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RESEARCH ARTICLE

Molecular Phylogenetic Analyses Reveal the Diversification and Dispersal Processes of the Tribe Shoreae (Dipterocarpaceae)

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ABSTRACT

Aim: The tribe Shoreae, part of the family Dipterocarpaceae, encompasses about 330 species and ten genera, namely *Anthoshorea*, *Doona*, *Hopea*, *Neobalanocarpus*, *Neohopea*, *Pentacma*, *Parashorea*, *Richetia*, *Rubroshorea* and *Shorea*. It has been hypothesized that Shoreae ancestors likely migrated from the Indian subcontinent and underwent rapid diversification within Southeast Asian rainforests. However, the phylogenetic relationships among genera and the specific processes of dispersal and diversification within this tribe remain unclear. This research conducted molecular phylogenetic analyses of the tribe Shoreae, aiming to establish a comprehensive framework for the evolutionary past of this group.

Location: South and Southeast Asia.

Time Period: The Cretaceous to present.

Major Taxa Studies: Tribe Shoreae (Dipterocarpaceae).

Methods: We conducted Bayesian molecular phylogeny inference, ancestral area and distributable climate reconstruction, and divergence time estimation by utilising the molecular data sourced from GenBank. The molecular data included four partial chloroplast DNA regions (*trnL–trnF*, *rbcL*, *trnH–psbA* and *matK*) and the partial *ITS* region of nuclear DNA from a total of 186 ingroup and five outgroup species (*Dryobalanops*). Based on these results, we also evaluated temporal and in situ diversification.

Results: The Bayesian molecular phylogeny identified two major clades within the tribe Shoreae with high posterior probabilities and confirmed the monophyly of the genera *Anthoshorea*, *Doona*, *Hopea*, *Parashorea*, *Richetia* and *Rubroshorea*. Furthermore, our results supported the origin of the tribe prior to the collision of the Indian subcontinent with Asia, the migration of the Shoreae ancestors to Southeast Asia, and subsequently, diversification in tropical Southeast Asia after the Oligocene.

Main Conclusions: Molecular phylogenetic analyses suggest that the formation of the tropical climate in Southeast Asia may have played a role in the diversification of Shoreae species. This study proposes a novel hypothesis regarding the distribution and diversification processes of Shoreae, highlighting the mechanisms driving plant diversification in response to changing climatic conditions.

1 | Introduction

The tribe Shoreae (Dipterocarpaceae) is composed of approximately 330 species, the most species-rich dipterocarp lineage forming a prominent group of tropical tree species (Ashton et al. 2021; Ashton and Heckenhauer 2022; POWO 2024; WFO 2024). Shoreae encompasses diverse species with various ecological adaptations and morphological traits, particularly in Southern and Southeast Asia (Ashton et al. 2021). The species diversity within Dipterocarpaceae, including Shoreae, is believed to have been shaped by plate tectonics, for example, India-Asia collision and climate fluctuations in South and Southeast Asia (Kooyman et al. 2019; Ashton et al. 2021; Bansal et al. 2022). The modern distribution of Dipterocarpaceae suggests an origin in Africa, with subsequent migration to Southeast Asia through the Asiatic floristic interchange (Kooyman et al. 2019; Bansal et al. 2022). The successful migration of dipterocarps enabled not only colonisation but also diversification and their rise to become one of the key taxa in the forest ecosystems of Southeast Asia (Klaus et al. 2016; Morley 2018; Kooyman et al. 2019; Ashton et al. 2021; Bansal et al. 2022). Therefore, understanding the evolutionary processes of the tribe Shoreae serves as an important model for investigating diversification and colonisation patterns of organisms in Southeast Asia, driven by migration from the Indian subcontinent.

The phylogenetic relationship between genera, the exact hotspot and the historical dynamics within this tribe have not been well understood (Heckenhauer et al. 2017, 2018; Kooyman et al. 2019; Ashton et al. 2021; Bansal et al. 2022; Cvetković et al. 2022). The genus *Shorea* was previously divided into seven sections—*Anthoshorea*, *Doona*, *Neohopea*, *Pentacma*, *Richetia*, *Rubroshorea* and *Shorea*—a recent reclassification has elevated them to generic level (Heckenhauer et al. 2018; Ashton et al. 2021). However, the phylogenetic topology of *Parashorea*, *Neohopea* and *Pentacma* and sectional and subsectional classifications among *Hopea*, *Rubroshorea* and *Shorea* remain unresolved (Table 1; Ashton 1982; Heckenhauer et al. 2017, 2018; POWO 2024; WFO 2024). Two hypotheses exist for the topology of *Parashorea*: either ((*Richetia* + *Parashorea*) + (*Shorea* + *Rubroshorea*)) or (*Richetia* + (*Parashorea* + (*Rubroshorea* + *Shorea*))) (Heckenhauer et al. 2017, 2019; Bansal et al. 2022; Cvetković et al. 2022). *Pentacme* has been suggested to be related to *Doona* based on morphological traits such as larger flowers and elongated anthers (Ashton et al. 2021; Ashton and Heckenhauer 2022); however, no molecular phylogenetic studies have included this genus. Although the evolutionary history of Dipterocarpaceae has also been updated (Bansal et al. 2022) and the dispersal and diversification hypothesis of Dipterocarpaceae is well-established, the specific processes among the species of

TABLE 1 | The classifications of tribe Shoreae (POWO 2024; WFO 2024).

		No. of species			
Tribe	**Genus**	**POWO (2024)**	**WFO (2024)**	**Section**	**Subsection**
Shoreae	*Anthoshorea*	23	24		
	Doona	10	10		
	Hopea[a]	114	121	Dryobalanoides	Dryobalanoides
					Sphaerocarpae
				Hopea	Hopea
					Pierrea
	Neobalanocarpus	1	1		
	Neohopea	1	1		
	Parashorea	13	14		
	Pentacme	2	2		
	Richetia	32	33		
	Rubroshorea[a]	71	71	Brachyptera	
				Ovalis	
				Pachycarpae	
				Rubella	
				Rubroshorea	Auriculatae
					Rubroshorea
	Shorea[a]	50	52	Barbata	
				Shorea[b]	Shorea

[a] Not all species within each genus are classified into sections.
[b] Not all species within each section are classified into subsections.

Shoreae remain elusive. It has been hypothesized that Shoreae originated in Africa and later migrated to Southeast Asia via the Asiatic floristic interchange, with the Oriental region serving as a centre of diversification, shaped by historical climate conditions (Ashton 2004, 2014; Ashton et al. 2021; Cvetković et al. 2022). However, the diversification hotspots and distribution processes, along with their association with ancestral climatic conditions, remain unexplained in these hypotheses.

Here, we explored these research gaps by testing the following hypotheses related to the diversification of Shoreae. (1) *Parashorea* is a sister clade to *Richetia*, (2) the phylogenetic position of *Pentacme* is close to or within the *Doona* clade and (3) Shoreae species have dispersed in response to palaeoclimate and primarily diversified under the climatic conditions of the Oriental region, particularly within tropical climates.

To test these hypotheses, this research conducted molecular phylogenetic analyses of the tribe Shoreae, aiming to establish a comprehensive framework for unravelling the evolutionary past of this group. Utilising molecular sequence data, distribution data with its climate status and palaeoclimate data available in open-access resources, our study seeks to clarify the following aspects: (1) the phylogenetic relationships among genera, sections and subsections, (2) the distribution processes with detailed geographical and climatic partitioning, (3) divergence times and (4) the centre of diversification within Shoreae.

2 | Materials and Methods

2.1 | Taxon Sampling

According to Ashton and Heckenhauer (2022), Shoreae comprises approximately 313 species, but recent summaries differed in the number of accepted species, ranging from 317 species (POWO 2024) to 329 species (WFO 2024).

