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Authors

Chaitanya, Ramamoorthi

McGuire, Jimmy A

Karanth, Praveen

et al.

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Author for correspondence:

Ramamoorthi Chaitanya
 e-mail: chaitanyar@mail.tau.ac.il

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Their fates intertwined: diversification patterns of the Asian gliding vertebrates may have been forged by dipterocarp trees

Ramamoorthi Chaitanya¹, Jimmy A. McGuire², Praveen Karanth³ and Shai Meiri¹

¹School of Zoology, Tel Aviv University 6997801, Tel Aviv, Israel

²Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720, USA

³Centre for Ecological Sciences, Indian Institute of Science, Bangalore, Karnataka 560012, India

ORCID RC, 0000-0002-0833-852X; JAM, 0000-0002-9562-5585; PK, 0000-0003-4364-6381; SM, 0000-0003-3839-6330

The repeated evolution of gliding in diverse Asian vertebrate lineages is hypothesized to have been triggered by the dominance of tall dipterocarp trees in the tropical forests of Southeast Asia. These dipterocarp forests have acted as both centres of diversification and climatic refugia for gliding vertebrates, and support most of their extant diversity. We predict similarities in the diversification patterns of dipterocarp trees and gliding vertebrates, and specifically test whether episodic diversification events such as rate shifts and/or mass extinctions were temporally congruent in these groups. We analysed diversification patterns in reconstructed timetrees of Asian dipterocarps, the most speciose gliding vertebrates from different classes (*Draco* lizards, gliding frogs and Pteromyini squirrels) and compared them with similar-sized clades of non-gliding relatives (*Diploderma* lizards, *Philautus* frogs and Callosciurinae squirrels) from Southeast Asia. We found significant declines in net-diversification rates of dipterocarps and the gliding vertebrates during the Pliocene–Pleistocene, but not in the non-gliding groups. We conclude that the homogeneity and temporal coincidence of these rate declines point to a viable ecological correlation between dipterocarps and the gliding vertebrates. Further, we suggest that while the diversification decay in dipterocarps was precipitated by post-Miocene aridification of Asia, the crises in the gliding vertebrates were induced by both events concomitantly.

1. Introduction

Gliding is a key innovation that has evolved at least thirty times in phylogenetically unrelated vertebrate lineages [1,2]. The evolution of this specialized locomotor mode may represent a natural extension of arboreality, and signals adaptive progression in an arboreal context [3]. The ability to glide likely accelerated the diversification of vertebrate lineages that evolved it, by exposing them to a plethora of ecological opportunities. These include facilitating the occupation of tall canopies, exploitation and partitioning of resources in these new habitats, and escape from predation [4,5].

The tropical forests of Asia harbour a remarkable extant diversity of gliding vertebrates, more than any other region in the world [6–9]. Gliding evolved in phylogenetically distant groups such as squirrels (tribe: Pteromyini, 49 out of 52 species), colugos (order: Dermoptera, 2 species), three clades within distantly related genera of gekkonid geckos (*Luperosaurus*, *Hemidactylus*, *Gekko*, 23 species), *Chrysopelea* snakes (5 species), 40 species of *Draco* lizards and a clade of gliding frogs (genera: *Rhacophorus*, *Leptomantis* and *Zhangixalus*, 92 species) [3,10–13].

Among these taxa, Pteromyini may have had an early-Miocene European origin [14,15] while all the other clades likely evolved in Asia considering they are not distributed elsewhere.

What caused this profusion of gliding forms? The tropical forests of Asia were thought to be structurally different from the tropics of South America and Africa in their low liana content, which are walkways for arboreal animals [16]. One hypothesis suggests that fewer lianas interlacing the Asian canopies may have necessitated the evolution of gliding in arboreal vertebrates for among-tree locomotion [16,17]. However, subsequent studies have found that pantropical biomes are structurally similar, especially in the constitution, abundance and species richness of lianas [6,18].

