Ma for the root age of *L. elongata* based on a broader divergence-time analysis of the *Litsea* complex (Qin et al., 2023) and calculated the 95% HPD interval based on the results of the MSC-I analysis. We extracted samples from the Himalayas-Hengduan Mountains Clades (XZ-ZM, XZ-TYPE) and the karst regions of southwest China (LES) clades that were used in the MSC-M analysis for the MSC-I analysis.

2.4 | Estimation of divergence times and environmental niche

To estimate a chronogram of divergence times for *Litsea elongata*, we used SNAPP (Bryant et al., 2012), which implements coalescent models suitable for genome-wide SNV data (Stange et al., 2018). Due

to the high computational demands of SNAPP, we limited the input to 11,350 SNVs separated by $>100,000$ bp between sites and 21 individuals representing the major clades of *L. elongata*. The forward (*u*) and reverse (*v*) mutation rates were estimated, whereas the remaining parameters were fixed at default values. The Ruby script *snapp_prep.rb* (https://github.com/mmatschiner/snapp_prep) was used to generate XML files for this analysis. We used the TREEMIX topology as the starting tree and constrained the crown age of *L. elongata* to 8.75 Ma, with a normal distribution and a standard deviation of 1, yielding a 95% HPD interval of 6.75–10.75 Ma. We also used the Pliocene fossil from Nepal (Paudyal, 2015) to constrain the crown age of the XZ-TYPE clade, applying a lognormal distribution with a mean of 3.61 Ma and a standard deviation of 0.5, because its vein angles match those of the modern XZ-TYPE clade. The Markov Chain Monte Carlo (MCMC) analysis was run for 500,000 generations, sampling every 250 generations. Effective sample sizes (>200) were confirmed using Tracer v1.7 (Rambaut et al., 2018) and visualized using DensiTree (Bouckaert, 2010).

Owing to the significant gene flow detected from the karst regions of southwest China (LES) to both the eastern montane region (EC) and the Himalayas and Hengduan Mountains (XZ-ZM) (see Section 3). We hypothesize that the gene flow among these disjunct clades may be associated with historical range shifts in *L. elongata*. Therefore, to investigate how its present range formed, and whether the LES clade had a more widespread distribution in the past, we reconstructed the historical niche of the LES clade using the maximum entropy niche model (MAXENT v3.4.1) (Phillips et al., 2006) to simulate its potential distribution during key paleoclimatic periods: the MIS M2 glacial period (~ 3.3 Ma), the mid-Pliocene Warm Period (~ 3.264 – 3.025 Ma), the Last Glacial Maximum (LGM, 21 Ka), and the present day. Five climatic variables common to both paleoclimate and modern climate (Bio1, Bio4, Bio12, Bio14, and Bio15; Table S1) were selected based on correlation filtering ($r < 0.8$; Qin, Zuo, et al., 2024), and corresponding data at a spatial resolution of 2.5 arc minutes were downloaded from WorldClim v1.4 (Hijmans et al., 2005) and PaleoClim (Brown et al., 2018). The accuracy of model predictions was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC). Distribution records were obtained from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>), and duplicate localities within 5 km were removed to reduce spatial bias. A total of 62 reliable occurrence records of the LES clade were retained for the MAXENT analysis.

2.5 | Inference of ancestral demography

To investigate historical changes in effective population size (N_e) among different montane regions in subtropical East Asia, we used the Pairwise Sequentially Markovian Coalescent (PSMC) model (Li & Durbin, 2011) to infer Pleistocene N_e dynamics for major clades of *Litsea elongata*. To meet the high sequencing depth recommended for PSMC, we sequenced 18 samples representing the major clades of *L. elongata*, with each sample yielding 50 Gb of raw data, resulting in

an average sequencing depth of $21.7\times$ (Table S2). Those high-depth samples mapped to the same reference genome, and we used a mutation rate of 3.02×10^{-9} per year and a generation time of 14 years (Qin, Zuo, et al., 2024). To minimize false positives, we excluded sites with sequencing depths below $3\times$ and above $80\times$, and other PSMC parameters were set as recommended by the authors (N25 -t15 -r5 -p “4 + 25*2 + 4 + 6”; <https://github.com/lh3/psmc>).

2.6 | Comparative analysis of leaf traits in living and fossil samples

To address how morphological variation aligns with genetic structure, geography, and the fossil record, we measured seven leaf morphological traits in *Litsea elongata*. We selected two to three mature leaves from each of the individuals. A total of 634 leaves were dried at 70°C for 24 h. We measured leaf length (LL), leaf width (LW), length to width ratio (LL/LW), leaf area (LA), leaf dry weight (LDW), specific leaf area (SLA), and angles between principal veins. Leaf area was measured by scanning leaves with a CanoScan LiDE 210 scanner and analyzing the images using ImageJ (Abramoff et al., 2004). We also measured the angles between principal veins in the two well-preserved leaf fossils of *L. elongata*, as this trait has been shown to exhibit important variation across clades. We performed PCA using the prcomp function in R to examine multivariate variation in non-ratio traits among clades. The first two principal components were visualized. To test for significant differences among clades, we conducted PERMANOVA using the vegan package (Oksanen et al., 2013). Pairwise comparisons were assessed using the pairwiseAdonis package in R (Arbizu, 2017). In addition, we evaluated differences in SLA among clades using ANOVA in R (Method S1).

3 | RESULTS

3.1 | Phylogenomic analyses

The ML trees constructed using concatenated genome-wide SNVs under Strategies 1–3 showed a consistent topology, dividing *Litsea elongata* into distinct geographic clades (Figures 1a and S1a–c and Table 1). The clades identified are as follows: The XZ-TYPE and XZ-ZM clades in the Himalayas and Hengduan Mountains, XZ-TYPE shows reddish bark, whereas XZ-ZM has gray-green bark; the LES clade (corresponding to *Litsea elongata* var. *subverticillata*) in the karst regions of southwest China with gray-green bark, and the remaining clades all have reddish bark, including the LEF clade (corresponding to *Litsea elongata* var. *faberi*) in the Yunnan-Guizhou Plateau; the SC clade, which forms an arc-shaped distribution encircling the southern Sichuan Basin; the GX clade, distributed in the Nanling Mountains; the WL clade, primarily in the Wuling Mountains; the CC + XF clade, present in the Xuefeng and Luoxiao Mountains in subtropical central China; and the EC clade, primarily distributed in the Wuyi Mountains of eastern China. Surprisingly, the XZ-ZM clade, sympatrically

distributed with the XZ-TYPE clade in the Himalayas and Hengduan Mountains, is sister to the LES clade from the karst regions (Figures 1a and S1a–c). In concatenated analyses excluding the XZ-ZM clade (Strategies 4–6), the LES clade from the karst region is strongly supported as sister to the geographically distant EC clade in eastern China (Figures 1b and S1c–e). The ASTRAL tree shows geographic clades that are largely consistent with the concatenated analyses (Figure 1c), with two key differences: The LEF clade is split into a western Yungui Plateau clade (LEF_W) and eastern clade (LEF_E), and the XZ-TYPE and XZ-ZM clades in the Himalayas and Hengduan Mountains group with LEF_W. The consensus tree constructed using SVDquartets largely agrees with the concatenated topology, except that its XZ-ZM clade diverges first (Figure S2).

3.2 | Population genetic structure and diversity

ADMIXTURE analysis indicated optimal values of $K = 4$ and 7 based on cross-validation errors (Figure S3). At $K = 4$, genetic clusters are distributed along a longitudinal gradient, with centers in the Himalaya-Hengduan Mountains, karst region of southwest China, Yunnan-Guizhou Plateau, and central subtropical China (Figures 1d and S4). The Himalaya-Hengduan cluster corresponds to the XZ-TYPE and XZ-ZM clades, with the latter showing admixture with the geographically isolated karst clade (LES) in southwestern China. The Sichuan Basin clade SC primarily consists of a mixture of the adjacent clades LEF and WL, whereas the GX clade in the Nanling Mountain region of Guangxi Province exhibits a more complex genetic mixture compared to other clades. The eastern China clade EC shows a high degree of gene flow from the geographically disjunct LES clade (Figure 1d).

