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Research article

Ecological trait divergence over evolutionary time underlies the origin and maintenance of tropical spider diversity

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Relative to its size, tropical Asia is likely to be the richest region in terms of biodiversity. However, the factors of species diversity formation and maintenance in Southeast (SE) Asia and neighboring regions remain poorly understood. Here we infer the evolutionary relationships within psilodercid spiders by incorporating fossil information into a robust, unprecedentedly complete species-level phylogeny of 202 extant species to explore potential abiotic drivers and ecological features underlying their stable diversification history. The combination of extant and extinct historical biogeographic data indicates that in situ speciation is the predominant form of diversification in tropical Asia but diverse Cretaceous psilodercids in Myanmar ambers were replaced by other biogeographical lineages during the northward movements of the Burma Terrane. Furthermore, our diversification analyses show no diversification rate changes through time and across geographic space in this family, but the genus *Althepus* displays an accelerated rate of species diversification driven by the remarkable expansion of leg length. Trait evolution analysis shows that ecological trait divergence contributes to the diversification and accumulation of tropical spiders by facilitating species coexistence. These findings provide empirical evidence that the ecological trait divergence over evolutionary time scales is key to forming species diversity hotspots in SE Asia. Thus, this study integrating molecular evidence and paleontological interpretation provides a new framework for understanding the evolution of tropical species diversity.

Keywords: biodiversity hotspots, biogeography, diversification, ecological traits, spider, tropics

Introduction

Tropical forests hold nearly two-thirds of Earth's biodiversity, and their astonishing species richness has attracted biologists to explore the evolution of these biodiversity

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hotspots (Weir and Schluter 2007, Estoque et al. 2019, Harvey et al. 2020, Liu et al. 2021). Specifically, Borneo and Indochina have proven to be major evolutionary hotspots for Southeast (SE) Asian biodiversity (de Bruyn et al. 2014). The diversity of species in SE Asia has long been explained by traditional abiotic factors related to colonization, speciation, and extinction rates, such as ancient geological history and long-time climatic stability (Wiens et al. 2006, Li and Wiens 2019). Since the Mesozoic, the Asian land area has increased, providing suitable habitat for the immigration of terrestrial species and opportunities for subsequent in situ speciation. For example, the Burma–Asia collision mediated the biotic interchange between the Burma Terrane and mainland Asia (Wood and Wunderlich 2023). In addition, divergent traits contributing to variation in niche use are also a major generator of diversity (Arnegard et al. 2014). Divergence in traits underlying niche use is an effective way to maintain high species diversity in the tropics with high levels of habitat heterogeneity (Merckx et al. 2015). However, the ways in which biotic and abiotic factors interact to promote and sustain species diversity in tropical Asia remain uncertain. Additionally, most large-scale biodiversity studies have focus on plants, vertebrates and marine invertebrates (Moyle et al. 2016, Bansal et al. 2022, Tian et al. 2024), leaving the diversity patterns of terrestrial invertebrates largely unexplored.

Spiders are not only among the most diverse invertebrates on Earth, with more than 50 000 species (World Spider Catalog 2024), but are also representative in the study of key phenotypic evolution, evolutionary diversity, and tropical Asian biodiversity hotspots (Piel 2018, Wolff et al. 2022). These makes spiders an ideal model for exploring biodiversity patterns and their underlying causes. Despite the advances in spider molecular phylogenetics, we know little about spider diversification through space and time, especially in tropical regions (Dimitrov and Hormiga 2021). Here, we focus on the species-rich family Psilodercidae (Araneae), one of the ancient and endemic web-building spider groups distributed in tropical Asia. Species diversity of extinct psilodercids in Myanmar suggests they were already an important and diverse component of tropical rainforests in SE Asia during the Cretaceous (Magalhaes et al. 2021). However, the largely unresolved relationships within the family have hampered our understanding of diversification in this large SE Asian group and limited examination of the broader drivers of tropical evolution.

Aiming to assess the relative role of classic biogeographical and ecological drivers in generating the hotspots of species diversity in SE Asia, we use molecular phylogenetics and biogeographical and diversification analyses for 202 living and five extinct species of the ancient family Psilodercidae. Psilodercidae currently contains 224 species in ten extant genera, and eighteen species in two extinct genera from mid-Cretaceous Burmese amber (Wunderlich 2012, 2015, 2017, Wunderlich and Muller 2018, Magalhaes et al. 2021, Xin et al. 2022). Most genera are endemic to limited geographic areas, whereas the genus *Althepus* with divergent body size, leg length and spinneret spigots is widespread and coexists with other genera across the SE Asian continent and numerous islands (Fig. 1, Supporting information). Furthermore, the fossil record of psilodercids provides a unique and complementary window to studying species generation in SE Asia. Psilodercid species are considered short-range endemics with ancient evolutionary histories (Deeleman-Reinhold 1995, Harvey 2002), making them excellent candidate models for studying the evolution of SE Asian biological diversity in deep time. Here, we used a total-evidence analysis to clarify the diverse evolution of psilodercid spiders, revealing ecological divergence and time are the main factors to promote the formation and maintenance of the SE Asian biodiversity hotspots.