The more widely accepted hypothesis implicates the dominance of Dipterocarpaceae trees in the Asian tropics for the evolution (or proliferation, in the case of Pteromyini) of gliding in vertebrates [6,8–10]. Dipterocarps originated in tropical Africa around the mid-Cretaceous (*ca* 103 million years ago, Ma) and colonized Southeast Asia during the middle Eocene (*ca* 50 Ma), using the northward drifting Indian plate as a ‘biotic ferry’ [19–21]. They proliferated through the Oligocene–Miocene and were the dominant tree flora in Southeast Asia by *ca* 20 Ma [21–23]. The Asian dipterocarps (subfamily: Dipterocarpoideae) are remarkably diverse with roughly 509 species [21]. Further, the Southeast Asian canopies are the tallest among the tropics of the world, ranging on average between 40 and 50 m with many emergent trees such as *Shorea* spp. consistently exceeding heights of 70 m [24–26]. Shenkin *et al.* [27] reported the tallest tropical tree in the world, a *Shorea faguetiana* individual, that rises above 100 m from the rainforest floor of Sabah, Borneo. The dominance of tall dipterocarps in Southeast Asian rainforests likely triggered the evolution of gliding in arboreal vertebrates as an energy-efficient means to locomote between trees. Further, taller trees provide for higher take-off points, resulting in longer glides that in turn provide substantial energetic advantages [6,28]. Reinforcing this association, Heinicke *et al.* [10] showed how the repeated evolution of gliding in Southeast Asian vertebrate groups is temporally congruent with the establishment and dominance of dipterocarp forests (50–20 Ma).

Asian gliding vertebrate clades are largely restricted to regions dominated by Dipterocarpoideae (figure 1). Chaitanya & Meiri [29] show that gliding vertebrates such as the peninsular Indian *Draco dussumieri* seem unable to disperse into regions that are devoid of tall trees like dipterocarps, despite climatic suitability [29] (but see flying squirrels; figure 1*d*). Globally, gliding vertebrates are most speciose in Southeast Asia that harbours the greatest diversity of dipterocarps. Moreover, the most speciose Asian gliding clades (Pteromyini, *Draco* and gliding frogs) and Dipterocarpoideae each exhibit matching as well as similarly disjunct distributions, with most species in all clades inhabiting Southeast Asia and fewer species on the Indian subcontinent (figure 1).

Considering this intricate ecological association between Asian dipterocarps and gliding vertebrates, we examine if these groups have had similar macroevolutionary histories. Specifically, we hypothesize that episodic shifts in diversification rates, or mass extinction events, during the evolution of Asian dipterocarps were temporally correlated with similar events in the history of gliding vertebrates. Recent reviews based on the fossil record suggest that the post-Miocene aridification of the Indian subcontinent may have led to the

extinction of most dipterocarp flora from the region [30,31]. This is corroborated in the diversification analyses conducted by Bansal *et al.* [21] who report a significant drop in global dipterocarp diversification rates during the Pliocene–Pleistocene (*ca* 3 Ma). Correspondingly, Lu *et al.* [14] and Casanovas-Vilar *et al.* [15] suggested that flying squirrels were abundant during the mid-Miocene but were confronted with a ‘severe crisis’ after the late Miocene due to changing palaeoclimates, especially in Asia. Based on these studies, we predict that gliding vertebrate clades and dipterocarps may have undergone similar crises in their diversification during the Pliocene–Pleistocene (5.3–0.01 Ma).

2. Material and methods

To test our hypothesis, we reconstructed timetrees of dipterocarps and the more speciose gliding clades ($n > 40$; Agamidae: *Draco*, Sciuridae: Pteromyini and Rhacophoridae: the genera *Rhacophorus*, *Zhangixalus* and *Leptomantis*) and conducted several analyses to detect rate shifts and mass extinctions in their evolutionary histories. Further, we accounted for phylogenetic uncertainty given clade sizes and ages, by estimating support for our diversification models on 100 empirical trees for each group against a constant birth–death null model.

Some methods that discern episodic rate shifts have been criticized to produce spurious signals that do not reflect real biological processes, but are merely artefacts of the data, i.e. clade sizes, tree topology, crown age of the clade, or sampling probability in the phylogeny (see Discussion) [32–34]. Furthermore, the signals we recover may reflect a general diversification trend in predominantly Southeast Asian arboreal groups due to localized climatic and/or geological processes in the region. To control for these factors, we repeated our analyses on closely related, arboreal, non-gliding, ‘control’ clades predominantly from Southeast Asia (the agamid *Diploderma* compared to *Draco*, the sciurid Callosciurinae compared with Pteromyini and the rhacophorid genus *Philautus* compared with the gliding frogs). These ‘control’ groups have comparable clade sizes and crown ages as our gliding groups [11,35–38]. We test if similar patterns of diversification persist in the gliding and non-gliding clades.