Nucleotide diversity (π) showed a gradual decrease from west to east (Table 1). The Himalaya-Hengduan Mountains clades (XZ-TYPE and XZ-ZM), along with the admixed clade GX, had the highest π values. These are followed by the SC, LEF, and LES clades in the Yungui Plateau and karst regions from southwest China, whereas the eastern clades (EC, WL, CC, and XF) showed the lowest π values (Table 1). Estimates of F_{st} indicated that genetic divergences between the western and eastern clades are substantial (Figure 2a). The highest F_{st} value was observed between the XZ-TYPE clade and the CC and XF clades, followed by XZ-TYPE and EC clades (Figure 2a). By contrast, the lowest F_{st} values were observed between the XF, WL, and CC clades. Notably, both the XZ-ZM clade and the EC clades had the lowest F_{st} values with the LES clade (Figure 2a). In addition, the inbreeding coefficient also showed a decreasing trend from west to east (Table 1), consistent with patterns of nucleotide diversity and phylogenetic branching.

3.3 | Estimation of gene flow

Analyses of D statistics on the concatenation topology showed that values of D_{min} were significantly different from zero in 83% of triplets (Z score > 3 and p value $< .002$), indicating pervasive gene flow among

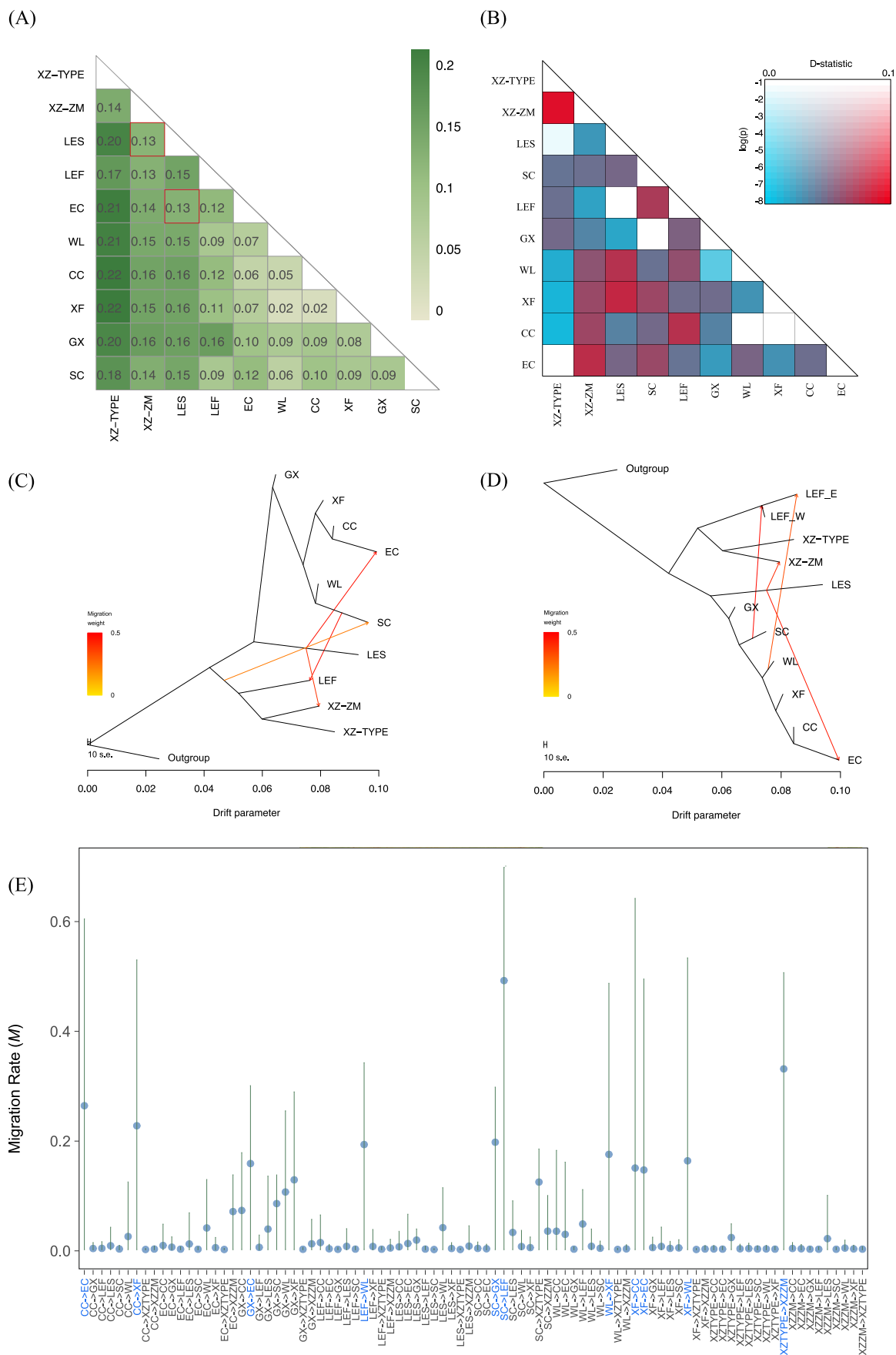


FIGURE 2 Legend on next page.

the major clades. The highest D values were between XZ-TYPE and XZ-ZM, and SC and LEF (Figure 2b). Repeating the analysis on the ASTRAL topology yielded similar results (Figure S5). The MSC-M model detected higher migration between geographically adjacent clades, for example, from SC into LEF, from XZ-TYPE into XZ-ZM, and from CC into EC (Figure 2e). By contrast, many of the gene flow events inferred by TREEMIX occurred between geographically distant clades (Figures 2c,d, S6, and S7). For example, TREEMIX detected gene flow from the LES clade into the EC and XZ-ZM clades, as well as from the SC clade into the LEF clade (Figure 2c,d). The MSC-I model inferred that the XZ-ZM clade originated via ancient gene flow between the XZ-TYPE and LES clades approximately 3.27 million years ago (95% HPD: 3.16–3.78 Ma; Figure 3c), with genomic contributions of 96% and 4%, respectively (Figure 3c).

Weightings of all possible tree topologies across the reference genome showed that the dominant topology is the same as the ASTRAL tree (topo1 in Figure S8a), with a largely uniform distribution across 12 chromosomes (Figure S8b). This topology supports XZ-ZM and XZ-TYPE as sister clades and EC and CC + XF as sister clades. Sister relationships of EC with LES and XZ-ZM with LES, as inferred by concatenated methods, were among the top five most frequently supported topologies out of the 105 possible topologies across the genomes (Figure S8a,b).

We tested the effect of gene flow on phylogenetic reconstruction under two hypotheses. For Hypothesis 1: (([LES, EC], CC), Outgroup), when reconstructing the phylogenetic tree using SNV sites most affected by gene flow (top 5% of D -statistic values; 480,168 SNVs), EC and CC clustered together as a single clade (Figure S8c). However, when using SNVs least affected by gene flow ($D < 0.01$; 240,702 SNVs), the LES and EC clades merged instead (Figure S8d). This suggests that gene flow significantly influenced the observed topologies. For Hypothesis 2: (([CC, EC], LES), Outgroup), a similar pattern was observed. When using the top 5% of SNVs with high D -statistic values (531,343 SNVs), LES and EC clustered together (Figure S8e). In contrast, when using SNVs least affected by gene flow ($D < 0.01$; 368,529 SNVs), EC and CC formed a single clade (Figure S8f).

3.4 | Historical analysis of divergence times, environmental niche, and demography

Divergence age estimates suggest that all clades of *Litsea elongata* had already originated before circa 2.2 million years ago (Figure 3a), indicating that *L. elongata* occupied a wide subtropical niche as a dominant species of evergreen broad-leaved forests before the Pleistocene.