Shoreae is comprised of ten genera, namely *Anthoshorea*, *Doona*, *Hopea*, *Neobalanocarpus*, *Neohopea*, *Pentacma*, *Parashorea*, *Richetia*, *Rubroshorea* and *Shorea* (Ashton and Heckenhauer 2022; POWO 2024; WFO 2024). Genetic sequences of 185 Shoreae species and five outgroup species of *Dryobalanops*, considered to be the sister clade to the Shoreae tribe (Ashton and Heckenhauer 2022; Bansal et al. 2022; Cvetković et al. 2022), were retrieved from GenBank (https://www.ncbi.nlm.nih.gov/genbank/). *Neohopea* was excluded from the subsequent analyses, as the sequence data of this genus (which comprises only one species, *N. isopteran*) was unpublished and may have been misplaced. Detailed information on the datasets used in the analyses, including GenBank accession numbers, is provided in Table S1.

2.2 | Phylogenetic Analyses

We generated a concatenated matrix incorporating sequences of four chloroplast DNA (chlDNA) regions (*trnL–trnF*, *rbcL*, *trnH–psbA* and *matK*) and the partial *ITS* region of nuclear DNA (nrDNA). The regions were aligned using MAFFT v.7.490 (Kuraku et al. 2013) with default settings, followed by visual inspection and corrections. In this study, we focused on regions where at least 78 species of the Shoreae sequence data (25%) are available from GenBank. Using PartitionFinder v.2.1 (Lanfear et al. 2017), the best-fitted substitution model for each region was selected and subsequently employed in Bayesian inference of phylogeny and maximum likelihood (ML) phylogenetic analyses (Table 2). The Bayesian phylogenetic hypotheses were reconstructed with MrBayes v.3.2.7a (Ronquist et al. 2012), using the substitution model for each partition based on Bayesian information criterion. The Markov chain Monte Carlo (MCMC) Metropolis Hastings algorithm for the Bayesian phylogenetic analysis was run for 10 million generations, sampling every 200 generations. Two output log files were evaluated based on the effective sample size (ESS) greater than 200 after removing the 25% burn-in using Tracer v.1.7.2 (Rambaut et al. 2018). Markov chains reached a stationary distribution, and the initial 12,501 trees were discarded as burn-in. To cross-check its phylogenetic topology, the ML phylogeny was also reconstructed with RAxML-NG v.1.2.0 (Kozlov et al. 2019) using the best-fitted substitution model for each region based on Akaike's information criterion (AIC) (Table 2). Each phylogenetic branch support value on the ML phylogeny was evaluated using bootstrapping with 100 replications. The phylogenetic hypotheses were visualised using FigTree v.1.4.4 (Rambaut 2018).

TABLE 2 | The best-fitted substitution model for each region using Bayesian and maximum likelihood (ML) phylogenetic analyses.

				Substitution model	
Data set	**Regions**	**No. of sequences**	**No. of sites**	**Bayesian tree**	**ML tree**[b]
chlDNA	*trnL–trnF*	163	2351	GTR + I + G	TVM + I + G
	rbcL	109	726	HKY + I + G	HKY + I + G
	trnH–psbA	94	1709	HKY + I + G	TVM + I + G
	matK	136	2332	GTR + I + G	TVM + I + G
nrDNA	*ITS*	78	6039	GTR + I + G	GTR + I + G
Combined		191	13,157	GTR + I + G[a]	

[a] Substitution model for BEAST analysis.
[b] See result Figure S1.

2.3 | Ancestral Area and Ancestral Distributable Climate Reconstruction Analyses

To investigate the historical biogeography of Shoreae within the given phylogeny, we conducted ancestral area reconstruction analysis using BioGeoBEARS v.1.1.3 (Matzke 2013) in R v.4.3.2 (R Core Team 2023). BioGeoBEARS performs different biogeographic models of ancestral area estimation, compares these results, and produces best-fitted historical biogeography outputs. We utilised biogeographic distribution data for each species (Table S1), which were obtained from Plants of the World Online (POWO 2024). Distribution regions were defined based on previous studies (Woodruff 2010; Morley 2018) as follows: China (Ch), Indochina = Indo-Burma sensu Myers et al. (2000) (Ic), Philippines (Ph), South Asia (Sa), Sundaic (Su) and Wallacea (Wa) (detailed region definition in Figure 1). We evaluated six models implemented in the programmes: DEC (dispersal-extinction-cladogenesis), DEC+J (including founder-event speciation), DIVALIKE (a likelihood version of dispersal-vicariance), DIVALIKE+J (including founder-event speciation), BAYAREALIKE (a likelihood version of the Bayesian inference of historical biogeography for discrete areas), and BAYAREALIKE+J (including founder-event speciation). The likelihood values of these models were compared using the likelihood ratio test, in which we used the AICc values of different models to select the most likely biogeographical scenario. The most likely scenario model was selected with the lowest AICc value.

To investigate the historical distributable climate of Shoreae within the given phylogeny, we conducted ancestral distributable climate reconstruction analysis using BayesTraits v.4 (Pagel et al. 2004). We utilised distributable climate data (Table S1) for each species. To obtain distributable climate data, we used species distribution data and climate classification (Beck et al. 2023). Species distribution data were initially collected from GBIF (https://www.gbif.org) and the IUCN Red List of Threatened Species (https://www.iucnredlist.org). The distributable climate was then determined based on these distribution data and a climate classification map. The climate classification, as defined by Beck et al. (2023), includes the following categories: tropical-rainforest (Af), tropical-monsoon (Am), tropical-savannah (Aw) and temperate-dry winter-hot summer (Cwa). BayesTraits was run using a multistate MCMC analysis with default settings, consisting of 5.5 million iterations, sampling every 1000 iterations. Two output log files were evaluated for ESS (> 200) after the Markov chains had reached a stationary distribution, with the initial 0.5 million iterations discarded as burn-in. The ancestral state at each node was determined using a 95% threshold. We calculated the sum of posterior probabilities for the most likely state at each node, and states that contributed to 95% of the PP were included in the result. For instance, if the posterior probabilities for states A, B, C and D were 0.50, 0.42, 0.06 and 0.02, at node X, the inferred states at node X would be A, B and C. To confirm the area of distributable climate in the past, a palaeoclimate map was reconstructed. An overview of the Köppen-Geiger climate classes, including the defining criteria, is based on Peel et al. (2007) and Beck et al. (2023). The climate datasets (i.e., monthly mean near-surface air temperature [°C] and monthly total precipitation [mm]) from 75 to 3 Ma were adopted from Valdes et al. (2020).

In these analyses, we used a molecular phylogenetic tree reconstructed with MrBayes (see Section 3; Figure 1). Since molecular phylogenetic trees were reconstructed with MrBayes and BEAST (see below), different substitution models were employed—one for each partition in MrBayes and one for the combined partition in BEAST. We opted to use the tree from MrBayes, which provides better resolution for the relationships between Shoreae species. *Dryobalanops* (outgroup genus) was excluded in these analyses.

2.4 | Divergence Time Estimation

To estimate the divergence time among Shoreae species, we employed BEAST version v.2.7.6 (Bouckaert et al. 2014) with the optimised relaxed clock model and tree prior based on the birth-death model (Gernhard 2008). This model was chosen based on preliminary analyses using the phytools R package (Revell 2012), in which the birth-death model (AIC = −241.5026) better explains the data compared to the Yule model (pure-birth model, Yule 1925) (AIC = −233.4644) for the BEAST tree of the tribe Shoreae. The analysis combined the entire partition datasets (Table 2). Seven monophyletic clade sets were defined according to the results of Bayesian molecular phylogeny as follows: (1) Shoreae, (2) *Anthoshorea*, *Doona*, *Neobalanocarpus* and *Hopea*, (3) *Parashorea*, *Pentacma*, *Richetia*, *Rubroshorea* and *Shorea*, (4) *Parashorea*, (5) *Richetia*, (6) *Rubroshorea* and (7) *Pentacma* and *Shorea* (see Section 3; Figure 1). Calibration points were defined with the lognormal prior (crown node of Shoreae at 75.82 million years ago [Ma] with a standard deviation of 0.05) considering the results of Bansal et al. (2022). Two independent MCMC algorithms were run for 30 million generations, sampling every 1000 generations. All output files were evaluated based on the ESS (> 200) after the removal of 10% burn-in and were combined using Tracer v.1.7.2 (Rambaut et al. 2018). The output tree files from the two independent runs were pooled into a single combined file after removing the initial 3000 trees as burn-in using LogCombiner v.2.7.6 (in the BEAST package), and then a maximum clade credibility tree with mean node height was summarised using TreeAnnotator v.2.7.6 (in the BEAST package) before visualisation with FigTree v.1.4.4 (Rambaut 2018). Each phylogenetic branch's support for the resulting phylogeny was evaluated based on Bayesian posterior probabilities.