(a) Compilation of sequence matrices and phylogenetic data

We assembled the most comprehensive data now available, in terms of taxa and gene coverage, for Asian gliding vertebrates (*Draco*, Pteromyini, gliding frogs) and the non-gliding ‘control’ groups (*Diploderma*, Callosciurinae, *Philautus*). Species lists were collated from the Reptile Database (<https://reptile-database.reptarium.cz/>) for *Draco* and *Diploderma*, AmphibiaWeb (<https://amphibiaweb.org/>) for gliding frogs and *Philautus*, and ASM Mammal Diversity Database (<https://www.mammal-diversity.org/>) for Pteromyini and Callosciurinae.

For *Draco*, we generated sequences of mitochondrial and nuclear gene fragments for 12 species (NADH dehydrogenase subunit 2—ND2, 12S ribosomal RNA and 16S ribosomal RNA; totalling 1994 bp, brain derived neurotrophic factor—BDNF, oocyte maturation factor Mos—CMOS and Pinin—PNN; totalling 1825 bp). Details on primers and protocols are listed in electronic supplementary material, table S1. Mitochondrial sequences for 21 other species of *Draco* were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Our final *Draco* sequence matrix comprised a mitochondrial dataset containing 33 of the 40 extant species, a nuclear dataset of 12 species (electronic supplementary material, table S2) and

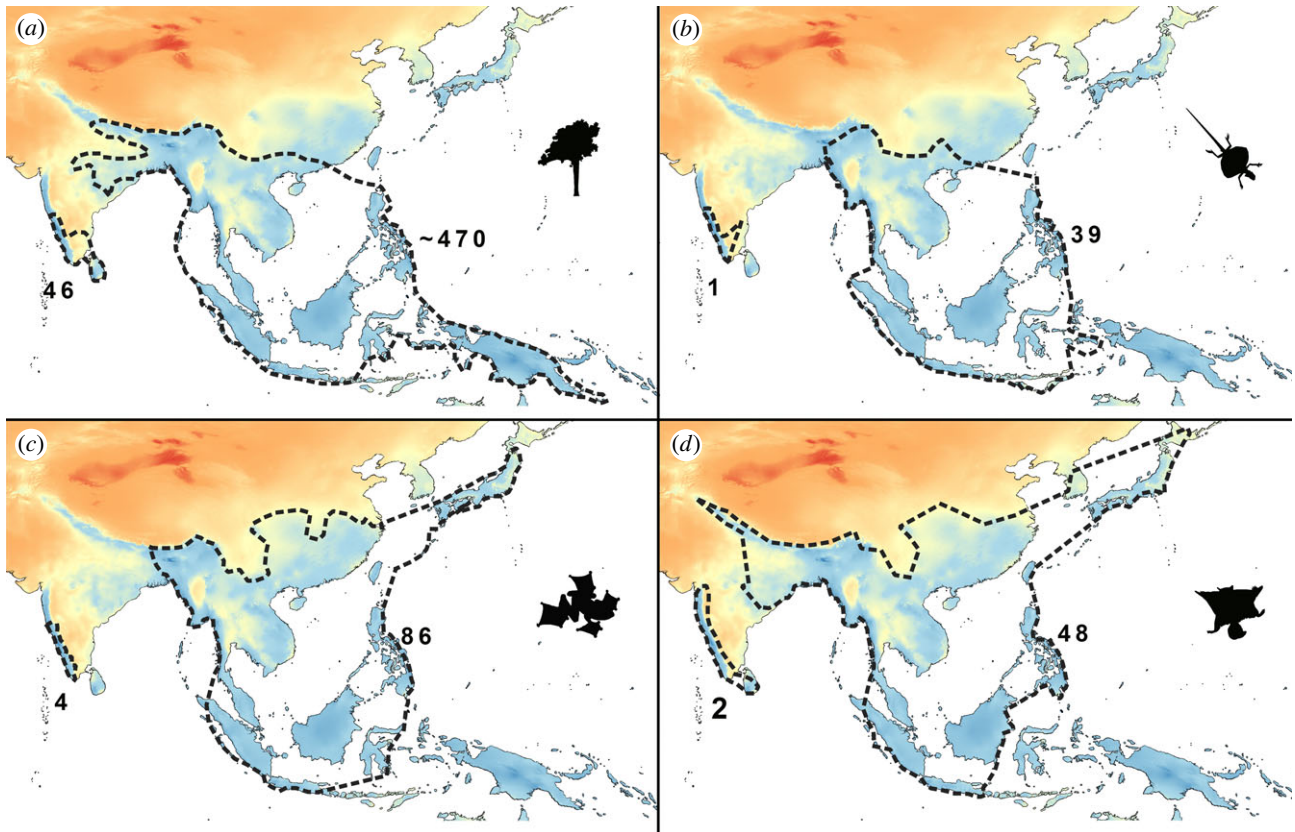


Figure 1. Mean annual precipitation maps of South and Southeast Asia showing the distributions of (a) Dipterocarpoideae, (b) *Draco*, (c) gliding frogs, and (d) Pteromyini (excluding the range of the Siberian flying squirrel, *Pteromys volans*). Numbers against polygons indicate the number of species in those regions. Polygons were created based on occurrence data for these groups, downloaded from GBIF.

included two outgroups—*Japalura tricarinata* and *Ptyctolaemus gularis* based on Wang *et al.* [36].