Paleoecological niche modeling based on MAXENT showed substantial predictive power ($AUC > 0.9$) and indicated that the suitable habitats for the LES clade once extended broadly across subtropical East Asia, with particularly high suitability in the Himalayas, Hengduan Mountains, and eastern China during the M2 glacial period (~3.3 Ma; Figure 3b). These areas encompassed the current ranges of both the XZ-ZM and EC clades. As the climate warmed, suitable habitats in the Himalayas and Hengduan Mountains contracted, whereas the Yungui Plateau exhibited higher habitat suitability during the mid-Pliocene Warm Period (~3.264–3.025 Ma; Figure 3b). Central China, where the CC and XF clade now occur, was never inferred as highly suitable habitat in the Pliocene. During the Last Glacial Maximum (LGM, 21 Ka; Figure 3b), suitable niches retreated southward but remained relatively continuous. In the present, suitable habitats are primarily concentrated in the karst regions of Southwest China and the Wuyi Mountains in eastern China (Figure S9).

Ancestral population sizes of clades within *L. elongata* fluctuated over the past 3 million years, displaying similar overall trends (Figure 3d). All clades underwent a gradual population increase from approximately 3 million years ago (Ma) to 1.5 Ma, followed by a decline from around 1.5 Ma to 200 thousand years ago (ka). Interestingly, the population size of the XZ-TYPE from the Himalayan and Hengduan Mountains continued declining from 200 to 10 ka, whereas the populations from the Yungui Plateau remained relatively stable. By contrast, the populations from central to eastern subtropical China increased until approximately 90 ka, after which they began to decline, following a pattern similar to that observed in the Himalayas and Yungui Plateau.

3.5 | Comparative analysis of leaf traits

We find that leaf variation exhibits geographic conservatism; PCA of leaf traits showed separation among clades (Figure S10), with the first two axes explaining 53.2% and 15.1% of the total variance, respectively. Pairwise PERMANOVA identified significant differences between most clade pairs ($p < .05$). However, some comparisons showed marginal or non-significant differences, including clades CC versus EC ($p = .087$), CC versus LEF ($p = .054$), WL versus XZ-TYPE ($p = .062$), and LES versus SC ($p = .061$). Interestingly, similar leaf forms can occur in distantly genetic related clades, the XZ-ZM, SC, and LES clades have longer leaves (LL) compared to other clades (Figure S11a), whereas the XZ-ZM and GX clades have wider leaves (Figure S11b). Clades SC and LES have the narrowest leaves, with a median leaf length-to-width (LL/LW) ratio greater than

FIGURE 2 (a) Matrix of genetic divergence (F_{st}) across the clades of *Litsea elongata*. Red boxes highlight F_{st} values for LES vs. XZ-ZM and LES versus EC. (b) Heatmap showing pairwise D statistics estimated using *Dsuite*. (c, d) Maximum likelihood tree and migration edges from TreeMIX based on analyses of 10 clades (concatenated ML) and 11 clades (ASTRAL), respectively. (e) Migration rates inferred between each clade using the MSC-M model in BPP. Clade pairs with higher inferred migration rates are highlighted in blue. Abbreviations: CC, Subtropical Central China clade; EC, Subtropical Eastern China clade; GX, Guangxi clade; LEF, *Litsea elongata* var. *faberi*; LES, *Litsea elongata* var. *subverticillata*; SC, Sichuan clade; WL, Wuling Mountains clade; XF, Xuefeng Mountains clade; XZ-TYPE, Xi-Zang (Tibet) type-bearing clade; XZ-ZM, Xi-Zang-Zhangmu clade.

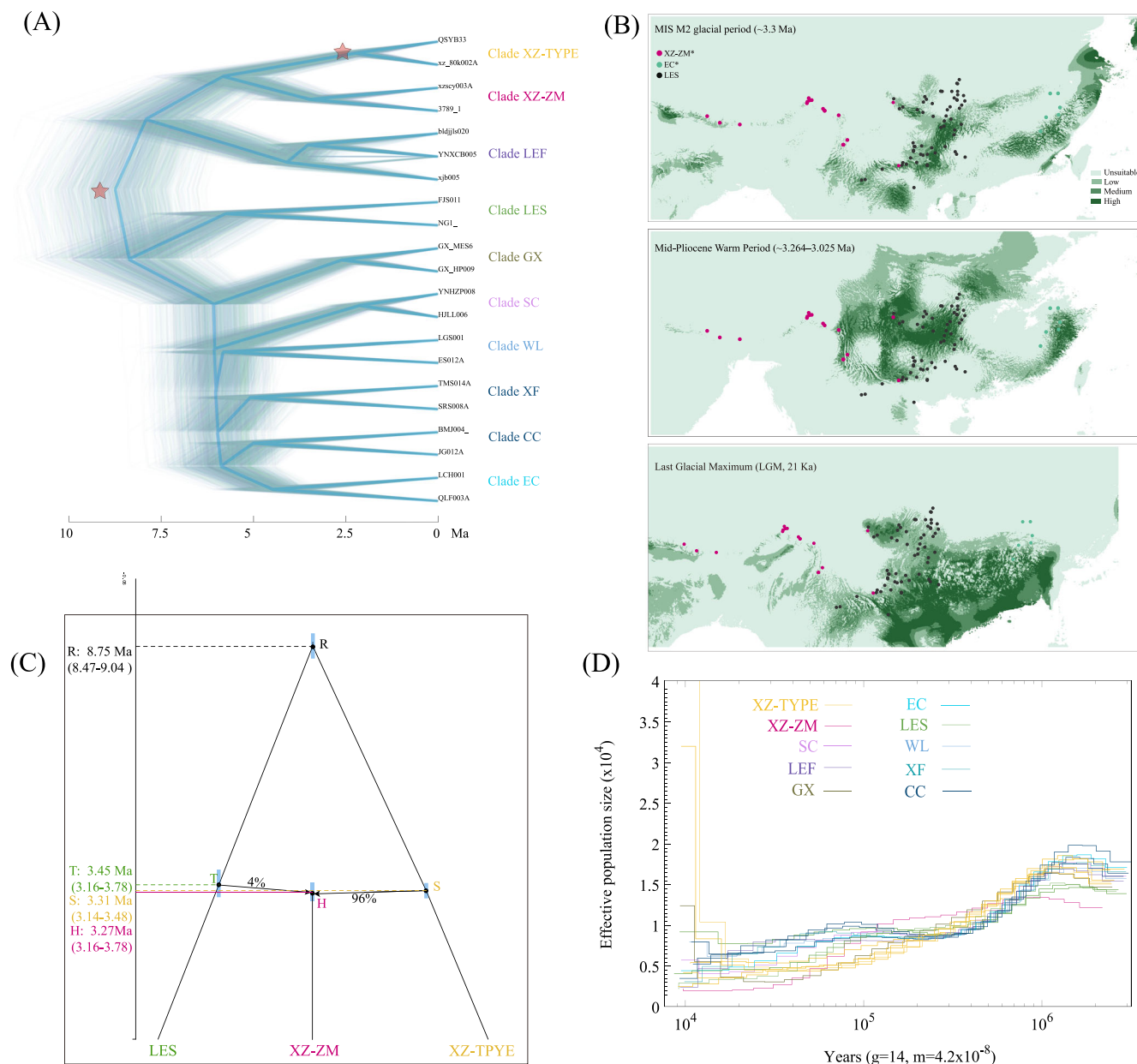


FIGURE 3 (a) Divergence-time estimates for *Litsea elongata* inferred with SNAPP. The DensiTree plot summarizes 2000 posterior trees, illustrating the posterior distributions of divergence times. Red stars indicate two calibration nodes. The light blue topology represents the consensus tree. (b) Potential habitat of the LES clade inferred from ecological niche modeling. From top to bottom, the panels represent the MIS M2 glacial period (~3.3 Ma), the Mid-Pliocene warm period (~3.264–3.025 Ma), and the Last Glacial Maximum (LGM, 21 Ka), respectively. Black dots indicate LES distribution records used in the MaxEnt analysis, whereas orange and blue dots represent field-collected occurrence data of the Himalayan and Hengduan Mountains (XZ) and eastern China (EC) clades, respectively. (c) MSC-I model showing the estimated time and genomic contributions in the ancient gene flow of the XZ-ZM clade. (d) Population demographic histories of geographic clades since the Quaternary, inferred from PSMC analysis. Abbreviations: CC, Subtropical Central China clade; EC, Subtropical Eastern China clade; GX, Guangxi clade; LEF, *Litsea elongata* var. *faberi*; LES, *Litsea elongata* var. *subverticillata*; SC, Sichuan clade; WL, Wuling Mountains clade; XF, Xuefeng Mountains clade; XZ-TYPE, Xi-Zang (Tibet) type-bearing clade; XZ-ZM, Xi-Zang-Zhangmu clade. [Correction added on 13 April 2026, after first online publication: Figure 1 image panel D has been updated for accuracy.]