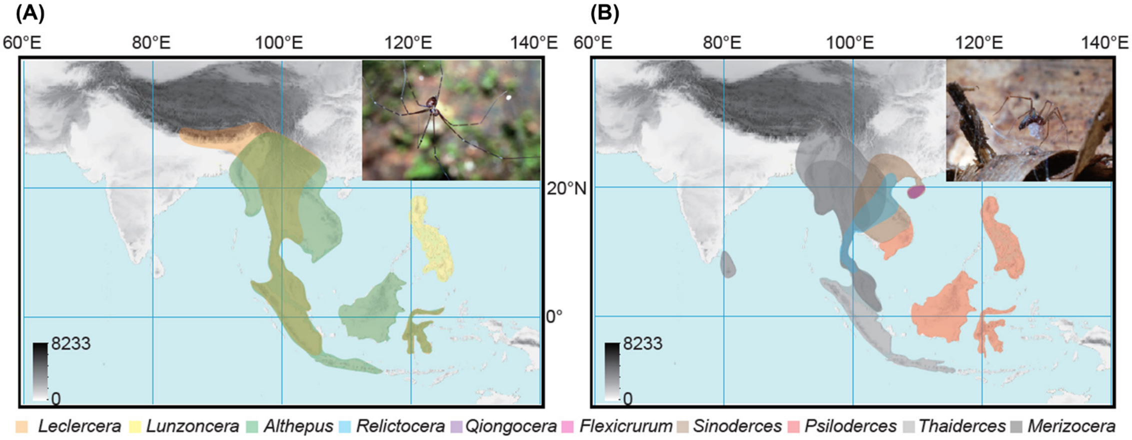

Figure 1. Geographic distribution of ten extant genera of sampled psilodercid spiders in SE Asia and neighboring regions. (A) The distribution pattern of clade I, including *Leclercera*, *Luzoncera* and *Althepus*. (B) The distribution pattern of clade II, including *Psiloderces*, *Sinoderces*, *Merizocera*, *Thaiderces*, *Flexicrurum*, *Relictocera* and *Qiongocera*.

Material and methods

Morphological and molecular data

The lack of a fully resolved phylogeny for Psilodercidae still hinders an understanding of the relationships among genera and the evolution of diversity within the family. In particular, the phylogenetic positions of the extinct genus *Priscaleclercera*, and the extant genera *Althepus* and *Leclercera* have been strongly debated. Due to the poor preservation of the extinct genus *Aculeatosoma* and the absence of defining characteristics typical of psilodercids (such as a bulbus attached to the basal part of the cymbium and spigots on posterior spinnerets arranged in a row) (Wunderlich 2017), it cannot be confidently classified within Psilodercidae. Therefore, *Priscaleclercera*, which includes numerous well-preserved fossil species, was selected for study. Firstly, to resolve the phylogenetic relationships between them, we have established a total-evidence dataset comprising 202 of 267 extant (75.7%) and five extinct psilodercid species, representing all ten extant and one extinct genus. Based on a previous morphological matrix (Tong and Li 2008) and identification keys (Deeleman-Reinhold 1995, Liu 2017, Magalhaes et al. 2021), the dataset comprises 46 morphological characters and 6013 molecular characters, consisting of five nuclear markers (*18s*, *28s*, *h3*, *wingless,* and *actin 5c*) and two mitochondrial genes (*16s* and *cox1*) (for details see Supporting information). Moreover, we also established a molecular dataset only comprising 202 extant species for downstream analyses. Of these, 900 sequences are novel and 418 sequences are from previous studies. In the above datasets, an additional species, *Loxosceles rufescens*, which is inferred to be sister to Psilodercidae, was used as the outgroup. DNA extraction, polymerase chain reaction, sequencing procedures, and primers were reported in Li et al. (2020). We aligned sequences using different methods of MAFFT 7 (http://mafft.cbrc.jp/alignment/server). Alignments of the protein-coding *h3*, *wingless*, *actin 5c* and *cox1* genes were produced using the L-INS-i method due to the lack of gaps and manually adjusted in MEGA X using the genetic codes (Kumar et al. 2018). Due to the highly variable nature of ribosomal genes, the E-INS-i method, which incorporates affine gap costs, was used to generate alignments of *16s*, *28s* and *18s*.

Furthermore, the genus *Althepus* prefer to build webs in tree buttresses and river embankments, while other genera build lower webs in leaf litter. Aerial web builders tend to have evolved longer legs than spiders of other guilds (Wolff et al. 2022). Therefore, we collected and analyzed morphological data associated with web height, such as leg length, body size, and relative leg length (leg/carapace ratio) to characterize the ecological niches of psilodercid genera (see the Supporting information for morphological data from all records). We compared traits of genera using Tukey's test with GraphPad Prism ver. 9.5.0 for Windows (GraphPad Software, www.graphpad.com). This approach aimed to explore the relationship between biotic factors and diversity, focusing on these morphological traits, which significantly vary across different ecological niches (Wolff et al. 2022, Shao et al. 2023).

Phylogenetic reconstruction and divergence time analyses

We used PartitionFinder ver. 2.1.1 (Lanfear et al. 2017) to select best-fit partitioning schemes and models for the molecular data only comprising extant species based on the Bayesian information criterion. The phylogenetic analysis using molecular dataset was performed in RAxML ver. 7.2.6 (Stamatakis 2014) using the best nucleotide substitution model for each partition (Supporting information) and rapid bootstrap analyses with 1000 replicates. The total-evidence dataset comprising both extant and extinct species was analyzed in IQ-TREE ver. 2.2.0 (Minh et al. 2020) using the best nucleotide substitution model for each partition (Supporting information) selected by *ModelFinder*. To evaluate the stability of the topology, we also inferred Bayesian inference (BI) topologies with MrBayes ver. 3.2.7 (Ronquist et al. 2012) using the best partitioning strategy and the best nucleotide substitution model.

We estimated divergence times of the molecular dataset using an uncorrelated relaxed clock model in BEAST ver. 1.10.4 (Drummond et al. 2012). We used three secondary calibrations derived from recent molecular dating estimates of Araneae (Li et al. 2020) to provide an even distribution of calibrations across the phylogeny. This recent molecular study used ten fossil calibrations to calibrate the Araneae phylogeny. The resulting tree sparsely sampled Psilodercidae (seven species) but included nodes shared with our sampling. First, the oldest calibration point was placed as the crown age of Psilodercidae at 154–97 Ma. Second, the ancestral node of *Sinoderces* and *Flexicrurum* was set to 80–31 Ma. Third, the timing of the common ancestor of *Merizocera*, *Sinoderces*, and *Flexicrurum* was constrained at 128–68 Ma (Supporting information). Further, we ran analyses using GTR substitution model with Gamma + Invariant category count of 4 under Yule prior and birth–death prior, separately. Each analysis was run using a tree sampled every 1000 generations in the three independent MCMC runs with 60 million generations. The stationarity of runs was examined using Tracer ver. 1.6 with an ESS > 200 for all parameters after combining all runs. Path sampling and stepping-stone sampling were used for model selection, employing 100 path steps with each chain running for 500 000 iterations (Supporting information).