Sequences for Pteromyini, gliding frogs and the ‘control’ groups were obtained entirely from GenBank. The Pteromyini dataset (electronic supplementary material, table S3) comprised mitochondrial (12S, 16S and Cytochrome-b; 2585 bp) and nuclear (interphotoreceptor retinoid-binding protein—IRBP; 1179 bp) gene fragments and contained 32 out of the 52 extant species, including *Sciurus carolinensis* as the outgroup [15]. For gliding frogs (electronic supplementary material, table S4), we obtained data for mitochondrial (12S and 16S) and nuclear (Rhodopsin—RHO) gene fragments totalling 1786 bp that covered 72 out of 90 extant species and used two outgroup taxa (*Polypedates cruciger* and *Polypedates megacephalus* [39]). Among the ‘control’ groups, the *Diploderma* dataset (electronic supplementary material, table S5) comprised the mitochondrial ND2, the nuclear RNA fingerprint protein 35—R35 and BDNF gene fragments totalling 2419 bp, covering 39 out of 42 species and included *Pseudocalotes kingdonwardi* as outgroup following Wang *et al.* [36]. We compiled genetic data for 49 out of 64 species of the squirrel subfamily Callosciurinae, comprising the mitochondrial genes 12S, 16S and Cytochrome-b and the nuclear gene IRBP, totalling 3836 bp (electronic supplementary material, table S6). The *Philautus* dataset consisted of the mitochondrial 12S, 16S and Cytochrome-b, totalling 1574 bp (electronic supplementary material, table S7) for 33 out of 55 species.

The sequence matrices were then aligned gene-wise for each group using the MUSCLE algorithm implemented in the program MEGA 11 [40] for further analyses. Alignments of protein-coding DNA sequences were translated to amino acids to detect pseudogenes or premature stop codons that are indicative of frame shifts in the alignment.

For Asian dipterocarps, we used a published chronogram of Dipterocarpaceae from a recent study (see [21]) that was

reconstructed using a dataset of nine nuclear and chloroplast loci (totalling 10 023 bp) and 9 fossil calibrations. The clade comprising the African+South American species (subfamily Monoitoideae, Clade M from [21]) was eventually pruned out from the chronogram to include only the Asian clade Dipterocarpoideae, and covered 296 out of 509 extant species (Clade I–IV from [21]).

(b) Reconstructing chronograms of focal and ‘control’ groups

We reconstructed chronograms based on divergence dates estimated from the most comprehensive studies conducted to date that included our focal and ‘control’ groups (table 1). We chose these studies based on gene coverage and the number of fossils that were used to assess divergence times. Estimates from these studies were used as secondary calibrations to inform our prior mean and σ (95% highest posterior density, HPD) for either divergence dates between our groups of interest and their sister groups, or as crown ages for our clades of interest (table 1).

For *Draco*, we did not combine the mitochondrial and nuclear datasets owing to low species coverage (12 species) in the nuclear dataset. We first built a chronogram using mitochondrial data (ND2, 12S and 16S) using BEAST2 [41]. We unlinked the site and clock models for the three genes to allow varying rates of substitution between them, but their tree models were linked to generate a single phylogeny due to the lack of recombination and the linked nature of mitochondrial DNA. The best-suited model of sequence evolution was estimated using the model-test algorithm implemented in BEAST2. We used a relaxed, uncorrelated lognormal clock model for each gene, to allow for between-lineage rate variation, and a Yule model of diversification (following [42]) to reconstruct the phylogeny. The analysis

Table 1. Divergence times between our focal groups and their phylogenetic sisters derived from previously published chronograms and the phylogenetic constraints enforced in the present study. Asterisk (*) indicates that the calibration was enforced on the crown group.