2.5 | Temporal-Based Diversification Analyses

To assess the temporal diversification of the Shoreae tribe, lineage-through-time (LTT) plot analysis was conducted based on a phylogenetic tree reconstructed with BEAST analysis using the phytools R package (Revell 2012). The LTT plot analysis involved 100 simulations based on the birth-death process (with a birth rate of 0.115 and an extinction rate of 0.040, as estimated from RevBayes analyses below). These simulations were computed using the R package APE (Paradis et al. 2004) based on the phylogenetic tree reconstructed with BEAST analysis. To assess the variability in evolutionary rates within the tribe Shoreae, additional analyses using RevBayes v.1.2.4 (Höhna et al. 2016) were performed based on a phylogenetic tree reconstructed with BEAST analysis. We examined how speciation, extinction and net-diversification rates change throughout the evolutionary process of Shoreae by performing an episodic diversification rate estimation. We followed the tutorial (https://revbayes.github.io/tutorials/divrate/ebd) with $\rho = 0.587$ (186 out of 317 total samples) and a chain length of 50 thousand generations, sampling every 200 generations. The R package RevGadgets v.1.2.1 (Tribble et al. 2022) was used to visualise these rate changes within Shoreae. We estimated branch-specific diversification rates to identify branches that shifted their diversification rates during

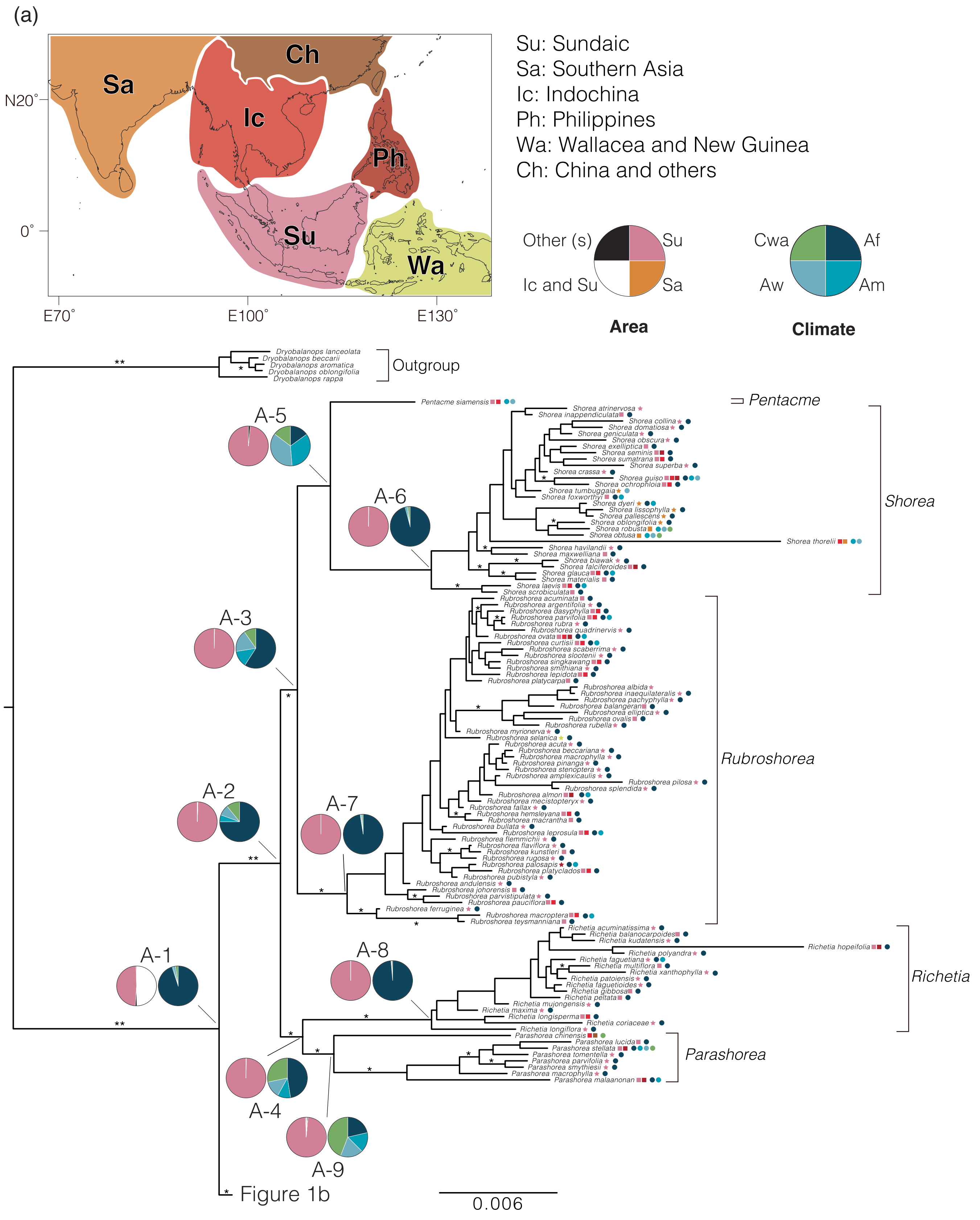

FIGURE 1 | Legend on next page.

FIGURE 1 | Bayesian molecular phylogenetic tree of the tribe Shoreae (Figure 1b is connected to the bottom branch of the phylogenetic tree in Figure 1a) was reconstructed using molecular data from partial *trnL–trnF*, *rbcL*, *trnH–psbA* and *matK* and *ITS* regions. Asterisk(s) positioned near each branch denote the Bayesian posterior probability (PP, *: > 0.7. **: > 0.99). Pie charts on a node show the results of ancestral area (left) and distributable climate (right) reconstruction based on the Bayesian phylogeny (colour legend in the upper right). Present distribution and climate class are denoted on the right side of the species name. Region-specific and non-region-specific species are denoted by stars and squares, respectively (colours in the symbols correspond to coloured regions in the map). Distributable climate class of each species is denoted by circles (colours in the symbols correspond to coloured legend in the upper right). The map delineates regions defined in BioGeoBEARS: Ch, China (China mainland and others); Ic, Indochina (Myanmar, Thailand, Laos, Vietnam, Cambodia, Andaman Island and Hainan Island); Ph, Philippines (Philippine); Sa, South Asia (India, Assam area, Bangladesh, Bhutan, Nepal, Tibet area, Himalaya area and Sri Lanka); Su, Sundaic (Malaya, Sumatra, Borneo and Java); Wa, Wallacea (Sulawesi, Sulawesi, Lesser Sunda Islands, Maluku Islands and New Guinea). Climate class defined in BayesTraits4: Af, tropical-rainforest; Am, tropical-monsoon; Aw, tropical-savannah; Cwa, temperate-dry winter-hot summer.