Biogeographic reconstruction with and without fossil taxa

Biogeographic areas and habitats were assigned as traits for each species in the dated phylogeny. Based on previous phyloregions defined by de Bruyn et al. (2014), and paleoclimate and paleogeography (Westerweel et al. 2019), we delimited nine biogeographic areas: A) India and Sri Lanka; B) south China; C) Indochina; D) Thai-Malay Peninsula and Sumatra, and Java (Sumatra); E) Borneo; F) Philippines; G) Sulawesi; H) Himalayas; I) Burma Terrane. Among them, the Burma Terrane was once part of a Trans-Tethyan island arc, located at a near-equatorial southern latitude around 95 million years ago, indicating the Burma Terrane should be treated separately. Areas C+D+E+F+G+I represent SE Asia and areas A+B+H represent the neighboring regions. Psilodercidae species were assigned to areas according to their distributional data (Supporting information). As psilodercids lack the ability to jump between remote geographical regions (Deeleman-Reinhold 1995, Ree and Sanmartin 2018), the evolutionary history of the family was inferred using a dispe rsal-extinction-cladogenesis (DEC) model (Ree et al. 2005, Ree and Smith 2008), a likelihood version of dispersal-vicariance (DIVALIKE) model (Ronquist 1997), and a likelihood version of the BayArea (BAYAREALIKE) model (Landis et al. 2013) in BioGeoBEARS (Matzke 2013). The maximum range size was set to two. The models were evaluated by AICc and AICc_wt values (Supporting information). The time-stratified analysis used four time slices (130–90 Ma, 90–60 Ma, 60–30 Ma and 30–0 Ma) to reflect the changing connectivity of biogeographic areas caused by plate tectonics (Supporting information). The connectivity of areas in each analysis was modeled with four dispersal probability categories (1, 0.5, 0.1 and 0.01). Considering that fossil occurrences may affect the final inference, we also reconstructed the biogeographical history with extinct taxa. Because taxa in the genus *Priscaleclercera* are morphologically highly similar and all of them are from mid-Cretaceous amber from northern Myanmar (Dunlop et al. 2019), we incorporated one fossil species into the dated phylogeny based on its phylogenetic placement and minimum age. Third, we ran the models with the same settings to evaluate the impact of fossil occurrences on biogeographic inference.

To test the relationship between orogeny and diversity evolution, we reconstructed the ancestral state of living psilodercid spiders. Based on previous studies, we categorized the habitat into four elevation states (Toussaint et al. 2014): lowland < 700 m, Premontane 700–1500 m, Montane 1500–3000 m, and Alpine > 3000 m (Supporting information). Further, we used the Bayesian binary MCMC (BBM) analysis implemented in RASP (Yu et al. 2015) to reconstruct the ancestral habitat with JC (Jukes–Cantor) and 10 million cycles, sampling every 1000 cycles.

Diversification analysis through time, among lineages, and across geographic space

As combining taxonomy and phylogeny can improve the performance of the diversification rate, we added unsampled species at the genus level based on the number of species via taxonomic addition for complete trees (TATC) method (Chang et al. 2020) following the World Spider Catalog (2024). Based on this tree, we explored the diversification dynamics through time, and among lineages. Firstly, we explored the pulled diversification index proposed by Louca and Pennell (2020). Secondly, we used the 'TESS' library (Höhna et al. 2016) in R to estimate parameters under any time-dependent birth–death process, which assumes the diversification rates are constant but can change episodically through time across all lineages. The number, timing, and magnitude of shifts in diversification rates are then run using reversible-jump MCMC until ESS values are ≥ 200. In addition, we used Bayesian analysis of macroevolutionary mixtures (BAMM; Rabosky et al. 2013) to detect and quantify heterogeneity in evolutionary rates through time and among lineages. The BAMM analysis was run for 10 million generations, sampling every 1000 generations. Convergence of the run was assessed by the log-likelihood trace and ESS of the log-likelihood. BAMM has been criticized by Laudanno et al. (2021) for giving spurious results. We thus used the lineage-specific birth–death-shift model (LSBDS) implemented in RevBayes (Höhna et al. 2019) and the cladogenetic diversification rate shift (ClaDS) model (Maliet et al. 2019) to estimate shifts in diversification rates dynamically. The code used for diversification analysis can be found at Dryad (Li et al. 2024).

To assess diversification rates across different geographic spaces, we used the regional LTT (Schenk et al. 2013) and the hidden state-dependent speciation and extinction (HiSSE) (Beaulieu and O'Meara 2016) on the molecular tree comprising 202 extant species. There is a major biogeographic boundary on the Kangar–Pattani (KP) line where the climate changes from Malay-type evergreen rain forest to Thai–Burmese type wet seasonal evergreen rain forest (Woodruff 2003). Thus, we used the KP line as the boundary to divide the distribution into two geographic spaces: north of the line including A, B, C, F and H, and south of the line including D, E and G. We compared the lineage accumulations between the two geographic spaces. As the HiSSE reduces the possibility of falsely associating a character with diversification rate heterogeneity by incorporating a second, unobserved character, we explored the speciation, extinction, and net diversification rates of the two geographic spaces using this model. HiSSE also accounts for unsampled species and traits by applying a specified sampling fraction (202/267). We employed MCMC with the model to estimate spatial diversification rates for 5000 generations, and used RevGadgets (Tribble et al. 2022) to generate plots and visually explore the posterior distributions of sampled parameters.