clade	outgroup	divergence time (Ma); mean (HPD)	reference	phylogenetic constraints
Dipterocarpoideae	Monotoideae	102.9 (88.0–108.0)	Bansal <i>et al.</i> [21]	NA
Draco	<i>Japalura</i> , <i>Ptyctolaemus</i>	53 (50.0–68.0)	Grismer <i>et al.</i> [35]	none
Pteromyini	Sciurini	30 (25.0–37.5)	Casanovas-Vilar <i>et al.</i> [15]	monophyly on subtribes Glaucomyina and Pteromyina
gliding frogs	<i>Polypedates</i>	32.56 (29–37)	Chen <i>et al.</i> [37]	monophyly on genera <i>Rhacophorus</i> , <i>Leptomantis</i> and <i>Zhangixalus</i>
<i>Diploderma</i>	<i>Pseudocalotes</i>	37.4 (30–44.5)	Grismer <i>et al.</i> [35]	none
Callosciurinae	NA	28.22 (32.2–24.2)*	Menendez <i>et al.</i> [38]	monophyly on genera <i>Callosciurus</i> , <i>Funambulus</i> , <i>Dremomys</i> , <i>Tamiops</i> and <i>Sundasciurus</i>
<i>Philautus</i>	NA	21.12 (19.2–23.2)*	Chen <i>et al.</i> [37]	none

was conducted using two runs of four chains (1 cold and 3 heated) each for up to 100 million generations, sampling every 10 000 generations from the posterior distribution of trees. We inferred convergence of the runs using Tracer v1.7.2 [43] when the effective sample size (ESS) for each parameter was >200. The first 10% of the samples was discarded as burn-in and the tree with maximum clade credibility (MCC) was selected using the program TreeAnnotator v2.6.6 [44].

Next, we analysed the nuclear dataset (BDNF, CMOS and PNN) for 12 *Draco* species to ratify the broad relationships recovered from the mitochondrial phylogeny. To account for the disparate evolutionary histories of nuclear DNA (i.e. unlinked nuclear genes that undergo recombination), we used the program StarBEAST2 [45] that uses a Bayesian multispecies coalescent approach to estimating species tree topologies. The three nuclear loci were treated as separate partitions by unlinking the site, clock and tree models, allowing for the estimation of three separate gene tree topologies. Other MCMC parameters and selection of the MCC tree follow the methods mentioned in the mitochondrial analysis. The mitochondrial *Draco* MCC chronogram was subsequently used in all further analyses. Due to unavailability of nuclear data for the non-gliding frog group *Philautus*, we followed the BEAST2 concatenated method described above to reconstruct the mitochondrial chronogram.

Due to the availability of mitochondrial and nuclear data for most species of Pteromyini, gliding frogs, *Diploderma*, and Callosciurinae, we followed the methods used in the analysis of the *Draco* nuclear dataset, i.e. a multi-species coalescent method implemented in StarBEAST2. User prior specifications and phylogenetic constraints for these analyses are listed in table 1.

(c) Detecting patterns of diversification

All subsequent analyses were conducted in the R platform, version 4.1.2. Diversification analyses were conducted on the gliding vertebrate clades and *Diploderma* after removing the outgroups from their respective MCC trees (the Callosciurinae and *Philautus* datasets did not include outgroups). We first constructed lineage-through-time plots (LTTs) for all groups using the R package APE 5.0 [46] to visualize trends in diversification. We then used three methods to discern patterns of diversification in our focal and ‘control’ groups. We primarily rely on the results of the CoMET analyses implemented in the R package TESS 2.1 [47,48], since it infers episodic rate shifts and mass extinctions

together, and allows for model comparison for the occurrence of such events at pre-defined time intervals in the history of the group. However, CoMET has recently been criticized for detecting episodic rate shifts due to inherent biases in the data [49] (and see Discussion). To substantiate our conclusions, we used two alternative methods to cross-validate the results obtained using CoMET.

Since we did not have *a priori* hypotheses on the number and timings of episodic rate shifts in diversification, mass extinctions, and their combinations in our focal and ‘control’ groups (but see [21] for Diptercarps), we chose the CoMET algorithm (function: *tess.analysis*) that treats these uncertainties in diversification models as random variables and integrates them over a vast model space. It detects discrete changes in speciation and extinction rates concurrently affecting all lineages in a tree, and can also infer whether mass extinctions have occurred in these time intervals. Speciation and extinction rates are allowed to change between time intervals but remain constant within them. The algorithm implements a reversible-jump MCMC approach over all possible episodically varying birth–death models, rate shifts and mass extinction events, and estimates their joint posterior probabilities. It allows for model comparison for each of these parameters using Bayes factor scores.