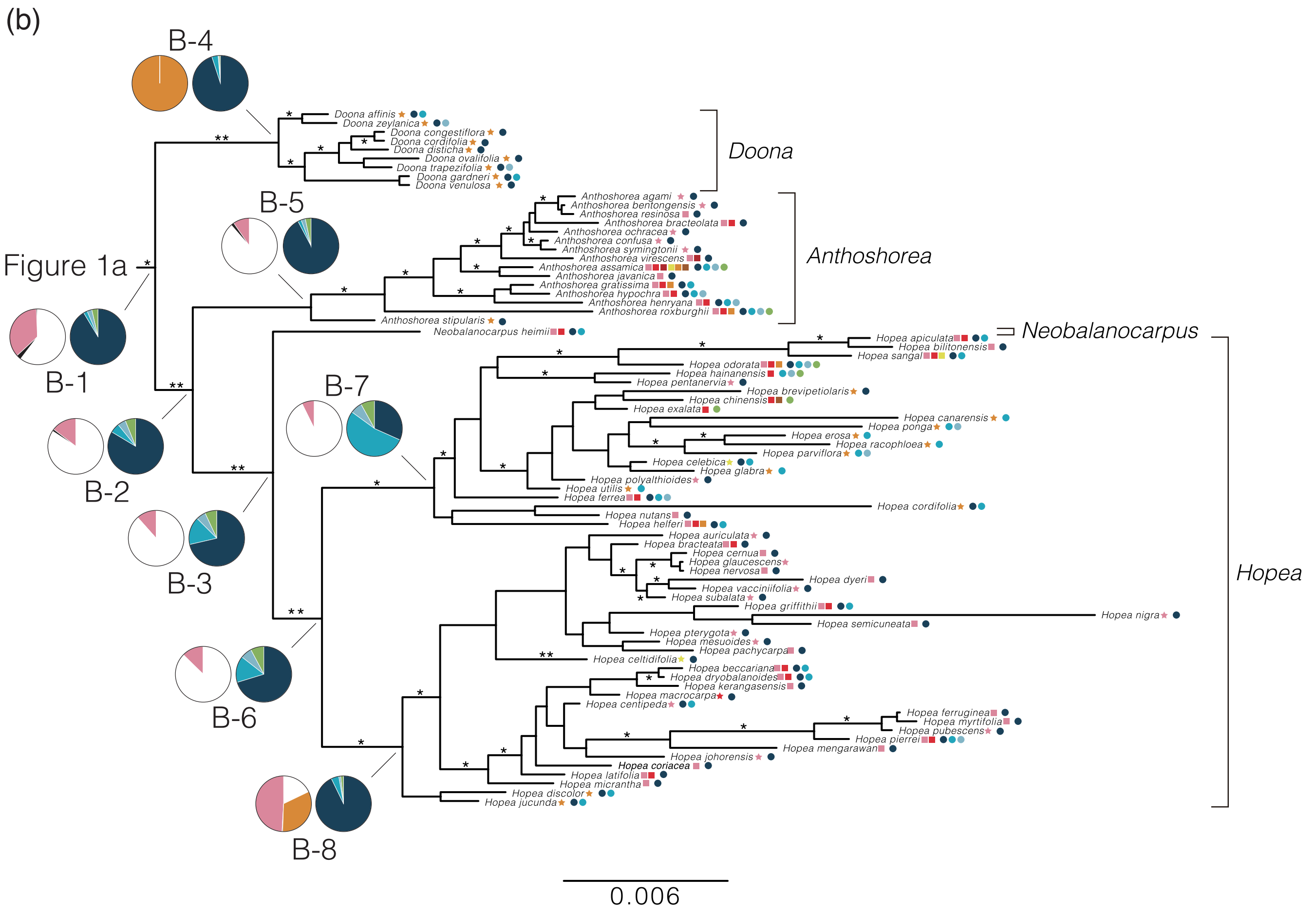

FIGURE 1 | (Continued)

Shoreae's evolutionary process. This followed the tutorial (https://revbayes.github.io/tutorials/divrate/branch_specific) with $\rho = 0.587$ (186 out of 317 total samples) and a chain length of 50 thousand generations, sampling every 200 generations. Again, we used RevGadgets v.1.2.1 (Tribble et al. 2022) for visualising shifts in diversification rates within Shoreae. Additionally, the Bayesian Analysis of Macroevolutionary Mixture (BAMM; http://bamm-project.org) was used to evaluate the variability in evolutionary rates within the tribe Shoreae, utilising the phylogenetic tree reconstructed with BEAST analysis. The evolutionary rate parameters (expected number of shifts = 1.0, lambdaInitPrior = 3.385, lambdaShiftPrior = 0.015 and muInitPrior = 3.385) were assessed using the setBAMMpriors function in the R package BAMMtools (Rabosky et al. 2014). The global sampling fraction was set at 0.587 (186 out of 317 total samples). The analysis was carried out by running four independent chains simultaneously for 10 million generations, assuming convergence when the ESS value exceeded 200, and discarding the first 10% as burn-in. Rate shift inferences and visualisations were performed using the BAMMtools R package (Rabosky et al. 2014). The Bayes factor (BF) calculations between models were utilised to select the optimal model. A BF value of less than 1 indicates negative support, a BF between 1 and 3 suggests minimal significance, a BF between 3 and 12 indicates positive support, and a BF greater than 12 is considered strong support for one model over another (Raftery 1996).

Although these analyses typically require an ultrametric phylogenetic tree, the phylogenetic tree reconstructed in this study using BEAST analysis was not ultrametric due to the presence of some negative branch lengths. We, therefore, applied a small branch length (0.000001) to the negative branches and converted the BEAST-reconstructed tree into an ultrametric tree using the chronos function in the R package Ape (Paradis et al. 2004).

2.6 | Estimation of Species Colonisation

To explore changes in the colonisation rates between and within regions and distributable climate classes, we employed the rolling estimates previously employed by Xing and Ree (2017). This method quantifies the contribution of each state to the Shoreae diversification process. The colonisation rates through time were estimated as $d_{ij}(t)=c_{ij}(t)/n_i(\mathrm{t}-1)$, where $c_{ij}(t)$ is the number of inferred colonisation events of area *j* from area *i*. For each node, $\sum c_{ij}(t)=1$. Areas and climate classes were plotted for all nodes based on the results of the BioGeoBEARS and BayesTraits analyses, respectively, and a score (rate) for each node was calculated. The total scores for each area and climate class were subsequently calculated.

3 | Results

3.1 | Phylogenetic Analysis

The Bayesian consensus phylogenetic hypothesis based on 13,125 sites recovered two major lineages with $PP>0.7$. The first one included the genera *Parashorea*, *Pentacme*, *Richetia*, *Rubroshorea* and *Shorea* (Clade A, Figure 1a), whereas the other one consisted of the genera *Anthoshorea*, *Doona*, *Hopea* and *Neobalanocarpus* (Clade B, Figure 1b). Except for *Shorea*, all genera were recovered as monophyla with $PP>0.7$. The genus *Parashorea* formed a sister clade of *Richetia*. These two genera formed the sister clade to a clade comprising *Pentacme*, *Rubroshorea* and *Shorea*. The species-poor genus *Pentacme* was found to be sister to *Shorea*. In the second lineage, the genus *Doona* was found as sister to a clade comprising *Anthoshorea*, *Hopea* and *Neobalanocarpus*. The latter monotypic genus was sister to *Hopea*. A nearly identical topology was displayed by the optimal phylogenetic tree recovered in the ML analyses (see Figure S1). The main difference was the placement of *Pentacme*, which was recovered as sister to a clade comprising *Rubroshorea* and *Shorea*. It is important to note that the theme Bayesian consensus phylogenetic hypothesis recovered the sister relationship of *Pentacme* and *Shorea* with $PP<0.7$. Species belonging to the species-rich genus *Hopea* were nested in two major clades with $PP>0.7$ in clade B (Figure 1b).

Species of *Rubroshorea* did not nest in a topology that corresponded to the proposed five sections (Brachyptera, Rubroshorea, Ovalis, Pachycarpae and Rubella) and two subsections (Auriculatae, Rubroshorea belonging to section Rubroshorea). Similarly, among *Shorea*, two sections (Barbata and Shorea) were not shown as monophyletic in our analysis. In clade B (Figure 1b), the two sections and four subsections (subsections Pierrea and Hopea in section Hopea and subsections Dryobalanoides and Sphaerocarpa in section Dryobalanoides) belonging to *Hopea* were not recovered as monophyletic.