Results

Phylogeny and divergence time

We constructed a comprehensive species-level dataset for the family Psilodercidae, which includes seven gene markers from 202 species belonging to all ten extant genera. BI and ML analyses of this dataset yielded a consistent topology (Supporting information). Extant psilodercids can be divided into two major clades: clade I, with relatively larger body size (Supporting information), contains *Leclercera*, *Althepus* and *Luzonacera*, and clade II consists of *Psiloderces*, *Sinoderces*, *Merizocera*, *Thaiderces*, *Flexicrurum*, *Relictocera* and *Qiongocera*. All psilodercid genera except for *Qiongcera* and *Sinoderces* were recovered as monophyletic. *Qiongcera* is monophyletic only in the topology inferred from the BEAST analysis. *Psiloderces fredstonei* is more closely related to *Sinoderces* than to the remaining species of *Psiloderces*. In addition, the unresolved relationships between extant and extinct species also need to be specified. Thus, a genus-level phylogenetic tree including the extinct genus *Priscaleclercera* was constructed by total evidence analysis. The total-evidence dataset comprised 202 extant species and five extinct species. The results showed that monophylic *Priscaleclercera* was the sister group of the insular *Leclercera*, which had multiple strong setae in the palpal femur of *Leclercera* males (Supporting information). The relationship of *Priscaleclercera* with other extant genera generally agrees with the previous study (Magalhaes et al. 2021). Moreover, the morphological analysis showed that only the genus *Althepus* is significantly different from all other genera in relative leg length ($p < 0.0001$).

For divergence time estimation, path sampling and stepping-stone sampling supported the Yule model, based on the comparison of marginal likelihoods between Yule and birth–death models (Supporting information). The chronogram based on the molecular data suggests an early Cretaceous divergence of Psilodercidae at 129.85 Ma (95% credibility interval (CI) 143–115 Ma). Subsequently, clades I and II began to diversify at 120.63 Ma (135.73–105.28 Ma) and 110.38 Ma (122.31–97.91 Ma) (Fig. 2A, Supporting information). In clade I, the Philippine genus *Luzonacera* split from the widespread genus *Althepus* in the late Cretaceous. In clade II, the mainland genus *Relictocera* diverged from the other three genera, and the genus *Sinoderces* diverged from the remaining two Hainan Island genera in the late Cretaceous. In addition, the split of *Psiloderces* from the remaining two insular genera, and the divergence of *Thaiderces* from the genus *Merizocera*, also occurred in the late Cretaceous. The genera *Leclercera*, *Althepus*, *Merizocera*, *Psiloderces* and *Thaiderces* dating back to the Cretaceous, survived the Cretaceous–Paleogene (K–Pg) event. For example, the diversification of the genus *Althepus* began at the K–Pg boundary age of 70.43 Ma (81–59 Ma), similar to previous studies (Li and Li 2018). However, other genera began to diversify from the middle Paleocene to the early Miocene.

Biogeographic and habitat inference

The DEC model with the highest AICc_wt value was selected as the best model (Supporting information). The biogeographic analyses in BioGeoBEARS based on DEC models with or without extinct taxa produced consistent scenarios for major lineages (Fig. 3, Supporting information). The results inferred with or without fossils are similar because *Priscaleclercera* does not belong to the basal lineage of the phylogeny. Incorporating fossils as terminal taxa enables the inference of evolutionary history for both fossil taxa and their living relatives. Thus, the calibrated tree including both extinct and extant taxa was used in the subsequent analysis. The ancestor of Psilodercidae inhabited Indochina and Sumatra during the early Cretaceous when Sibumasu and Indochina formed a single landmass, followed by the vicariance between the two clades. Clade I and clade II have similar evolutionary routes. They both separately originated from Indochina and Sumatra, and Indochina, respectively, then dispersed into other areas following the collision events between major land masses in SE Asia. Specifically, during the early Cretaceous, *Leclercera* (including their fossil relative *Priscaleclercera*) have an estimated ancestral range in the Indochina and Sumatra. In the mid-Cretaceous, *Leclercera* dispersed from Sumatra to Burma and diversified as a dominant Burmese amber taxon. During the Paleocene, there were two events of range expansion out of Indochina and into the Himalayas. At the same time, psilodercid spiders colonized the Indian subcontinent from Sumatra around 62 Ma (71–53 Ma). During the Eocene to Oligocene, clade I and clade II separately dispersed eastward and eventually colonized the Philippines. Taken together, the diversity of the dispersal-limited Psilodercidae arose through the combination of 177 in situ diversification events and 25 colonizations between nine biogeographic areas.

For ancestral state reconstruction, results inferred using RASP recovered a lowland origin with strong support (probability: 99.65) (Fig. 3, Supporting information). This character state also was recovered in the ancestors of clade I and clade II with strong support (probability: 98.69 and 99.75). The lowland habitat preference is shared with species distributed in Indochina. However, some species in the Himalayas and Burma developed a stronger bond with higher altitudes. The adaption to high-altitude habitats is estimated to have occurred independently four or five times and follows colonization events from Indochina to the Himalayas and Burma (Fig. 3).

Diversification dynamics

Combining the results of the pulled diversification rates, TESS, LSBDS, ClaDS and BAMM, we found that psilodercid diversification has been relatively steady since the origin of this family, lacking an early burst. Psilodercid lineages have accumulated gradually through time (Fig. 4A, Supporting information). Diversification through time analyses did not find evidence for shifts in diversification rate over the history of the group aside from a drop within the past 1 Ma likely resulting from unsampled intraspecific diversity (Fig. 1A, Supporting information). We further calculated the diversification rate on the phylogenetic tree. LSBDS shows that *Althepus* experienced an accelerated rate of species diversification near the origin of this clade (Fig. 4C). BAMM says that 12% posterior has a shift on the branches of *Althepus* (Supporting information). ClaDS reveals that *Althepus* have a higher probability of speciating and having offspring than other lineages (Supporting information). To test whether the remarkable lineage diversification of *Althepus* was associated with ecological factors, we now focus on the traits that help distinguish *Althepus* from other Psilodercidae. Ancestral state