5 (Figure S11c). Leaf area of the XZ-ZM clade is the largest, whereas the LEF and CC + XF clades have relatively small leaf areas (Figure S11d). Additionally, leaf dry weight data indicated that the XZ-ZM and SC clades had heavier leaves than the other clades (Figure S11e). Specific leaf area (SLA) differed significantly among clades (ANOVA: $F = 47.88, p < .001$; Table S3; Figure S11f). Tukey's

HSD test revealed that LES had significantly higher SLA than all other clades. The largest differences were observed between LES and LEF, XZ-TYPE, and CC. By contrast, the smallest differences were found between LES and EC and between LES and XZ-ZM (Table S3). Elevational ranges of the XZ-ZM, XZ-TYPE, and LEF clades are significantly higher than other clades (Figure S11g). Vein angle exhibited significant

differences across clades (Figures 4 and S11h), with values of the EC and CC clades generally greater than 60 degrees (Figure 4a–c), and those from the Himalayan clades (XZ-ZM and XZ-TYPE) and the type specimens collected from Nepal in 1821 typically less than 50° (Figure 4e–g). Vein angles of Pliocene fossils from Nepal and Late Miocene to Pliocene fossils from Tiantai, Zhejiang, correspond to their respective geographic clades (Figures 4 and S11h).

4 | DISCUSSION

4.1 | Phylogenetic relationships and ancient gene flow of *Litsea elongata*

Our study revealed geographically structured clades within *Litsea elongata* (Figure 1; Table 1) characterized by conflicting phylogenetic

relationships across different analysis types, a dynamic history of past gene flow events between now-disjunct clades, and ongoing gene flow between geographically proximate populations. An unexpected result was that two distinct clades, XZ-TYPE and XZ-ZM, co-occur sympatrically in the Himalaya-Hengduan Mountains, with the XZ-ZM clade appearing to have formed through ancient gene flow between XZ-TYPE and the LES clade from the karst region of southwest China. This latter inference, from multiple phylogenetic and population genetic analyses, is also supported by morphological evidence: The XZ-ZM and LES clades share gray-green bark and whorled leaves, whereas all other clades, including the sympatric XZ-TYPE clade, exhibit reddish bark and alternate leaves (Figures 1c and S12). We speculate that the shared bark color observed in XZ-ZM may be maintained in sympatry with XZ-TYPE through selection on the minor genomic component introgressed from LES, in a manner similar to that shown in *Heliconius* butterflies (Rosser et al., 2024).

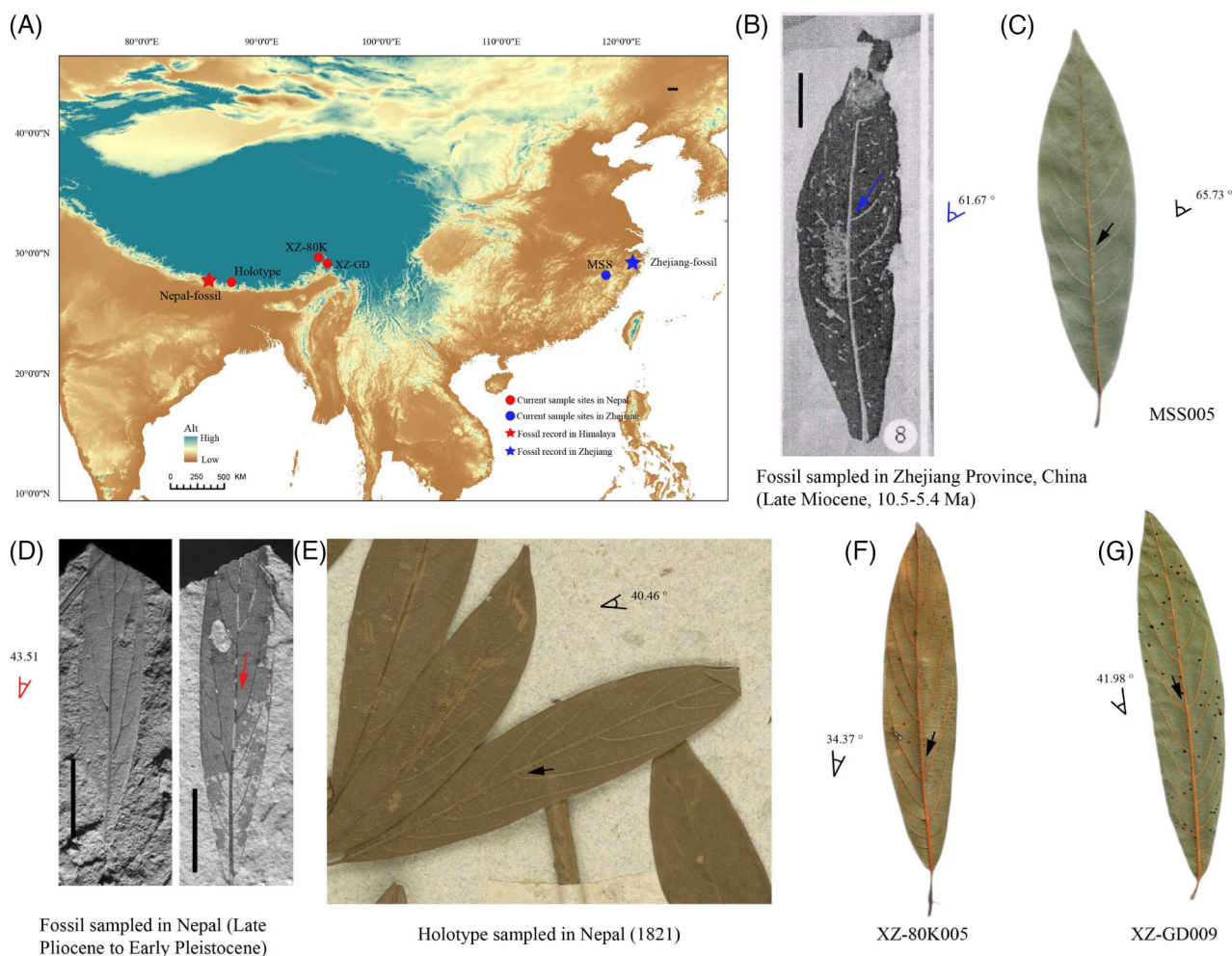


FIGURE 4 Differences in leaf vein angles between extant and fossil samples of *Litsea elongata*. (a) Geographical distribution of extant and fossil clades, with red star representing fossil collected from the Upper Pliocene to Early Pleistocene in Nepal and blue star representing fossil collected from the Late Miocene to Upper Pliocene in eastern China (Tiantai, Zhejiang province); red circles indicate the collection locations of extant individuals from the Himalayan, whereas blue circles indicate the collection locations of extant individuals from eastern China; measurements of leaf vein angles are shown for (b) Eastern China fossil specimen (adapted from He et al., 2023). (c) Extant eastern China clade (EC), (d) Nepal fossil specimen (adapted from Paudyal, 2015), (e) holotype collected from Nepal, and (f, g) extant individuals from the Himalayan and Hengduan Mountains clades (XZ-TYPE).

Topological relationships among clades differed across analyses, introducing uncertainty about the true dominant history. The LES clade figured prominently in these differences. In ML analyses of concatenated SNVs, LES is sister to XZ-ZM; in the ASTRAL analysis, it is nested within the group of clades east of the Hengduan Mountains; and in the population tree inferred by TREEMIX, it is sister to the eastern clades, with historical gene flow events into XZ-ZM and EC, the easternmost clade. XZ-ZM and EC are precisely the clades that are each inferred as sister to LES in concatenated-ML phylogenetic analyses with and without XZ-ZM, respectively (Figure 1), leading us to suspect that those analyses were misled by the effects of historical gene flow. It may be that the TREEMIX topology (Figure 2c,d), with its basal split between a higher-elevation western clade and lower-elevation eastern clade, is closest to the truth.