CoMET is sensitive to the initial speciation and extinction hyperpriors, so we ran the CoMET analyses using both *a priori*, and empirically calculated values for initial speciation and extinction hyperpriors. For the *a priori* analyses, we used the function *fit.bd* implemented in the R package *Phytools* [50] to inform our initial speciation and extinction rates for all groups. Since speciation and extinction rates must be greater than 0, we used a lognormal prior distribution to incorporate this condition. We specified these hyperparameters (means using the values from the *fit.bd* function and standard deviation) in real space and then transformed them to reflect the mean and standard deviation of the log-transformed speciation and extinction rates. Next, due to the lack of *a priori* information on mass extinction events in these groups, we used a beta distribution to vary the survival probability (intensity of a mass extinction event) from a mass extinction event. We set the initial survival probability to 0.1 (i.e. 90% species diversity was lost due to a mass extinction event) and computed the α and β parameters of the beta distribution. We set the value of β to be large, allowing us to focus on the prior density more tightly around the expected survival probability. Then, we computed α based on the expected

Table 2. Inferred crown ages of focal and ‘control’ groups and previously published reference chronograms. Asterisk (*) indicates that the calibration was enforced on the crown group.

clade	mean crown age (Ma)	95% HPD interval (Ma)	geological time of the mean crown age	reference
<i>Draco</i>	33	36.3–29.6	Eocene–Oligocene	Heinicke <i>et al.</i> [10]; Grismer <i>et al.</i> [35]
Pteromyini	22.8	25.4–20.2	Miocene	Mercer & Roth [55]; Fabre <i>et al.</i> [56]
gliding frogs	31.8	33.9–28.6 Ma	Oligocene	O’Connell <i>et al.</i> [57]; Chen <i>et al.</i> [37]
<i>Diploderma</i>	27.4	35.5–20.7	Oligocene	Grismer <i>et al.</i> [35]
Callosciurinae	29.2*	31.0–27.3	Oligocene	Menendez <i>et al.</i> [38]
<i>Philautus</i>	21.7*	23.7–19.7	Miocene	Chen <i>et al.</i> [37]

survival probability and the specified β value. The initial number of expected rate changes and number of expected mass extinctions for *Draco*, Pteromyini, gliding frogs and the non-gliding ‘control’ groups were set to 1, while the larger and older dipterocarpaceae clade allowed these parameters to be set to 2. The sampling probability (ρ) for each analysis was set to the fraction of extant species sampled in our phylogenies: 0.82 (*Draco*), 0.61 (Pteromyini), 0.8 (gliding frogs), 0.9 (*Diploderma*), 0.76 (Callosciurinae), 0.60 (*Philautus*) and 0.55 (Dipterocarpaceae, based on [21]) under a uniform sampling scheme.

We ran CoMET analyses on the MCC trees of our focal and our ‘control’ groups for 10^7 generations and estimated convergence by checking a stable Geweke statistic near zero for all time periods in the analyses and a large estimated sample size (ESS) value of >400 for all parameters. To account for CoMET’s sensitivity towards the initial hyperpriors (speciation and extinction rates), we reran the analyses described above for all groups, but using empirically calculated hyperpriors (empiricalHyperPriors = TRUE) for the initial speciation and extinction rates. We ran additional analyses varying the initial speciation and extinction rates, expected number of rate-shifts and mass extinctions to ensure that our results were not sensitive to these settings. We specifically under-sampled (sampling probability $\rho = 0.8$ and 0.7) the *Diploderma* dataset since it was the most complete, to ensure the patterns recovered were not sensitive to sampling probability. Model fit was compared using Bayes factors (2lnBf) to determine differences between focal and null models. We followed Kass & Raftery [51] in considering BF = 0 to 2 as ‘not worth more than a bare mention’, BF = 2 to 6 as ‘positive’ support, BF = 6 to 10 as ‘strong’ support, and BF > 10 as ‘decisive’ support.

As an alternative to CoMET, we used the function `bd.shifts.optim` implemented in the R package TreePar 2.5 [52] to detect shifts in diversification rates of our focal and ‘control’ groups. The likelihood function implemented in TreePar is identical to CoMET but differs in the inference framework (ML versus BI) and the method for model comparison (AICc versus BF). Further, CoMET uses independent compound Poisson processes (CPPs) to simultaneously detect rate shifts in diversification along with mass extinctions, but these parameters cannot be estimated together in TreePar. We set the sampling factor (ρ) for each phylogeny as in the CoMET analyses. The end time for each analysis was set to the crown age of the corresponding group and the start time to present day (0 Ma). We gridded the analysis into time-slices of 1 million years to infer episodic rate shifts or mass extinction events occurring within them. We allowed for 0–5 rate shifts in each group and used the χ^2 test to determine the best and the second-best rate shift models for each group. We considered $\chi^2 > 0.95$ as strong support while $0.95 < \chi^2 < 0.90$ as support that cannot be ignored.