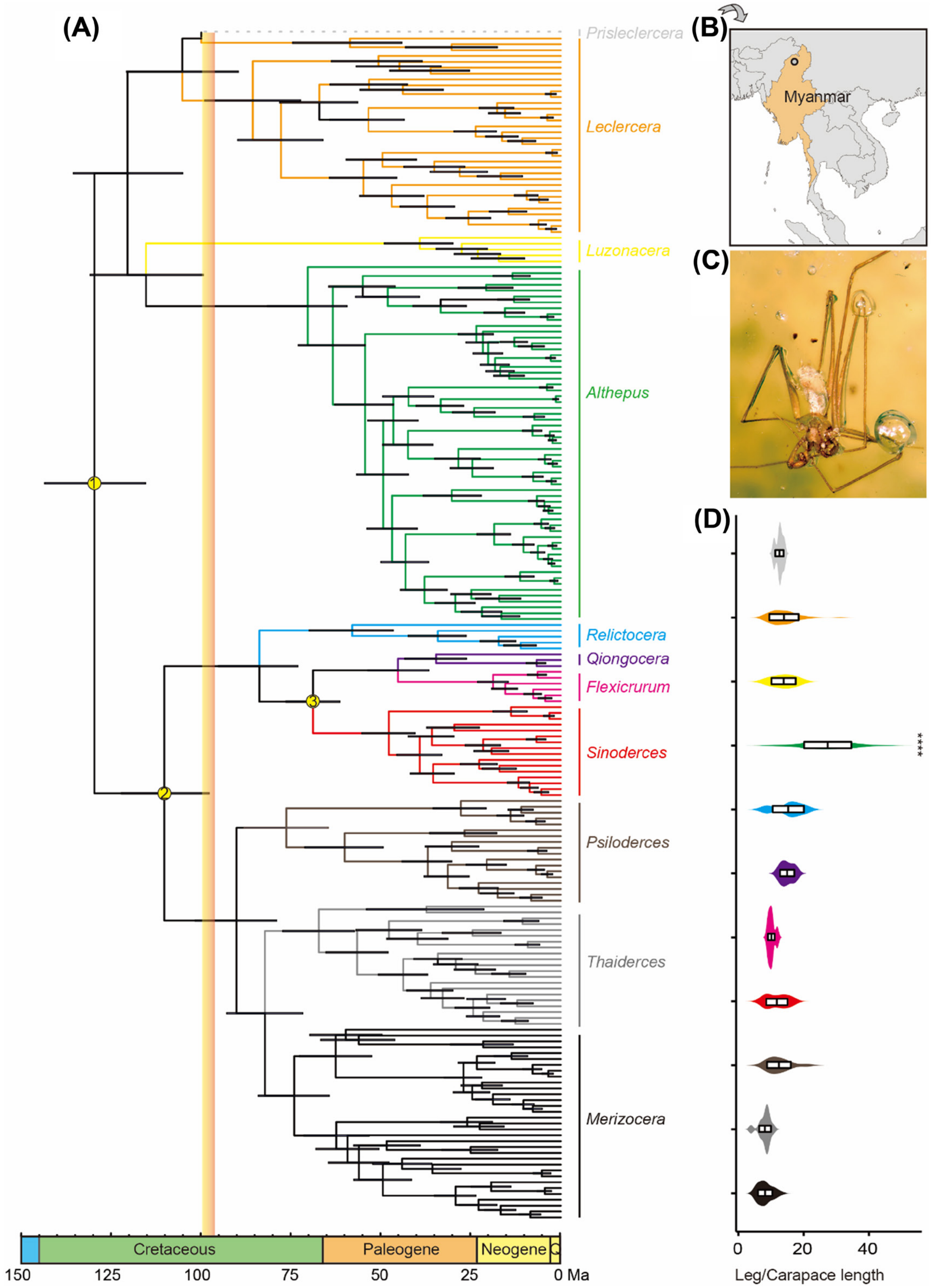

Figure 2. Dated phylogeny with morphological diversity. (A) Time-calibrated phylogenetic tree for Psilodercidae inferred from BEAST. Circles represent calibration points. Different colors refer to different genera. Purple bars represent 95% credible intervals for age estimation; A tree with tip labels is shown in the Supporting information. (B) The extinct genus *Priscaleclercera* was distributed in northern Myanmar during the middle Cretaceous. (C) Amber piece including *Priscaleclercera* species. (D) Leg:carapace ratio at the genus level. Tukey's test, ****$P < 0.0001$. The boxplots are colored according to figure (A).