The TREEMIX inference of gene flow from LES into EC, with no evidence of LES into any geographically intervening clades (GX, CC, XF, and WL; Figure 1d), is surprising in its disjunct pattern. Similarly, gene flow from LES into XZ-ZM involves disjunction across the range of the LEF clade. These inferences suggest that the LES lineage was formerly more widespread and co-occurred with both the high-western and low-eastern clades as they were diversifying, as inferred by ecological niche model (Figure 3b). Concordant evidence comes from leaf functional morphology: The karst LES clade has significantly higher SLA than all other clades (Figure S11f) yet shows the smallest pairwise SLA differences with EC and XZ-ZM (Figure S11f and Table S3), paralleling the genomic connections inferred by TREEMIX. The current restriction of LES to karst habitats in southwestern China may therefore reflect subsequent adaptive specialization and a loss of competitive ability in non-karst regions.

Our analyses of *Litsea elongata* are consistent with increasing evidence that intragenomic phylogenetic conflict caused by gene flow is common (Hibbins & Hahn, 2022), especially among closely related species (Morales-Briones et al., 2021; Zhang et al., 2021). In addition to cases of historical gene flow, we found evidence for ongoing gene flow between geographically adjacent clades (Figure 2e). Both ongoing and ancient gene flow likely contribute to the observed phylogenetic discordance. For example, ongoing gene flow from SC to LEF may explain the shifting position of the LEF clade across different analytical methods (Figure 1).

4.2 | Implications for the phylogeographic history of east Asian EBLFs

As a dominant species of East Asian subtropical evergreen broad-leaved forests, *Litsea elongata* currently spans a geographic range of over 50° of longitude and an elevational range from around 500 m to cloud forests up to 2500–2800 m (Figures 1d and S11g). Our findings suggest that this extensive range did not arise by a single wave of expansion and divergence from a common ancestral population. Instead, evidence of historical gene flow suggests that the LES clade expanded its range independently of the higher elevation western and lower elevation eastern clades and experienced gene flow with both

before contracting to its current distribution in karst habitats. Paleoecological niche modeling supports this hypothesis, indicating that suitable habitats for the LES clade extended into the Himalayas and eastern China during the Late Pliocene (~3.3 Ma; Figure 3b). Moreover, the only two published *L. elongata* fossils, one from the Pliocene of Himalayas (Paudyal, 2015) and the other from Late Miocene of eastern China (He et al., 2023), fall within the morphological range of extant clades in those regions (Figures 4 and S11h), providing strong evidence that *L. elongata* and EBLFs in general had a widespread distribution during the Late Miocene or Early Pliocene.

Recent genomic resequencing studies indicate that subtropical East Asian plants responded to Pleistocene climate changes in a largely synchronous manner, with population size fluctuations followed by a general decline (Chen et al., 2018; Zhao et al., 2019; Y. Chen, Ma, et al., 2020; Zhu et al., 2020; Li et al., 2023; Ren et al., 2024). Our analyses of ancestral demography and paleoclimatic niche models also suggest that during the Pleistocene, clades of *Litsea elongata* experienced fluctuations and ultimately contractions in population size. Although a larger effective population size does not necessarily translate into a broader geographic distribution, a broader past distribution relative to the present appears to be common among EBLF montane taxa, as supported by paleoecological evidence. For instance, fossil evidence from Chinese white pine (*Pinus armandii*) shows that during the Pleistocene, this montane species in subtropical China occupied a range broader than its present distribution (Huang, Li, Huang, Jin, & Oskolski, 2023). We estimated that *L. elongata* had significantly larger effective population sizes during the Early Pleistocene compared to the present (Figure 3d), followed by a decline possibly attributable to significant climatic shifts during this period (Xiong et al., 2020).

Despite the overall similarity in general trends, differences in demographic history across clades of *L. elongata* likely reflect regional histories of glaciation and climate change. For instance, the XZ-TYPE clade in the Himalayan and Hengduan Mountains experienced a continuous decline between 200 and 10 ka years ago (Figure 3d), whereas the southwestern clade showed a slow decline, and the central and eastern China clades exhibited an increase followed by a decrease. These response patterns are strongly correlated with elevation (Figure S11g). The Himalayas and Hengduan clades are found at high elevations (>2000 m). Although evergreen broad-leaved forests in this habitat were not covered by Pleistocene glaciers (Jin et al., 2020), the Himalayas and Hengduan were more impacted by the climate change of glaciations compared to the lower elevation central and eastern regions of subtropical China (Jin et al., 2020), likely leading to a persistent decline for the XZ-TYPE clade. However, the N_e for XZ-ZM is relatively stable compared to other clades, reflecting its unique evolutionary history. In central China, numerous refugia harbored subtropical flora and fauna (Fu & Wen, 2023; Liu et al., 2012). During the last interglacial period (120,000–70,000 years ago), the intensification of the East Asian summer monsoon led to significant increases in both precipitation and temperature (Ao et al., 2024). These favorable hydrothermal conditions may have contributed to an increase in N_e for subtropical evergreen broad-leaved forests in eastern regions until the onset of the Last Glacial

Maximum (ca. 70,000 to 10,000 years ago) when values of N_e for all clades began to decline once again. These results highlight strong geographic heterogeneity in demographic responses, suggesting that conservation of *L. elongata* (and EBLFs more broadly) should account for regional evolutionary histories. In particular, protecting climatically sensitive high-elevation habitats (Himalayas and Hengduan mountains), gene flow contact zones, and eastern refugial areas may be important for sustaining evolutionary potential under ongoing climate change and habitat fragmentation.

In conclusion, this study provides strong evidence that the formation of phylogeographic patterns in dominant EBLF species is more complex than previously understood. The montane EBLFs of subtropical East Asia, presently disjunct, may have been extensively connected in the past. The complex genetic structure of EBLF species observed today likely results from multiple episodes of expansion and contraction, and admixture during glacial periods. Despite their iconic status in subtropical East Asia, EBLFs are experiencing rising anthropogenic pressures, most notably habitat loss and fragmentation. Populations that were once widespread have become isolated, restricting contemporary gene flow; continued human disturbance across subtropical China is likely to deepen this isolation. Gaining a clearer picture of how the dominant species of EBLFs attained their current biogeographic distributions is therefore critical for safeguarding this vegetation and informing effective conservation planning.

AUTHOR CONTRIBUTIONS

De-Zhu Li conceived and designed the research and wrote the manuscript. Richard H. Ree and Peng-Fei Ma analyzed the data and wrote the manuscript. Sheng-Yuan Qin, Zheng-Yu Zuo, Chih-Chieh Yu, Shuang-Xiu Xu, and Jun Rong did the sampling, conducted the experiments, analyzed the data, and wrote the manuscript. [Correction added on 13 April 2026, after first online publication: Author contributions section been updated for accuracy.]

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Phylogenomic data in this study have been made available on Dryad (DOI: [10.5061/dryad.866t1g22w](https://doi.org/10.5061/dryad.866t1g22w)).

ETHICS STATEMENT

This study did not involve human participants.