Finally, we used an implementation of the CoMET model in the program RevBayes [53] in which speciation and extinction are allowed to vary at discrete time intervals as in CoMET, but are

autocorrelated (unlike TESS where they are independent). We used a Brownian model as implemented in Condamine *et al.* [54] to inform our speciation and extinction rates, with rates in the next time interval centred around those obtained for the current interval. The analyses were run for 10^6 generations with the first 5000 generations discarded as burn-in.

(d) Accounting for phylogenetic uncertainty

Since the occurrence and timing of episodic rate shifts are contingent on the tree topology and crown ages [47,48,52], we estimated marginal likelihoods for models under episodic and constant birth–death processes (function: `tess.likelihood`) for 100 trees sampled from the post burn-in posterior distributions obtained in our BEAST (for *Draco*, *Philautus*) and StarBEAST (for all other groups) analyses. We constructed models under a constant birth–death diversification process and compared these with models simulating episodic rate shifts during times estimated by the CoMET and TreePar analyses (S2c), while keeping extinction rates constant. Marginal likelihoods were estimated for the null and focal models using stepping-stone sampling (function: `tess-steppingStoneSampling`) with 1000 iterations, with 50 stepping stones and with the first 100 iterations discarded as burn-in. Model fit for each of the 100 trees in each group was then compared using Bayes factors (2lnBf) between focal and null models.

All R scripts used in S2c,d are presented in the electronic supplementary material (S8–S12).

3. Results

(a) Phylogenetic relationships and crown ages of gliding vertebrates and the ‘control’ groups

The reconstructed phylogenies of focal (gliding) and ‘control’ (non-gliding) groups were largely congruent with previously published studies that included them (electronic supplementary material, figures S13–S19). The recovered crown ages of groups either agreed with or overlapped greatly with past molecular estimates of these groups (table 2).

A detailed exposition of phylogenetic relationships for all groups is provided in the electronic supplementary material, section S20.

(b) Patterns of diversification in dipterocarps, gliding vertebrates and ‘control’ groups

(i) Dipterocarps

The Dipterocarpaceae LTT curve (figure 2a) shows a rather constant accumulation of lineages until *ca* 20 Ma where an