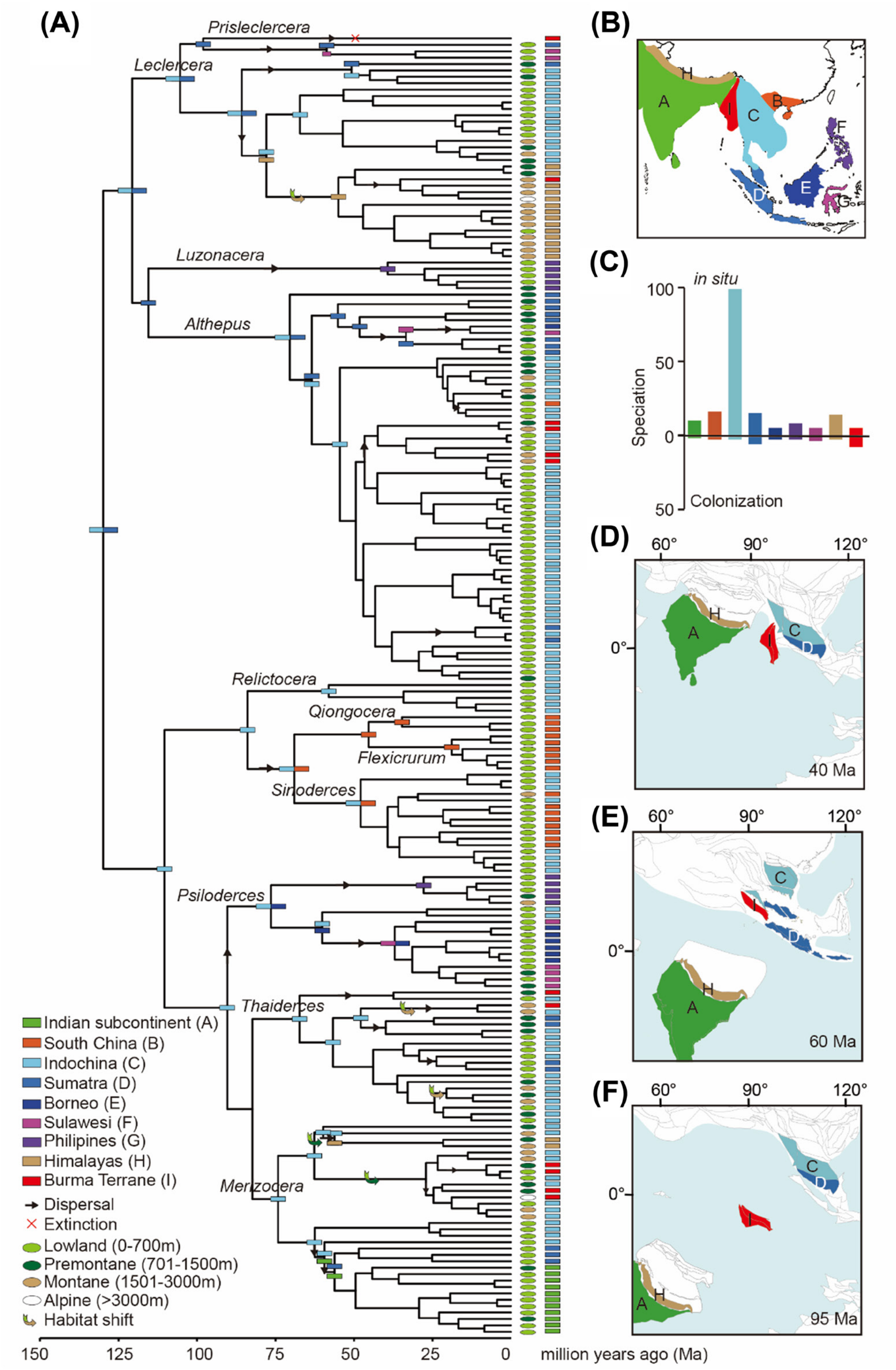

Figure 3. Biogeographic and habitat inference with fossils. Squares at tips indicate current distributions; dots at tips indicate current habitats. (A) AARs are shown using both extinct and extant species with the DEC model in BioGeoBEARS. A = Indian subcontinent; B = South China; C = Indochina; D = Sumatra; E = Borneo; F = Sulawesi; G = Philippines; H = Himalayas; I = Burma Terrane. (B) The distribution areas defined for ancestral area analyses. (C) Number of in situ diversification and immigration events observed for pre-defined areas. (D)–(F) Boundaries of land and sea at 40 Ma, 60 Ma and 95 Ma [modified from Westerweel et al. (2019)].

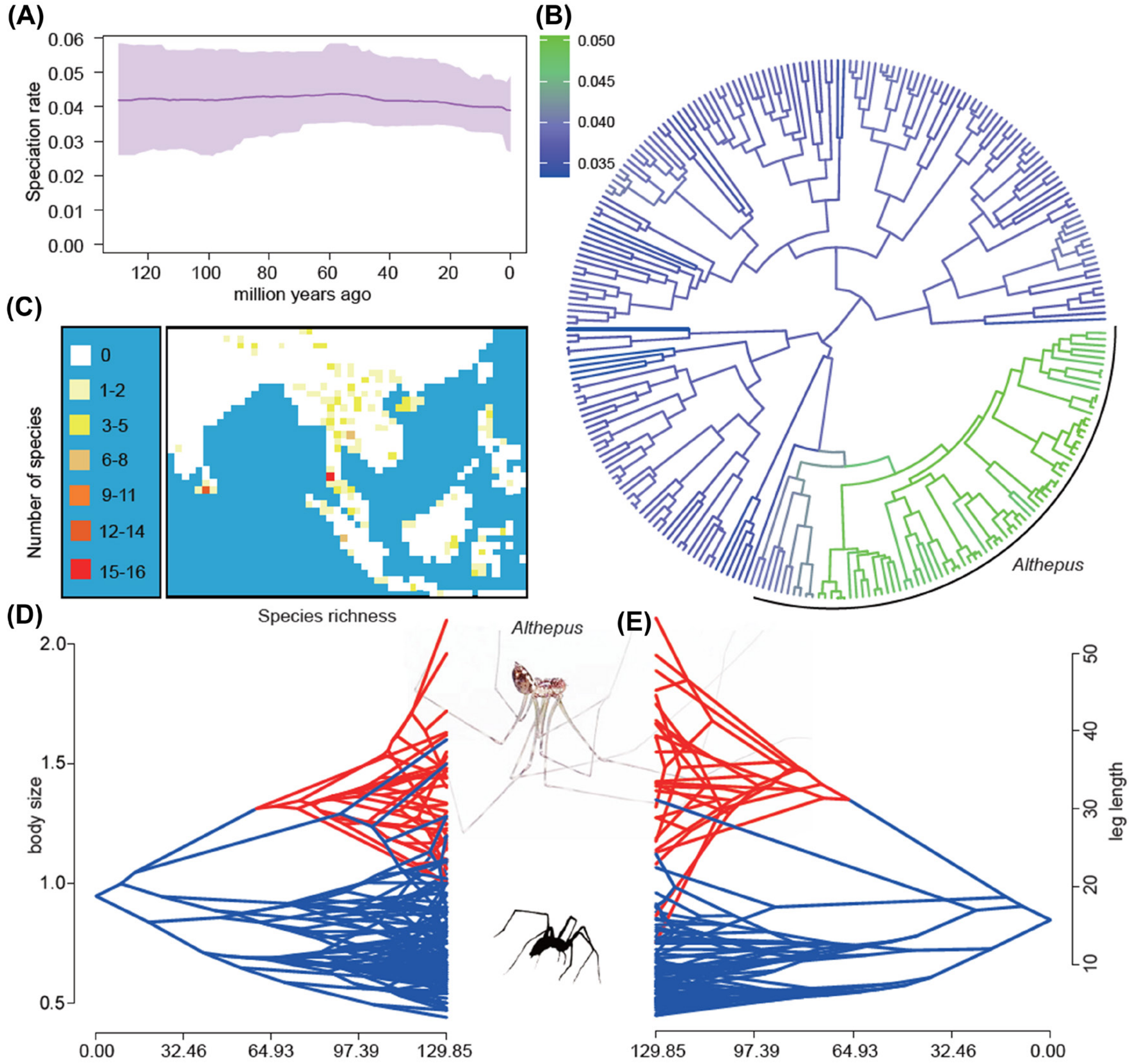

Figure 4. Diversification analysis through time, among lineages, and across geographic space. (A) TESS shows the gradual accumulation of species over time. (B) LSBDS shows that *Althepus* experienced accelerated rated of species diversification near the origin of this clade. (C) The distribution of species richness for the family Psilodercidae across geographic space. (D)–(E) Evolution of body size and leg length in the family Psilodercidae (*Althepus* are highlighted in red). The vertical positions of nodes in phenograms depict the reconstructed values of a given trait, whereas their horizontal position reflect the underlying phylogeny.