3.2 | Ancestral Area and Ancestral Distributable Climate Reconstruction and Divergence Time Estimation Analysis

In the ancestral area reconstruction analysis with BioGeoBEARS, the most likely biogeographical scenario model with the lowest AICc value was BAYAREALIKE+J (LnL = −360.79, AICc = 727.73, AICc_wt = 0.80; Table S2). The results of ancestral area reconstruction analysis, ancestral distributable climate reconstruction analysis, and divergence time estimation analyses are shown in Figure 1, Table 3 and Figures S2–S4. These results indicated that the split of Shoreae into two major clades (node A-1 in Figure 1a) occurred in the Indochina and Sundaic regions and in the tropical-rainforest climate class around 82.76–67.97 Ma (95% highest probability density [HPD]).

The genera *Parashorea*, *Pentacme*, *Richetia*, *Rubroshorea* and *Shorea* were split from the other clade after 54 Ma (64.73–30.60 Ma in 95% HPD), in the Sundaic region and in all of the climate classes (tropical-rainforest, tropical-monsoon, tropical-savannah and temperate-dry winter-hot summer climates) (nodes A-3–5 in Figure 1a, Table 3). The Sri Lanka endemic genus *Doona* was separated from its sister clade occurring in Indochina and Sundaic regions and in the tropical-rainforest, tropical-savannah and temperate-dry winter-hot summer climate classes around 80.73–62.37 Ma (95% HPD, node B-1 in Figure 1b), whereas the genera, *Anthoshorea*, *Neobalanocarpus* and *Hoepa* were split from the other clade after 67 Ma (75.18–45.45 Ma in 95% HPD), in the Indochina and Sundaic region and in all of the climate classes (nodes B-2 and B-3 in Figure 1b, Table 3). The two major clades of the genus *Hopea* differentiated in the Indochina and Sundaic regions and in all of the climate classes around 60.68–40.22 Ma (95% HPD, node B-6 in Figure 2b). The ages of the crown nodes of *Richetia*, *Rubroshorea* and *Shorea* were younger than 43 Ma in the Sundaic region and in the tropical-rainforest climate class (nodes A-6–8 in Figure 1a, Table 3). The age of the crown node of *Parashorea* was around 54.62–28.96 Ma (95% HPD) in the Sundaic region and in all of the climate classes (node A-9 in Figure 1a). The age of the crown node of *Doona* was around 30.82–7.75 Ma (95% HPD) in the South Asia region and in the tropical-rainforest climate class (node B-4 in Figure 2b). The age of the crown node of *Anthoshorea* was 49.75–21.92 Ma (95% HPD) in the Indochina and Sundaic regions and in the tropical-rainforest and temperate-dry winter-hot summer climate classes (node B-5 in Figure 2b). The age of the crown node of *Hopea* was around 60.68–40.22 Ma (95% HPD) in the Indochina and Sundaic regions and in all of the climate classes (node B-6 in Figure 2b). The ages of the two crown nodes in *Hopea* were around 53.91–29.67 Ma (95% HPD) in the Indochina and Sundaic regions and in all of the climate classes, and around 49.18–28.83 Ma (95% HPD) in the Sundaic regions and in the tropical-rainforest and tropical-monsoon climate classes, respectively (nodes B-7 and B-8 in Figure 2b).

TABLE 3 | Estimated divergence time with 95% HPD, biogeographic states and distributable states of the tribe Shoreae.

Node	Age (million years ago)	95% HPD	Biogeographic state based on the Bayesian phylogenetic tree	Distibutable climate state based on the Bayesian phylogenetic tree
A-1	76.71	82.76–67.97	Indochina and Sundaic regions	Tropical-rainforest
A-2	60.31	71.22–46.60	Sundaic region	All climates
A-3	53.38	64.73–39.61	Sundaic region	All climates
A-4	53.09	64.14–39.11	Sundaic region	All climates
A-5	45.71	57.93–30.60	Sundaic region	All climates
A-6	33.59	45.10–21.34	Sundaic region	Tropical-rainforest
A-7	42.13	53.58–27.97	Sundaic region	Tropical-rainforest
A-8	27.18	38.20–15.15	Sundaic region	Tropical-rainforest
A-9	42.98	54.62–28.96	Sundaic region	All climates
B-1	72.76	80.73–62.37	Indochina and Sundaic regions	Tropical-rainforest, Tropical-savannah and Temperate-dry winter-hot summer
B-2	66.44	75.18–54.77	Indochina and Sundaic regions	All climates
B-3	57.49	66.79–45.45	Indochina and Sundaic regions	All climates
B-4	19.40	30.82–7.57	South Asia regions	Tropical-rainforest
B-5	36.86	49.75–21.92	Indochina and Sundaic regions	Tropical-rainforest and Temperate-dry winter-hot summer
B-6	51.93	60.68–40.22	Indochina and Sundaic regions	All climates
B-7	42.82	53.91–29.67	Indochina and Sundaic regions	All climates
B-8	40.15	49.18–28.83	Sundaic region	Tropical-rainforest and Tropical-monsoon

Note: All climates, all of the climate classes (tropical-rainforest, tropical-monsoon, tropical-savannah and temperate-dry winter-hot summer climates).
Abbreviation: HPD, highest probability density.

3.3 | Temporal-Based Diversification Analyses and Estimation of Species Colonisation

The observed LTT plot on logarithmic scale fell within the range of simulated plots, suggesting that the diversification rate of Shoreae species followed the birth-death process (Figure 2a). The results of the diversification rate analyses conducted with RevBayes and BAMM are presented in Figure 2b–e. The RevBayes analyses converged as indicated by high ESS values (965.4 for the likelihood of the episodic diversification rate estimation and 1905.9 for the likelihood of the branch-specific diversification rates estimation). Although the RevBayes results did not detect any diversification rate shifts at specific nodes in the phylogeny, the net diversification and speciation rates increased after approximately 20 Ma, while the extinction rate remained consistently low (Figure 2b,d). The BAMM analysis converged as indicated by high ESS values (936.56 for log-likelihood, 1162.44 for number of shifts). The results of the BAMM analyses indicated the best scenario with a single evolutionary rate shift (Figure 2c, PP = 0.56). Compared to the null model, the BF for this scenario was 4.24, while the scenario with two shifts had a BF of 2.12, and the scenario with three or more shifts had a BF lower than 0.74. The BAMM analysis results showed an increase in net diversification and speciation rates, a stable and low extinction rate, and a single shift in diversification rate around 20 Ma within the *Rubroshorea* clade (Figure 2c,e).

The rolling estimates of colonisation rate over time among regions recovered three diversification hotspots, namely Indochina, South Asia and Sundaic. The results suggested that these regions were the main source of species distributed in China, Philippines and Wallacea (Figure 3a). Most species belonging to *Anthoshorea*, *Hopea*, *Parashorea*, *Richetia*, *Rubroshorea* and *Shorea* have originated in the Sundaic, while some other species and/or ancestral species have diversified after migrating from Sundaic to other regions (Figure S5). Species of *Doona* were likely to have diversified in Sri Lanka (Table S1, Figure S2).

The rolling estimates of colonisation rates across distributable climates identified the tropical rainforest as the primary diversification hotspot climate (Figure 3b). Most species belonging to *Anthoshorea*, *Doona*, *Hopea*, *Parashorea*, *Richetia*, *Rubroshorea* and *Shorea* were likely to have originated in the tropical rainforest climate, while some other species and/or ancestral species have diversified in other climates and migrated to other climates (Figure S6).