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REFERENCES

- Abramoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Bio Photonics International*, 11, 36–42.
- Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, 19(9), 1655–1664. <https://doi.org/10.1101/gr.094052.109>
- Ao, H., Ruan, J., Martín-Torres, M., Krapp, M., Liebrand, D., Dekkers, M. J., Caley, T., Jonell, T. N., Zhu, Z., & Huang, C. (2024). Concurrent Asian monsoon strengthening and early modern human dispersal to East Asia during the last interglacial. *Proceedings of the National Academy of Sciences of the United States of America*, 121(3), e2308994121. <https://doi.org/10.1073/pnas.2308994121>
- Arbizu, P. M. (2017). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 00, 2019, 1.
- Bouckaert, R. R. (2010). DensiTree: Making sense of sets of phylogenetic trees. *Bioinformatics*, 26(10), 1372–1373. <https://doi.org/10.1093/bioinformatics/btq110>
- Brown, J. L., Hill, D. J., Dolan, A. M., Carnaval, A. C., & Haywood, A. M. (2018). PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. *Scientific Data*, 5, 180254. <https://doi.org/10.1038/sdata.2018.254>
- Bryant, D., Bouckaert, R., Felsenstein, J., Rosenberg, N. A., & RoyChoudhury, A. (2012). Inferring species trees directly from Biallelic genetic markers: Bypassing gene trees in a full coalescent analysis. *Molecular Biology and Evolution*, 29(8), 1917–1932. <https://doi.org/10.1093/molbev/mss086>
- Chen, J., Hao, Z., Guang, X., Zhao, C., Wang, P., Xue, L., Zhu, Q., Yang, L., Sheng, Y., Zhou, Y., Xu, H., Xie, H., Long, X., Zhang, J., Wang, Z., Shi, M., Lu, Y., Liu, S., Guan, L., ... Shi, J. (2018). *Liriodendron* genome sheds light on angiosperm phylogeny and species-pair differentiation. *Nature Plants*, 5(1), 18–25. <https://doi.org/10.1038/s41477-018-0323-6>
- Chen, Y. C., Li, Z., Zhao, Y. X., Gao, M., Wang, J. Y., Liu, K. W., Wang, X., Wu, L. W., Jiao, Y. L., Xu, Z. L., He, W. G., Zhang, Q. Y., Liang, C. K., Hsiao, Y. Y., Zhang, D. Y., Lan, S. R., Huang, L., Xu, W., Tsai, W. C., ... Wang, Y. D. (2020). The *Litsea* genome and the evolution of the laurel family. *Nature Communications*, 11(1), 1675. <https://doi.org/10.1038/s41467-020-15493-5>
- Chen, Y., Ma, T., Zhang, L., Kang, M., Zhang, Z., Zheng, Z., Sun, P., Shrestha, N., Liu, J., & Yang, Y. (2020). Genomic analyses of a “living fossil”: The endangered dove-tree. *Molecular Ecology Resources*, 20(3), 756–769. <https://doi.org/10.1111/1755-0998.13138>
- DePristo, M. A., Banks, E., Poplin, R., Garimella, K. V., Maguire, J. R., Hartl, C., Philippakis, A. A., del Angel, G., Rivas, M. A., & Hanna, M. (2011). A framework for variation discovery and genotyping using next-generation DNA sequencing data. *Nature Genetics*, 43(5), 491–498. <https://doi.org/10.1038/ng.806>
- Dong, W., Li, E., Liu, Y., Xu, C., Wang, Y., Liu, K., Cui, X., Sun, J., Suo, Z., Zhang, Z., Wen, J., & Zhou, S. (2022). Phylogenomic approaches

- untangle early divergences and complex diversifications of the olive plant family. *BMC Biology*, 20(1), 92. <https://doi.org/10.1186/s12915-022-01297-0>
- Fan, D., Hu, W., Li, B., Morris, A. B., Zheng, M., Soltis, D. E., Soltis, P. S., & Zhang, Z. (2016). Idiosyncratic responses of evergreen broad-leaved forest constituents in China to the late Quaternary climate changes. *Scientific Reports*, 6(1), 31044. <https://doi.org/10.1038/srep31044>
- Flouri, T., Jiao, X., Huang, J., Rannala, B., & Yang, Z. (2023). Efficient Bayesian inference under the multispecies coalescent with migration. *Proceedings of the National Academy of Sciences*, 120(44), e2310708120. <https://doi.org/10.1073/pnas.2310708120>
- Flouri, T., Jiao, X., Rannala, B., & Yang, Z. (2018). Species tree inference with BPP using genomic sequences and the multispecies coalescent. *Molecular Biology and Evolution*, 35(10), 2585–2593. <https://doi.org/10.1093/molbev/msy147>
- Flouri, T., Jiao, X., Rannala, B., & Yang, Z. (2020). A Bayesian implementation of the multispecies coalescent model with introgression for phylogenomic analysis. *Molecular Biology and Evolution*, 37(4), 1211–1223. <https://doi.org/10.1093/molbev/msz296>
- Fu, J. Z., & Wen, L. Y. (2023). Impacts of quaternary glaciation, geological history and geography on animal species history in continental East Asia: A phylogeographic review. *Molecular Ecology*, 32, 4497–4514. <https://doi.org/10.1111/mec.17053>
- Fu, S., Chen, X., Wang, K., Chen, J., Zhou, J., Yi, W., Lyu, M., Ye, Z., & Bu, W. (2024). Shared phylogeographic patterns and environmental responses of co-distributed soybean pests: Insights from comparative phylogeographic studies of *Riptortus pedestris* and *Riptortus linearis* in the subtropics of East Asia. *Molecular Phylogenetics and Evolution*, 195, 108055. <https://doi.org/10.1016/j.ympev.2024.108055>
- Gauthier, O., & Lapointe, F. J. (2007). Hybrids and phylogenetics revisited: A statistical test of hybridization using quartets. *Systematic Botany*, 32(1), 8–15. <https://doi.org/10.1600/036364407780360238>
- Gong, W., Liu, W., Gu, L., Kaneko, S., Koch, M. A., & Zhang, D. (2015). From glacial refugia to wide distribution range: Demographic expansion of *Loropetalum chinense* (Hamamelidaceae) in Chinese subtropical evergreen broadleaved forest. *Organisms Diversity & Evolution*, 16(1), 23–38. <https://doi.org/10.1007/s13127-015-0252-4>
- Hai, L., Li, X. Q., Zhang, J. B., Xiang, X. G., Li, R. Q., Jabbour, F., Ortiz, R. D. C., Lu, A. M., Chen, Z. D., & Wang, W. (2022). Assembly dynamics of East Asian subtropical evergreen broadleaved forests: New insights from the dominant Fagaceae trees. *Journal of Integrative Plant Biology*, 64(11), 2126–2134. <https://doi.org/10.1111/jipb.13361>
- He, W. L., Roth-Nebelsick, A., & Sun, B. N. (2023). Leaf trait data of two Miocene floras from eastern China and its palaeoclimate implications. *Palaeontologia Electronica*, 26(2), a23.
- Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405(6789), 907–913. <https://doi.org/10.1038/35016000>
- Hewitt, G. (2004). Genetic consequences of climatic oscillations in the quaternary. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 359(1442), 183–195. <https://doi.org/10.1098/rstb.2003.1388>
- Hibbins, M. S., & Hahn, M. W. (2022). Phylogenomic approaches to detecting and characterizing introgression. *Genetics*, 220(2), iyab173. <https://doi.org/10.1093/genetics/iyab173>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Huang, L., Li, S., Huang, W., Jin, J., & Oskolski, A. A. (2024). Late Pleistocene glacial expansion of a low-latitude species *Magnolia insignis*: Megafossil evidence and species distribution modeling. *Ecological Indicators*, 158, 111519. <https://doi.org/10.1016/j.ecolind.2023.111519>
- Huang, L., Li, S., Huang, W., Xiang, H., Jin, J., & Oskolski, A. A. (2023). Glacial expansion of cold-tolerant species in low latitudes: Megafossil evidence and species distribution modelling. *National Science Review*, 10(4), nwad038. <https://doi.org/10.1093/nsr/nwad038>
- Huang, L., Li, W., Huang, W., Jin, J., & Oskolski, A. A. (2023). *Cryptocarya chinensis* from the Upper Pleistocene of South China and its biogeographic and paleoecological implications. *IScience*, 26(8), 107313. <https://doi.org/10.1016/j.isci.2023.107313>
- Jin, H. J., Jin, X. Y., He, R. X., Luo, D. L., Chang, X. L., Wang, S. L., Marchenko, S. S., Yang, S. Z., Yi, C. L., Li, S. J., & Harris, S. A. (2019). Evolution of permafrost in China during the last 20 ka. *Science China Earth Sciences*, 62, 1207–1223. <https://doi.org/10.1007/s11430-018-9272-0>
- Jin, H. J., Vandenberghe, J., Luo, D. L., Harris, S. A., He, R. X., Chen, X. L., Jin, X. Y., Wang, Q., Zhang, Z., & Spektor, V. (2020). Quaternary permafrost in China: Framework and discussions. *Quaternary*, 3(4), 32. <https://doi.org/10.3390/quat3040032>
- Kong, H., Condamine, F. L., Harris, A. J., Chen, J., Pan, B., Möller, M., Hoang, V. S., & Kang, M. (2017). Both temperature fluctuations and East Asian monsoons have driven plant diversification in the karst ecosystems from southern China. *Molecular Ecology*, 26(22), 6414–6429. <https://doi.org/10.1111/mec.14367>
- Leaché, A. D., Davis, H. R., Feldman, C. R., Fujita, M. K., & Singhal, S. (2024). Repeated patterns of reptile diversification in Western North America supported by the Northern Alligator Lizard (*Elgaria coerulea*). *Journal of Heredity*, 115(1), 57–71. <https://doi.org/10.1093/jhered/esad073>
- Li, D., Jiang, L., He, W., Fan, D., Cheng, S., Yang, Y., Wang, M., Tang, S., Kou, Y., & Zhang, Z. (2024). Allopatric speciation and secondary sympatry of *Fagus longipetiolata* and *F. lucida* (Fagaceae) in subtropical China. *Botanical Journal of the Linnean Society*, 205, boad077. <https://doi.org/10.1093/botlinnean/boad077>
- Li, D., Lin, H. Y., Wang, X., Bi, B., Gao, Y., Shao, L., Zhang, R., Liang, Y., Xia, Y., & Zhao, Y. P. (2023). Genome and whole-genome resequencing of *Cinnamomum camphora* elucidate its dominance in subtropical urban landscapes. *BMC Biology*, 21(1), 192. <https://doi.org/10.1186/s12915-023-01692-1>
- Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics*, 25(14), 1754–1760. <https://doi.org/10.1093/bioinformatics/btp324>
- Li, H., & Durbin, R. (2011). Inference of human population history from individual whole-genome sequences. *Nature*, 475(7357), 493–496. <https://doi.org/10.1038/nature10231>
- Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., & Durbin, R. (2009). The sequence alignment/map format and samtools. *Bioinformatics*, 25(16), 2078–2079. <https://doi.org/10.1093/bioinformatics/btp352>
- Li, H. W., Li, J., Huang, P. H., Wei, F. N., Cui, H. B., & van der W. H. (2008). Lauraceae. In Z. Y. Wu & P. H. Raven (Eds.), *Flora of China*, Vol. 7. *Calanthaceae–Schisandraceae*. Science Press and Missouri Botanical Garden Press.
- Liu, J. Q., Sun, Y. S., Ge, X. J., Gao, L. M., & Qiu, Y. X. (2012). Phylogeographic studies of plants in China: Advances in the past and directions in the future. *Journal of Systematics and Evolution*, 50(4), 267–275. <https://doi.org/10.1111/j.1759-6831.2012.00214.x>
- Lu, L. M., Mao, L.-F., Yang, T., Ye, J. F., Liu, B., Li, H. L., Sun, M., Miller, J. T., Mathews, S., & Hu, H.-H. (2018). Evolutionary history of the angiosperm flora of China. *Nature*, 554(7691), 234–238. <https://doi.org/10.1038/nature25485>
- Lu, R. S., Chen, Y., Tamaki, I., Sakaguchi, S., Ding, Y. Q., Takahashi, D., Li, P., Isaji, Y., Chen, J., & Qiu, Y. X. (2020). Pre-quaternary diversification and glacial demographic expansions of *Cardiocrinum* (Liliaceae) in temperate forest biomes of Sino-Japanese Floristic Region. *Molecular Phylogenetics and Evolution*, 143, 106693. <https://doi.org/10.1016/j.ympev.2019.106693>
- Luo, D., Xu, B., Li, Z. M., & Sun, H. (2021). Biogeographical divides delineated by the three-step landforms of China and the East China Sea:

- Insights from the phylogeography of *Kerria japonica*. *Journal of Biogeography*, 48(2), 372–385.
- Malinsky, M., Matschiner, M., & Svardal, H. (2021). Dsuite-fast D-statistics and related admixture evidence from VCF files. *Molecular Ecology Resources*, 21(2), 584–595. <https://doi.org/10.1111/1755-0998.13265>
- Martin, S. H., & van Belleghem, S. M. (2017). Exploring evolutionary relationships across the genome using topology weighting. *Genetics*, 206, 429–438. <https://doi.org/10.1534/genetics.116.194720>
- Meng, H. H., Song, Y. G., Hu, G. X., Huang, P. H., Li, M., Fang, O. Y., Su, R. P., Cao, G. L., Cai, X., Zhou, S. S., Tan, Y. H., Xiang, X. G., Wang, W., Zhou, Z. K., & Li, J. (2025). Evolution of East Asian subtropical evergreen broad-leaved forests: When and how? *Journal of Systematics and Evolution*, 63(5), 1045–1060. <https://doi.org/10.1111/jse.70001>
- Morales-Briones, D. F., Kadereit, G., Tefarikis, D. T., Moore, M. J., Smith, S. A., Brockington, S. F., Timoneda, A., Yim, W. C., Cushman, J. C., & Yang, Y. (2021). Disentangling sources of gene tree discordance in phylogenomic data sets: Testing ancient hybridizations in *Amaranthaceae* s.l. *Systematic Biology*, 70(2), 219–235. <https://doi.org/10.1093/sysbio/syaa066>
- Nguyen, L. T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32(1), 268–274. <https://doi.org/10.1093/molbev/msu300>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H., & Wagner, H. (2013). Package 'vegan'. *Community Ecology Package, Version*, 2(9), 1–295.
- Paudyal, K. N. (2015). Plio-Pleistocene plant megafossils from the Lukundol formation (Nakkhu Khola, Lalitpur District, Central Nepal)—First results. *Journal of Institute of Science and Technology*, 20(1), 141–144. <https://doi.org/10.3126/jist.v20i1.13938>
- Perrigo, A., Hoorn, C., & Antonelli, A. (2020). Why mountains matter for biodiversity. *Journal of Biogeography*, 47(2), 315–325. <https://doi.org/10.1111/jbi.13731>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259.
- Pickrell, J., & Pritchard, J. (2012). Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genetics*, 8(11), e1002967. <https://doi.org/10.1371/journal.pgen.1002967>
- Qian, H., & Ricklefs, R. E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, 407(6801), 180–182. <https://doi.org/10.1038/35025052>
- Qin, S. Y., Chen, K., Zhang, W. J., Xiang, X. G., Zuo, Z. Y., Guo, C., Zhao, Y., Li, L. F., Wang, Y. G., & Song, Z. P. (2024). Phylogenomic insights into the reticulate evolution of *Camellia* sect. *Paracamellia* Sealy (Theaceae). *Journal of Systematics and Evolution*, 62(1), 38–54. <https://doi.org/10.1111/jse.12948>
- Qin, S. Y., Zuo, Z. Y., Guo, C., Du, X. Y., Liu, S. Y., Yu, X. Q., Xiang, X. G., Rong, J., Liu, B., Liu, Z. F., Ma, P. F., & Li, D. Z. (2023). Phylogenomic insights into the origin and evolutionary history of evergreen broadleaved forests in East Asia under Cenozoic climate change. *Molecular Ecology*, 32(11), 2850–2868. <https://doi.org/10.1111/mec.16904>
- Qin, S. Y., Zuo, Z. Y., Xu, S. X., Liu, J., Yang, F. M., Luo, Y. H., Ye, J. W., Zhao, Y., Rong, J., & Liu, B. (2024). Anthropogenic disturbance driving population decline of a dominant tree in East Asia evergreen broad-leaved forests over the last 11,000 years. *Conservation Biology*, 38(1), e14180. <https://doi.org/10.1111/cobi.14180>
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67(5), 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ren, Y., Zhang, L., Yang, X., Lin, H., Sang, Y., Feng, L., Liu, J., & Kang, M. (2024). Cryptic divergences and repeated hybridizations within the endangered “living fossil” dove tree (*Davidia involucrata*) revealed by whole genome resequencing. *Plant Diversity*, 46(2), 169–180. <https://doi.org/10.1016/j.pld.2024.02.004>
- Rosser, N., Seixas, F., Queste, L. M., Cama, B., Mori-Pezo, R., Kryvokhyzha, D., Nelson, M., Waite-Hudson, R., Goringe, M., Costa, M., Elias, M., de Mens Eleres Figueiredo, C., Freitas, A. V. L., Joron, M., Kozak, K., Lamas, G., Martins, A. R. P., McMillan, W. O., Ready, J., ... Dasmahapatra, K. K. (2024). Hybrid speciation driven by multilocus introgression of ecological traits. *Nature*, 628, 1–7. <https://doi.org/10.1038/s41586-024-07263-w>
- Shafer, A. B., Cullingham, C. I., Côté, S. D., & Coltman, D. W. (2010). Of glaciers and refugia: A decade of study sheds new light on the phylogeography of northwestern North America. *Molecular Ecology*, 19(21), 4589–4621. <https://doi.org/10.1111/j.1365-294X.2010.04828.x>
- Song, Y., & Da, L. (2016). Evergreen broad-leaved forest of East Asia. In *Vegetation structure and function at multiple spatial, temporal and conceptual scales* (pp. 101–128). Springer.
- Song, Y., Yan, E., & Song, K. (2015). Synthetic comparison of eight dynamics plots in evergreen broadleaf forests, China. *Biodiversity Science*, 23(2), 139–148. <https://doi.org/10.17520/biods.2014140>
- Stange, M., Sánchez-Villagra, M. R., Salzburger, W., & Matschiner, M. (2018). Bayesian divergence-time estimation with genome-wide single-nucleotide polymorphism data of sea catfishes (Ariidae) supports Miocene closure of the Panamanian Isthmus. *Systematic Biology*, 67(4), 681–699. <https://doi.org/10.1093/sysbio/syy006>
- Tang, C. Q. (2015). *The subtropical vegetation of southwestern China: Plant distribution, diversity and ecology* (Vol. 11). Springer. <https://doi.org/10.1007/978-94-017-9741-2>
- Tang, C. Q., Matsui, T., Ohashi, H., Nualart, N., Herrando-Moraira, S., Dong, Y. F., Grote, P. J., van Ngoc, N., van Sam, H., & Li, S. (2022). Identifying long-term stable refugia for dominant *Castanopsis* species of evergreen broad-leaved forests in East Asia: A tool for ensuring their conservation. *Biological Conservation*, 273, 109663. <https://doi.org/10.1016/j.biocon.2022.109663>
- Tian, S., Lei, S. Q., Hu, W., Deng, L. L., Li, B. O., Meng, Q. L., Soltis, D. E., Soltis, P. S., Fan, D. M., & Zhang, Z. Y. (2015). Repeated range expansions and inter-/postglacial recolonization routes of *Sargentodoxa cuneata* (Oliv.) Rehd. et Wils. (Lardizabalaceae) in subtropical China revealed by chloroplast phylogeography. *Molecular Phylogenetics and Evolution*, 85, 238–246. <https://doi.org/10.1016/j.ympev.2015.02.016>
- Vachaspati, P., & Warnow, T. (2018). SVDquest: Improving SVDquartets species tree estimation using exact optimization within a constrained search space. *Molecular Phylogenetics and Evolution*, 124, 122–136. <https://doi.org/10.1016/j.ympev.2018.03.006>
- Wang, Y. H., Jiang, W. M., Comes, H. P., Hu, F. S., Qiu, Y. X., & Fu, C. X. (2015). Molecular phylogeography and ecological niche modelling of a widespread herbaceous climber, *Tetrastigma hemsleyanum* (Vitaceae): Insights into Plio-Pleistocene range dynamics of evergreen forest in subtropical China. *New Phytologist*, 206(2), 852–867. <https://doi.org/10.1111/nph.13261>
- Wang, Z., Zhang, M., Zhao, X., Xie, J., Peng, Y., Sheldon, F. H., & Zou, F. (2024). The Nanling Mountains of southern China played a variable role as a barrier and refuge for birds depending upon landscape structure and timing of events. *Journal of Avian Biology*, 2024(5–6), e03131. <https://doi.org/10.1111/jav.03131>
- Wei, X. P., & Zhang, X. C. (2022). Phylogeography of the widespread fern *Lemmaphyllum* in East Asia: Species differentiation and population dynamics in response to change in climate and geography. *Journal of Systematics and Evolution*, 60(2), 411–432.
- Wilgenbusch, J. C., & Swofford, D. (2003). Inferring evolutionary trees with PAUP. *Current Protocols in Bioinformatics*, 6.4.1–6.4.28.