reconstructions detect an increase in mean body size and leg length at the origin of *Althepus* and indicate that these traits maintained comparatively higher values within this genus throughout its entire diversification process (Fig. 4D, E).

When mapped onto geography, psilodercid species are evenly distributed across SE Asia. Based on the two geographic spaces, we found similar speciation rates and extinction rates between the north and the south regions of the KP line using the regional LTT and HiSSE model (Supporting information).

Discussion

Compared with the Afrotropical region and Latin American region, tropical Asia is likely to be proportionately richest for biodiversity in general for its size (Raven et al. 2020), but the evolution of its biodiversity is still poorly understood. We used the evolutionary history of psilodercid spiders that are endemic to SE Asia as a typical case to explore the evolution of the SE Asian biodiversity hotspots. Combining extant diversity dynamics with fossil records, we found that the long-term species accumulation due to a combination of ancient geological history and long-time climatic stability, and ecological divergence, mediated by leg length differentiation, likely played a critical role in evolution and maintenance of species diversity of the family Psilodercidae in SE Asia. This study provides an important perspective for understanding the rich spider diversity in tropical Asia. It also sheds light on the role of biotic and abiotic factors as evolutionary drivers of the distribution and dynamics of tropical terrestrial biodiversity.

Diversification since the Cretaceous

Based on a decade of diversity surveys, we constructed the most comprehensive phylogenetic tree of the family Psilodercidae at the species level, representing 202 of 267 species. The stable and mostly well-resolved tree topology was highly concordant with previous phylogenomic results, such as analyses of transcriptome data and hundreds of molecular markers (Li et al. 2020, Shao et al. 2023). Our study inferred that the earliest divergence of Psilodercidae dated back to the early Cretaceous. This is consistent with previous studies, such as the reconstructed phylogenomic relationship covering 105 families (Shao et al. 2023). Moreover, middle Cretaceous fossilized remains of psilodercid spiders comprising approximately two genera and 18 species indicate that a clade existed during a specific geological period (Wunderlich 2012, 2015, 2017, Wunderlich and Muller 2018, Xin et al. 2022). The oldest psilodercid assemblage preserved in amber provides insight into the potentially diverse mid-Cretaceous Paleotropics. Notably, *Leclercera* diverged 120.9–89.7 Ma, and the species-rich genera (*Althepus*, *Psiloderces*, *Merizocera* and *Thaiderces*) diverged within the last 10 Myr of the Cretaceous, and the other five genera diversified after the Cretaceous to Palaeogene (K–Pg) boundary. *Luzoncera*, restricted to the Philippines, presents a long branch in the chronogram from extinction events or sparse taxon sampling. Our timetree implies a late Cretaceous prehistory to 'modern spiders' with diversification that continued into the Palaeogene. Furthermore, our diversification analyses also supported no significant rate increases during the early or middle Eocene (Fig. 4, Supporting information). Therefore, the diversification dynamics of psilodercids rejected the radiation model following the K–Pg extinction.

Under the current dating scheme and fossil evidence, the diversity of psilodercids can be explained by the gradual accumulation of species. This macroevolutionary model is consistent with neotropical birds whose speciation is relatively stable over most of the group's history (Harvey et al. 2020). In addition, biodiversity across temporal and spatial dimensions is closely interconnected. Species diversity of Psilodercidae is shaped not only by time-related factors but is further complicated by spatial influences like SE Asian geological history and niche differentiation.

Indochina is the primary source of SE Asian biodiversity

Our results taking advantage of the relatively complete diversity information and ancient evolutionary histories of psilodercid spiders have significantly enhanced our understanding of how biodiversity has been shaped and assembled over evolutionary timescales. As sit-and-wait predators, their behavior reflects not only their hunting strategies but also their history of range expansion. Our results exemplify how biological groups dispersed and isolated in response to the geological changes in SE Asia. We reported a high level of in situ diversification and biotic interchange among SE Asian regions, totaling 177 in situ speciation events and 25 dispersal events (Fig. 3B). Among them, Indochina not only generated enormous in situ diversity (99 species across all genera) but also produced 17 lineages that dispersed to other regions throughout the Cretaceous. Although Indochina and Sumatra are both psilodercid ancestral areas, Indochina stands out as the primary source of diversity because of its larger size and the longer emergent history (de Bruyn et al. 2014). Most of these dispersal events were to Burma (5 lineages) and Sumatra (4 lineages), followed by dispersals into subtropical regions, such as the Himalayas and south China. We recorded a higher interchange of lineages between regions with similar environments than with environmental differences. Biotic interchange has taken place for > 120 million years and generally increased toward the present. The total amount of time lineages spend in a region appears to be the strongest predictor of migration events. Recent studies of 61 phylogenetic datasets have also shown Indochina, the largest SE Asian area, has been a major diversification hotspot through time and a key source for lineage dispersal across the region (de Bruyn et al. 2014). Therefore, the immigration of lineages into SE Asia has only occurred one or two times (Fig. 3B), which indicates that colonization is not a primary driver of elevated SE Asian diversity.