4 | Discussion

4.1 | Molecular Phylogeny of Shoreae

The Bayesian molecular phylogeny revealed two major clades within the tribe Shoreae with high posterior probabilities. While most of the genera (*Anthoshorea*, *Doona*, *Hopea*, *Parashorea*, *Richetia* and *Rubroshorea*) showed monophyly (Figure 1), sections and subsections within the genera *Hopea*, *Rubroshorea* and *Shorea*, proposed based on morphological characters considered of taxonomic value, were found to be polyphyletic. This finding is consistent with previous studies (Heckenhauer et al. 2018; Ashton and Heckenhauer 2022; Bansal et al. 2022; Cvetković et al. 2022). The result of molecular phylogeny in this study suggests that classifying these sections and subsections based solely on morphological traits is ineffective. While some valuable morphological features

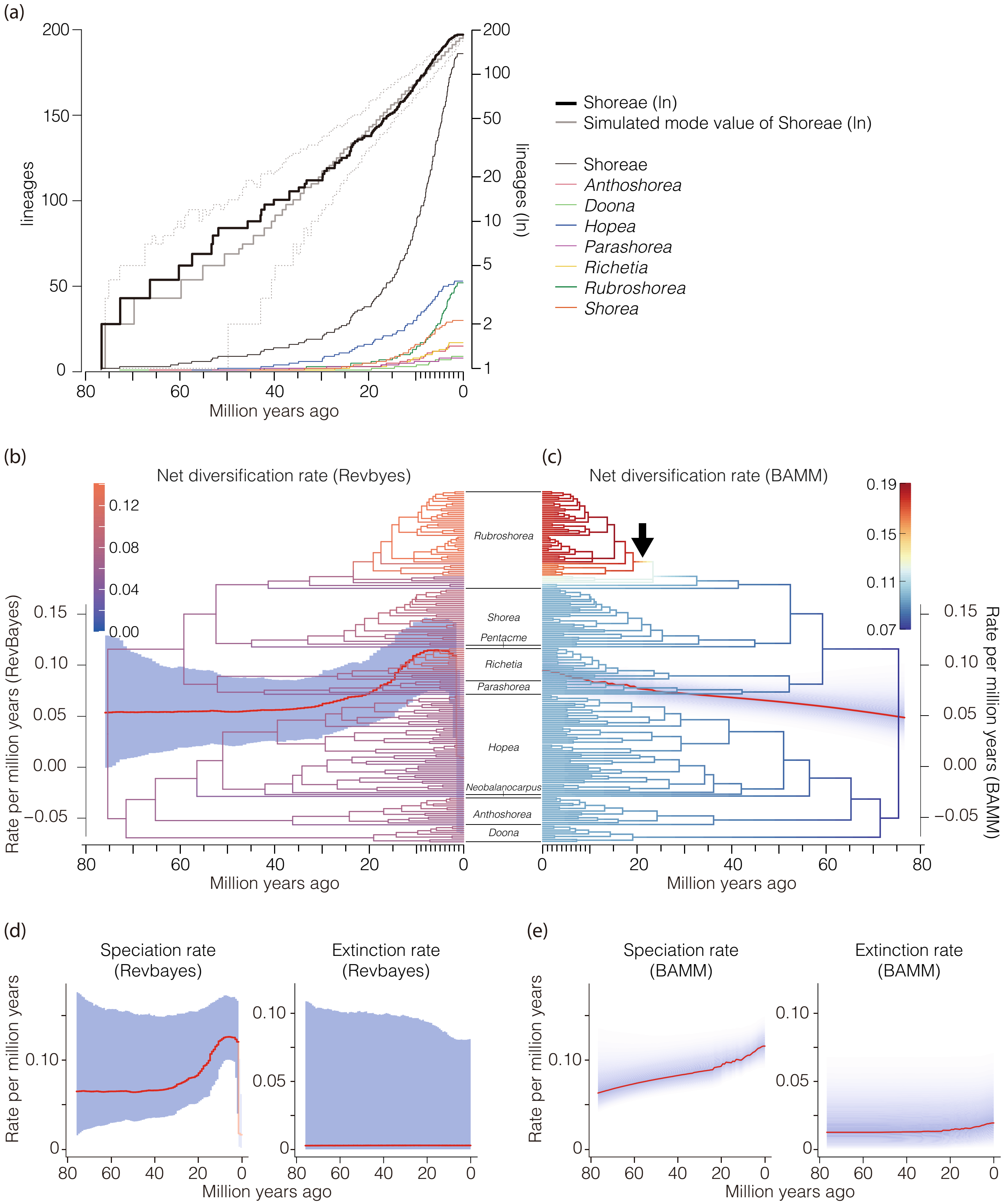

FIGURE 2 | Legend on next page.

FIGURE 2 | Results of diversification analyses within tribe Shoreae. (a) The LTT (lineage-through-time) plot illustrating the diversification rate of the tribe Shoreae. The solid black line and thick solid black line represent the diversification and logarithmic diversification of Shoreae, respectively. The solid grey line and broken line represent the mode value and 95% confidence intervals, respectively, in the simulated LTT plot. Coloured lines correspond to the diversification of genera within Shoreae, excluding *Pentacma* and *Neobaranocarpus*. (b) Molecular phylogenetic tree was reconstructed by BEAST with net diversification rate inferred by Revbayes. The graph displays the results from the episodic birth-death model implemented in RevBayes, where the red line represents the net diversification rate and the blue area indicates its 95% confidence intervals. Colour pattern illustrates the variation in net diversification rates within Shoreae. This coloured phylogeny was based on the scenario with no diversification rate shift. (c) Molecular phylogenetic tree was reconstructed by BEAST with net diversification rate inferred by BAMM. The graph displays the results from the episodic birth-death model implemented in BAMM, where the red line represents the net diversification rate and the blue area indicates its 95% confidence intervals. Colour pattern indicates variation of net diversification rates within Shoreae. This coloured phylogeny was based on scenario with one diversification rate shift. The arrow indicates the branch with a net diversification shift. (d, e) show the estimates of speciation and extinction rates from the episodic birth-death model implemented in RevBayes and BAMM, respectively. In both panels, the red line represents the speciation or extinction rate, and the blue area indicates its 95% confidence intervals. The faded lines in (b, d) indicate that the drops in diversification and speciation rates after the youngest splitting nodes are estimation artefacts.

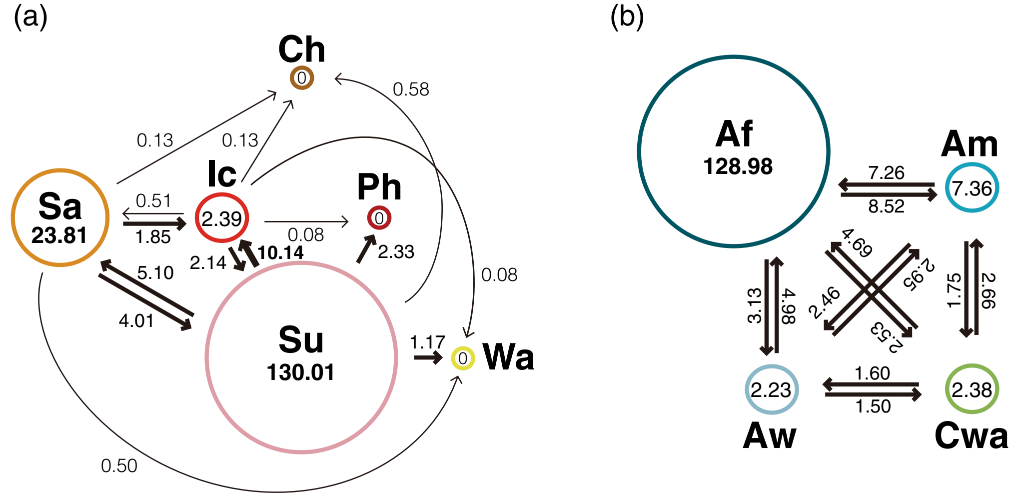

FIGURE 3 | Assembly of Shoreae species across different (a) regions and (b) climate classes, with colonisation rates (r) calculated by the rolling estimates through time. Numbers within circles represent colonisation rates per state within specific regions or climate classes, while numbers on arrows denote colonisation rates assocated with dispersal between regions or between climate classes (thin arrows: $0 < r < 1$, medium: $1 \leq r < 10$, thick: $10 \leq r$). Regions: Ch, China (China mainland and others); Ic, Indochina (Myanmar, Thailand, Laos, Vietnam, Cambodia, Andaman Island and Hainan Island); Ph, Philippines (Philippine); Sa, South Asia (India, Assam area, Bangladesh, Bhutan, Nepal, Tibet area, Himalaya area and Sri Lanka); Su, Sundaic (Malaya, Sumatra, Borneo and Java); Wa, Wallacea (Sulawesi, Lesser Sunda Islands, Maluku Islands and New Guinea). Climate classes: Af, tropical-rainforest; Am, tropical-monsoon; Aw, tropical-savannah; Cwa, temperate-dry winter-hot summer.

would exist, further research regarding feature-based taxonomic classification is warranted.