- Xiong, W., Zhu, L., Zhang, X., Guo, L., Ye, W., & Xiong, S. (2020). Middle Pleistocene transition and its environmental effects revealed by red earth of South China. *Quaternary Sciences*, 40(6), 1441–1452.
- Ye, J. W., & Li, D. Z. (2021). Distinct late Pleistocene subtropical-tropical divergence revealed by fifteen low-copy nuclear genes in a dominant species in South-East China. *Scientific Reports*, 11(1), 4147. <https://doi.org/10.1038/s41598-021-83473-w>
- Ye, J. W., & Li, D. Z. (2022). Diversification of East Asian subtropical evergreen broadleaved forests over the last 8 million years. *Ecology and Evolution*, 12(11), e9451. <https://doi.org/10.1002/ece3.9451>
- Ye, J. W., Li, D. Z., & Hampe, A. (2019). Differential quaternary dynamics of evergreen broadleaved forests in subtropical China revealed by phylogeography of *Lindera aggregata* (Lauraceae). *Journal of Biogeography*, 46(6), 1112–1123.
- Ye, J. W., Zhang, Y., & Wang, X. J. (2017). Phylogeographic history of broad-leaved forest plants in subtropical China. *Acta Ecologica Sinica*, 37(17), 5894–5904.
- Yu, X. Q., Gao, L. M., Soltis, D. E., Soltis, P. S., Yang, J. B., Fang, L., Yang, S. X., & Li, D. Z. (2017). Insights into the historical assembly of East Asian subtropical evergreen broadleaved forests revealed by the temporal history of the tea family. *New Phytologist*, 215(3), 1235–1248. <https://doi.org/10.1111/nph.14683>
- Zhang, C., Rabiee, M., Sayyari, E., & Mirarab, S. (2018). ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19(S6), 153. <https://doi.org/10.1186/s12859-018-2129-y>
- Zhang, D., Rheindt, F. E., She, H., Cheng, Y., Song, G., Jia, C., Qu, Y., Alström, P., & Lei, F. (2021). Most genomic loci misrepresent the phylogeny of an avian radiation because of ancient gene flow. *Systematic Biology*, 70(5), 961–975. <https://doi.org/10.1093/sysbio/syab024>
- Zhang, Q., Yang, Y., Liu, B., Lu, L., Sauquet, H., Li, D., & Chen, Z. (2024). Meta-analysis provides insights into the origin and evolution of East Asian evergreen broad-leaved forests. *New Phytologist*, 242(5), 2369–2379. <https://doi.org/10.1111/nph.19524>
- Zhao, J., Li, S., Huang, J., Ding, W., Wu, M., Su, T., Farnsworth, A., Valdes, P., Chen, L., Xing, Y., & Zhou, Z. (2024). Heterogeneous occurrence of evergreen broad-leaved forests in East Asia: Evidence from plant fossils. *Plant Diversity*, 47, 1–12. <https://doi.org/10.1016/j.pld.2024.07.004>
- Zhao, Y. P., Fan, G., Yin, P.-P., Sun, S., Li, N., Hong, X., Hu, G., Zhang, H., Zhang, F.-M., Han, J.-D., Hao, Y. J., Xu, Q., Yang, X., Xia, W., Chen, W., Lin, H. Y., Zhang, R., Chen, J., Zheng, X. M., ... Ge, S. (2019). Resequencing 545 ginkgo genomes across the world reveals the evolutionary history of the living fossil. *Nature Communications*, 10(1), 4201. <https://doi.org/10.1038/s41467-019-12133-5>
- Zhu, S., Chen, J., Zhao, J., Comes, H. P., Li, P., Fu, C., Xie, X., Lu, R., Xu, W., & Feng, Y. (2020). Genomic insights on the contribution of balancing selection and local adaptation to the long-term survival of a widespread living fossil tree, *Cercidiphyllum japonicum*. *New Phytologist*, 228(5), 1674–1689. <https://doi.org/10.1111/nph.16798>

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