Dispersal events of psilodercid spiders were influenced by changes in the geographical distribution of land, sea, and surface topography, especially the northward motion of the Burma Terrane coupled with the Indian Plate. Our phylogenetic analyses support the sister relationship between the Burmese *Priscaleclercera* and the Insular *Leclercera* (Fig. 2, Supporting information). The movement trajectory of the Burma Terrane, passing through the Insular region during the Cretaceous and moving northwards, might have induced the colonization of the amber lineage from Sumatra to Burma (Westerweel et al. 2019, Fig. 3F). In contrast to the Gondwana origin model, which suggests that the Burmese amber fauna has ties to Gondwana (Poinar 2018, Wood and Wunderlich 2023), the biogeographic pattern of Psilodercidae provides one new explanation for the origin and evolution of Cretaceous amber biota. The closure of the Neo-Tethys Ocean allowed the mainland *Leclercera* to disperse from Indochina to the Himalayas during the late Cretaceous. Subsequently, along with the Greater Indian lithosphere impinging northward into and subducting beneath the Asian lithosphere (Ding et al. 2022), two Paleocene colonization events of the genus *Merizocera* occurred from Indochina to the Indian subcontinent (Fig. 3E). The ancestral character state reconstructions reveal that ancestral psilodercids might have colonized lower altitudes and undergone passive uplift to the high altitudes. During the ~ 60–40 Ma stage of Himalaya uplift, two lowland lineages adapted to montane habitats. These biogeographic data reflect tectonism and surface uplift in SE Asia.

Geography and climate in SE Asia contribute to steady diversification

The steady dynamics of psilodercids are similar to the pattern found in many other groups in the Neotropics (Weir and Schluter 2007, Harvey et al. 2020). There are multiple potential causes for the absence of rate shifts (Wiens 2011, Rabosky and Hurlbert 2015). For instance, the psilodercid radiation may have been less subject to episodic ecological opportunity associated with the relative stability of geography and climate in SE Asia. Psilodercidae is an ancient group of spiders known from fossils and phylogenetic dating analyses and is believed to have originated in the Cretaceous (Li et al. 2020). The collision of land masses on the eastern edge of Gondwana with Eurasia during the late Triassic contributed to the formation of the Malay Peninsula (Metcalfe 2013). Thus, the appearance of the SE Asian continental core–Indochina and Sundaland since the end of the Mesozoic provides a stable geological environment for organisms that originated or diversified during the same period. Moreover, tropics are characterized by modest seasonality in temperature and precipitation and more minor changes in climate through geologic time. Recent studies indicated that environmental variables mediate the number of species in an area, which drives speciation variation (Harvey et al. 2020). Therefore, stable climatic environments have preserved the original biological richness of SE Asia (Raven et al. 2020).

Recently, Louca and Pennell (2020) clarified the limits of fully reconstructing diversification dynamics from extant timetrees because different parameterizations can lead to different inferences. Following the constantly improving fossil information of Psilodercidae, we will integrate the fossils and the molecular timetree into diversification analyses in future work. Fossils will correct the molecular timetree and provide greater insights for deep-time questions (Upham et al. 2021).

Ecological divergence is a major driver of biodiversity

Our model uncovered the universal associations of morphological innovations and diversification rate increases. Our analyses indicate that the increase in leg length in *Althepus* may correlate with a rise in its speciation rate (Fig. 4C–E). Spiders interact with their environments through varied webs and morphological features (Ceccarelli et al. 2019), with aerial web builders evolving longer legs compared to other groups (Wolff et al. 2022). In particular, the genus *Althepus* exhibits a notably longer leg and larger body size than other genera, which has enabled it to build webs in higher space rather than leaf litter. This vertical stratification, with species inhabiting different spatial heights within the same locality, may have facilitated its diversification. The genus *Althepus* is significantly different in ecological traits from other genera, meaning that the distinct body size, spinneret morphology, and vertically stratified habitat may promote the coexistence of different genera in SE Asia (Fig. 2D). Many arthropods including spiders use the complex and plentiful biological habitats to coexist in SE Asia.

We conclude that our comprehensive analyses combining fossil information and biogeographic history provide a strong insight into the fundamental importance of abiotic and ecological features in the generation and maintenance of psilodercid diversity. Meanwhile, our total-evidence analyses provide the Asian origin inference of Myanmar amber biota in the Cretaceous, which reveals that a series of geological events have shaped the spatiotemporal history of both extant and extinct lineages. Thus, reconstructing the diversity dynamics of the family Psilodercidae, a SE Asian representative group, offers the opportunity to reveal the causes of origin and evolution for relatively unknown invertebrate diversity in SE Asia. This study contributes to understanding the spatial and temporal dynamics of biodiversity in SE Asia, thereby preserving the integrity of biodiversity hotspots.

Significance statement

Compared with good dispersers, web-weaving psilodercid spiders with well-preserved fossils and poor dispersal capabilities are a more appropriate model to study how biotic and abiotic factors shape the spatial and temporal diversification patterns in Southeast Asian biodiversity hotspot. We combined biogeographic with ecological analyses to systematically resolve the evolutionary history of these tropical spiders and reveal the central role of ecological trait divergence over evolutionary time scales in the origin and maintenance of tropical spider diversity from a unique angle.

We integrated divergence time estimates, key trait measurements, biogeographic reconstruction, and diversification analyses for extant and extinct spiders to infer the evolutionary history of the family Psilodercidae and examine abiotic drivers and ecological features behind the evolution of diversity. These findings suggest that psilodercids were already an important and diverse component of tropical rainforests in SE Asia during the Cretaceous, which was maintained by ecological trait divergence over evolutionary time.

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Author contributions

Fengyuan Li and **Tongyao Jiang** contributed equally to this publication. **Fengyuan Li**: Conceptualization (equal), Data curation (equal), Formal analysis (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Writing - review and editing (equal). **Tongyao Jiang**: Formal analysis (equal), Methodology (equal). **Wei Zhang**: Conceptualization (equal), Writing - review and editing (equal). **Shuqiang Li**: Conceptualization (equal), Data curation (equal), Supervision (equal), Writing - review and editing (equal).

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Data availability statement

Sequence data are available from GenBank (Supporting information). Morphological alignment, concatenated alignment, phylogenetic trees, dated trees, species distribution, R scripts and codes are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8sf7m0ctb (Li et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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