This study identified a monophyletic clade composed of *Parashorea* and *Richetia* with a high PP. Previous studies have presented conflicting results concerning *Parashorea*. Our molecular phylogenetic analyses based on a dataset combining plastid and nuclear sequences with over 13K sites agree with our hypothesis: ((*Richetia* + *Parashorea*) + (*Shorea* + *Rubroshorea*)), and indicate a close relationship between *Parashorea* and *Richetia*.

We found that certain relationships among genera remained unclear due to low posterior probabilities. The results of the molecular phylogenetic analysis rejected our second hypothesis, suggesting that *Pentacma*, which comprises two species (*P. siamensis* and *P. paucinervis*; Ashton and Heckenhauer 2022), is associated with *Shorea*, not with *Doona*, although the PP was low. It is known that *Pentacma* and *Doona* species share characteristics (Ashton et al. 2021), which may have resulted from convergent evolution. Wines and Tiu (2012) suggested that incorporating taxa, even with incomplete sequences, can generally enhance phylogenetic accuracy. Thus, the inferred molecular phylogeny in this study sheds light on the unresolved topological complexity in Shorea. However, unresolved issues regarding the phylogenetic relationships among Shorea genera remain. Additional specimens and sequence data are necessary to reconstruct and update the phylogeny of Shorea, including the positioning of *Pentacma* and the monotypic genus *Neohopea*. Progress may be achieved by expanding the DNA sequence data from a few regions with the chloroplast genomes and nuclear DNA toward a comprehensively sampled phylogenomic dataset incorporating various loci.

4.2 | Diversification Analysis

The crown ages of the Shoreae genera in this study differ from those in the previous study (Bansal et al. 2022). The estimated ages of the major nodes in this study were generally younger than those in Bansal et al. (2022). For nodes A2–4, A6–9 and B1–6, the average difference was 8.19 Ma younger, with the range of differences spanning from 22.9 Ma younger to 2.9 Ma older. Differences in crown node ages of the major nodes are likely due to variations in age calibration methods, the size of sequences, specimens used, and, in particular, the algorithms used. While Bansal et al. (2022) utilised a broader range of taxa with multiple calibration points and specimens belonging to the whole Dipterocapeceae, our study was taxon-focused with one calibration point and only specimens belonging to the tribe Shoreae. The variation in estimated divergence times can be attributed primarily to methodological differences, particularly regarding calibration points and their numbers. Previous studies using other taxonomic groups also reported similar discrepancies (e.g., Yang and Yoder 2003). Additionally, our study utilised the secondary calibration method (calibrations based on the results of previous molecular dating studies), which is known to potentially result in younger divergence time estimates (Schenk 2016). Therefore, it is important to interpret the results carefully in light of such factors that potentially cause discrepancies in estimated divergence time.

The calibrated molecular phylogeny reveals the ages of splitting and crown nodes. Our estimated divergence ages among genera within the tribe Shoreae are acceptable. Three fossil records related to the tribe Shoreae (*Parashorea*, *Rubroshorea* and *Shorea* type fossils) from the Vastan Lignite Mine in India date back to 54 Ma (Bansal et al. 2022). Based on our divergence time estimation, which suggests a younger age than previous studies due to our secondary calibration method, these fossils closely align with the corresponding crown node ages within a 95% HPD estimated in this study. Furthermore, most of the estimated divergence ages are consistent with those of a recent study (Table 3; Bansal et al. 2022). The geographic occurrences of three fossil records from the Pondaung Formation in Myanmar (viz. *Shoeroxylon burmense*, *S. deomaliense* and *S. maomingensis*, representing *Shorea* type fossils from 39.5 Ma, Licht et al. 2014) and fossil records from Southern China (*Shorea maomingensis*, classified into *Doona*, *Parashorea*, *Shorea*, or extinct type; Feng et al. 2013; Ashton et al. 2021) suggest that these genera were distributed in the seasonal wet regions of Southeast Asia and Southern China during the late Eocene (37.7–33.9 Ma), as previously suggested based on pollen cores (Morley 2018). The reconstructed palaeoclimate in this study also indicates the distributable climate of *Parashorea* and *Shorea* in South and Southeast Asia and Southern China regions (Figure S7) and aligns with those fossil records.

This study performed an LTT plot with approximately 60% sampling of Shoreae species. While incomplete sampling can underestimate recent speciation rates (Helmstetter et al. 2022), a simulation study found that the trends in the slope of the LTT plot with subsampled OTUs were similar to that with a full set of OTUs (Cusimano and Renner 2010). Therefore, we consider the diversification process of Shoreae indicated by the LTT plot reliable. The observed LTT plot on a logarithmic scale fell within the range of the simulated plots, supporting the idea that a birth-death process adequately explains the diversification history of Shoreae species.

The results from the RevBayes and BAMM analyses indicated an increase in net diversification rate starting around 20 Ma, and this diversification, particularly within *Rubroshorea*, has contributed to the current number of species in Shoreae. This diversification likely occurred during climate changes that resulted in the development of tropical climates in Southeast Asia (Morley 2012). The reconstructed palaeoclimate during 31–20 Ma also indicates the formation of a tropical-rainforest climate in Southeast Asia following the collision of the Indian subcontinent (Figure S7). This diversification can be attributed to the transition into increasingly tropical climates favourable for common Shoreae species (Ashton et al. 2021). BAMM analyses showed a diversification scenario with a single evolutionary rate shift in *Rubroshorea*, which is not only distributed and diversified in Southeast Asia, especially in the Sundaic region, but also consists of various endemic species (32 out of 52 *Rubroshorea* species in this study are endemic to Borneo). Northwest Borneo boasts the richest dipterocarp flora, including the highest endemic species (Ashton et al. 2021). A palaeogeographic event forming a complex geological structure in the proto-northwest Borneo area occurred from the earliest Miocene to the Pliocene, contributing to the species richness in Northwest Borneo (Ashton et al. 2021). The diversification scenario within Shoreae is likely related to palaeogeographic events in the tropical proto-northwest Borneo area.

4.3 | Dispersal Processes of Shoreae From the Indian Subcontinent to Proto-Southeast Asia

The reconstructed common ancestral area of the tribe Shoreae suggested an origin in Indochina and the Sundaic regions (node A-1, 82.76–67.97 Ma in 95% HPD, Figure 1a), which is inconsistent with the proposal taken forward in the study focusing on the history of all dipterocarps (Bansal et al. 2022). This previous study assumed an expansion of the distribution range from India toward Southeast Asia after the collision between India and Asia began during the middle to late Eocene period (47.8–33.9 Ma; Dutta et al. 2011; Kooyman et al. 2019). This conflict may be explained by post-collision processes resulting in the extinction of the ancestors of Shoreae species in the Indian subcontinent, and the discovery of fossil evidence supporting the presence of Shoreae in western India reinforces this argument. Therefore, the reconstructed ancestral areas in Indochina and Sundaic before 48 Ma probably pertain to the areas where species migrated from the Indian subcontinent to proto-Southeast Asia, ultimately shaping the South Asian area. Essentially, these areas were part of the Indian subcontinent and contributed to the supply of certain species to proto-Southeast Asia. According to this scenario, the Shoreae genera would have already been present and speciated in the Indian subcontinent. The results of the ancestral distributable climate reconstruction and palaeoclimate map indicate the distributable area of these species in the Indian subcontinent (Figure 1, Table 3, Figure S7). Furthermore, the ancestral area reconstructed at the root node may best be assigned to Africa (Bansal et al. 2022), as Shoreae genera likely originated through dispersal from Africa via the Kohistan–Ladakh Island Arc. This is supported by the fact that the ancient Indian subcontinent was situated in the Indian Sea along with the Kohistan–Ladakh Island Arc from the late Cretaceous to the early Palaeocene (Morley 2018; Bansal et al. 2022) around 70–54 Ma, as supported by the results of divergence time estimation in this study. The climate transition from aseasonal to perhumid in the Indian subcontinent also suggests that Shoreae species may have been widespread across the region (Morley 2018; Bansal et al. 2022). Despite discovering three *Shorea* fossils in western India, *Shorea* species may have been present in the eastern region of the Indian subcontinent, facilitating their migration to proto-Southeast Asia. The reconstructed palaeoclimate supports this hypothesis, showing the distributable area with tropical climates in both Africa and the Indian subcontinent prior to their collision (Figure S7a). The dispersal of plants into perhumid proto-Southeast Asia from the Indian subcontinent likely began in the middle Eocene, supported by the earliest appearance of Indian-origin angiosperms in the Sundaic area around 49 Ma, with increased dispersal occurring after 45 Ma (Morley 2018; Klaus et al. 2016).

It is important to acknowledge the conflicts and limitations associated with the ancestral state reconstruction analyses presented in this study. It is well recognised that analyses based solely on extant taxa can lead to inaccurate inference of ancestral areas, especially at deeper nodes such as the root of the phylogeny. To improve the accuracy of biogeographic reconstructions, it is essential to incorporate fossils and extinct taxa (Wisniewski et al. 2022; Faurby et al. 2024). While the inferred ancestral states at more recent nodes are likely to be reliable, those at deeper nodes may be prone to misidentification and should be re-assessed in future studies with more comprehensive datasets. Accordingly, the rolling estimates of colonisation rates for each genus (Figures S5 and S6) can be considered broadly acceptable, though potential overestimation cannot be excluded. Notably, across most genera, the contribution values for the Sundaic region and tropical rainforest climate remained consistently higher than those for other states.

4.4 | Dispersal and Diversification Scenario of Shoreae Genera

Our study supported the third hypothesis by shedding light on the diversification and dispersal dynamics within the tribe Shoreae, which have been shaped by the dynamic geographic and climatic landscapes of South and Southeastern Asia. Existing research suggests that shifts from arid or seasonal climates to perhumid environments (Morley 2012, 2018) have played pivotal roles in speciation in this region.

The result of ancestral distributable climate reconstruction analysis showed that the distributable climate of ancestral Shoreae species was most of the climate classes (nodes A-2–4 and B-1–3 in Figure 1, Table 3). Some ecological traits that influence species distribution are thought to have evolved gradually (Donoghue 2008). For example, the evolution of tolerance to freezing temperatures and highly seasonal climates from a tropical climate is considered a slow process. Thus, certain traits that facilitate plant migration through climate change may have already evolved (Donoghue 2008). Our results suggest that Shoreae species were already adapted to the predominantly tropical climates.

Following this, we outline the dispersal and diversification scenarios for each genus within Shoreae. Our findings from ancestral area and distributable climate reconstruction, divergence time estimation, and rolling estimates of colonisation rates through time indicate that several ancestral species of *Anthoshorea*, *Hopea*, *Neobaranocarpus*, *Parashorea, Pentacma, Richetia, Rubroshorea* and *Shorea* migrated into Southeast Asia during the Eocene and subsequently diversified, particularly in the Sundaic region and in tropical climate. This is attributed to the perhumid climate, suitable for common Shoreae species, primarily located in the southern part of proto-Malesian until the late Oligocene (Morley 2018). The reconstructed palaeoclimate map also showed that tropical climate had been developed in proto-Southeast Asia after the Indo-Asian collision (Figure S7).

Among the tribe Shoreae, some *Shorea* and *Hopea* species may have dispersed from Southeast Asia to South Asia (clades including nodes A-6 and B-7, Figure 1). Plant dispersal between South Asia and the Indochina and Sundaic regions was restricted due to the Neogene uplift of the Indo-Burmese range (Morley 2018; Ashton et al. 2021). Thus, some (albeit rare) *Shorea* and *Hopea* ancestral species that diversified in proto-Southeast Asia underwent back-dispersion into South Asia through distributable climate areas along the proto-Bay of Bengal (Figure S7) before the uplift of the Indo-Burmese range. In addition, it was observed that some species, such as the Sri Lanka endemic species *Anthoshorea stipularis*, *Hopea discolour* and *H. jucunda*, are likely to have remained on the Indian subcontinent. Although these species may have been distributed in South Asia in the past, it is believed that the onset of the Indian monsoon, the post-Eocene Indo-Asian collision, and the shift toward a more arid climate in South Asia likely reduced the extent of perhumid regions, causing the distribution of these ancestral species to shift southward. This scenario is proposed to explain the present distribution of *Doona* species (Shukla et al. 2013; Morley 2018). Indeed, the reconstructed palaeoclimate map indicates an expansion of dry climate areas in South Asia following the Indo-Asian collision (Figure S7b).

To our surprise, the collisions of the Australian Craton and Southeast Asia resulting in the formation of the Malesian archipelago consisting of the Sundaic region, the Philippines and the Wallaceae Region in the last 20 million years (see Hall 2012, 2017) appeared to have a less significant impact on the Shoreae. Our results did not indicate significant effects on Shoreae diversification through geographic isolation caused by this collision, except for a few Wallacean species (*Rubroshorea selanica*, *Hopea celebica* and *H. celtidifolia*). During the late Miocene to the Pleistocene, the migration of organisms from Australia to Southeast Asia was less frequent than from Southeast Asia to Australia (de Bruyn et al. 2014). The dipterocarps are arguably an example supporting the latter. Besides, this collision profoundly influenced the region's climate by disrupting the Indonesian throughflow, a major interoceanic current passing through the Malay Archipelago (Morley 2006). The climate shift toward a wetter climate caused by this collision facilitated the emergence of the modern Malesian flora (Morley 2000). Therefore, the Asia–Australia collision may have played a role in the diversification of Shorea by altering the climate in Southeast Asia.

This study suggests that plant species have migrated into suitable habitats and diversified in response to historical climate change. Ancestral climate reconstruction in this study implies that Shoreae species had already adapted to tropical climates before the collision of the Indian subcontinent with Asia. However, a key question remains: why are the distributions of most species still restricted to certain areas despite the presence of suitable climatic conditions elsewhere? Further research is needed to identify the factors that determine plant distribution. Physiological studies may provide insights into this issue. For example, some Shorea species showed differences in physiological traits related to water use, such as seedling drought tolerance and leaf dehydration traits (Kawai et al. 2021; Ichie et al. 2023). Such traits may be critical for understanding the distribution patterns of Shoreae species.

Author Contributions

Y.I. conceptualised the study and performed all analyses. All authors contributed to manuscript preparation. Y.I. and A.N. wrote the manuscript with contributions from H.S.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data utilised in this study are accessible through GenBank (https://www.ncbi.nlm.nih.gov/genbank/), the Plants of the World Online website (http://www.plantsoftheworldonline.org/), the World Flora Online Plant List (https://wfoplantlist.org), GBIF (https://www.gbif.org) and the IUCN Red List of Threatened Species (https://www.iucnredlist.org).

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Supporting Information

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