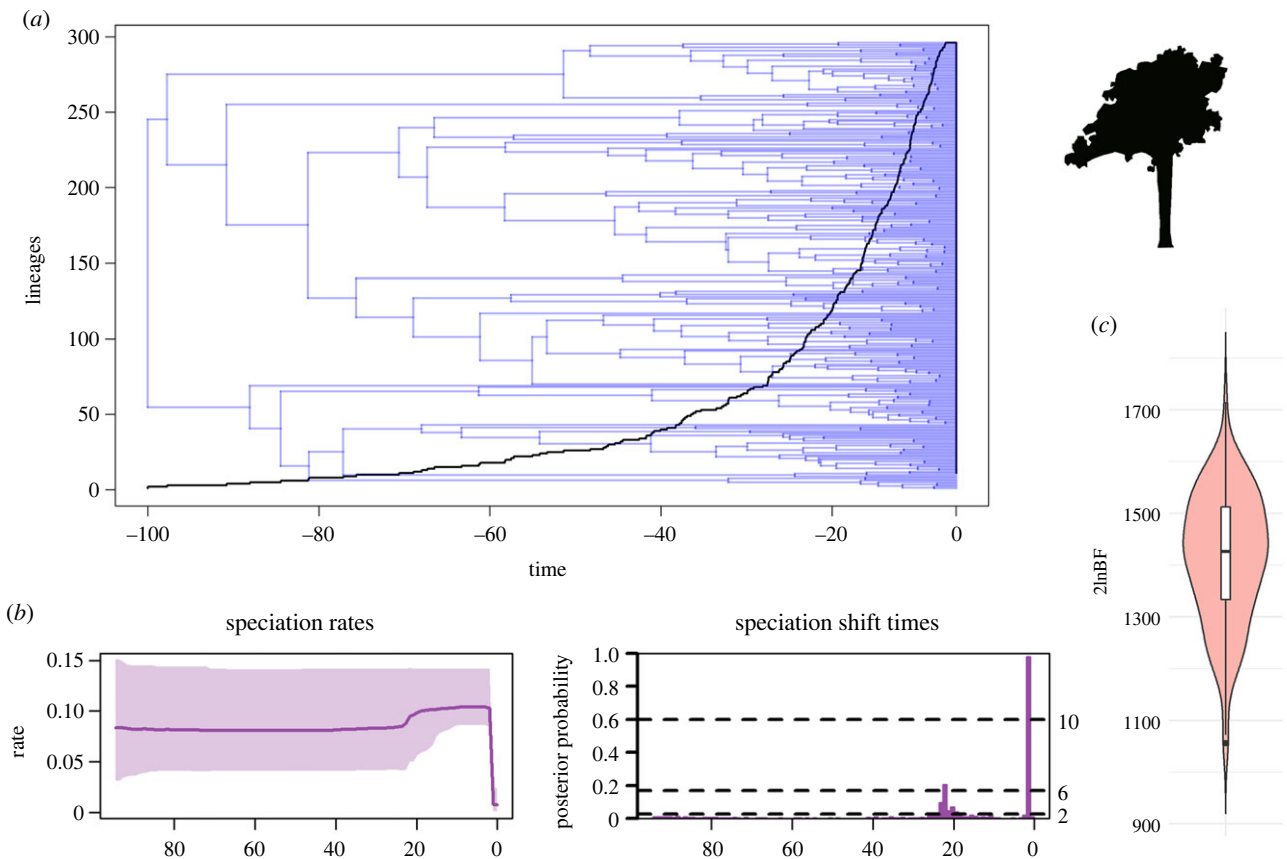


Figure 2. (a) LTT plot of the Dipterocarpoideae with the MCC tree from Bansal *et al.* [21] in the backdrop. (b) Speciation rates inferred using CoMET analysis with *a priori* hyperpriors and Bayes factors support for speciation shift times. (c) Bayes factors (2lnBF) support for models simulating an episodic decline in rates during the Pliocene–Pleistocene over a constant birth–death model for Dipterocarpoideae applied on 100 empirical trees retrieved from Bansal *et al.* [21].

increase in diversification rates is seen followed by a plateau during the Pleistocene, indicating a decline in diversification rates during this time. The CoMET analysis conducted on the Asian dipterocarp MCC tree using *a priori* hyperpriors indicates strong support (figure 2b) for an increase in speciation rate (2lnBF > 6) in the early Miocene (*ca* 20 Ma) followed by decisive support for a precipitous drop (2lnBF \sim 15) during the Pleistocene (*ca* 2 Ma). This pattern was also observed for all Dipterocarpaceae in the analyses conducted by Bansal *et al.* [21]. Extinction rates in dipterocarps were largely constant with no support for mass extinction events (electronic supplementary material, figure S21A). The analyses performed using empirical hyperpriors retrieved the Pleistocene decline in rates with slightly lower BF support, but not the early Miocene increase in rates (electronic supplementary material, figure S21B). The RevBayes analysis however, showed a decline in diversification rates in the Pliocene (*ca* 4 Ma), did not reveal the increase in rates during the early Miocene (electronic supplementary material, figure S22), and further suggested an increase in extinction rates during the Pleistocene. TreePar recovered two independent declines in diversification rates during the Pleistocene (table 2), but did not support an increase in rates during the early Miocene (*ca* 20 Ma). The model-fitting exercise conducted on 100 trees sampled from the post-burn-in treespace generated from the divergence dating analyses for dipterocarps yielded decisive support for an episodic rate-shift over a constant birth–death process (2lnBF > 900) during the Pliocene–Pleistocene (figure 2c). All 100 sampled trees in these groups supported the episodic rate-shift model over a constant birth–death model.

(ii) Inferring patterns from LTT plots of gliding vertebrates and their 'control' groups

Lineage through time plots for the gliding groups revealed plateaus in lineage numbers after 5 Ma (Pliocene–Pleistocene) indicating a decline in diversification rates during this time (figure 3a). Gliding frogs showed a steep increase in lineage accumulation *ca* 4 Ma followed by a plateau *ca* 1 Ma. Among the non-gliding groups, *Diploderma* and *Philautus* underwent constant lineage accumulation throughout their history (figure 3b), while Callosciurinae rates plateaued between *ca* 10 and 6 Ma and again at *ca* 3 Ma.

(iii) Gliding vertebrates

The CoMET analyses run using hyperpriors specified *a priori* on the gliding clades recovered drops in speciation rates during the Pliocene–Pleistocene in all clades (figure 4a–c). The rate shifts were decisively supported for gliding frogs (2lnBF > 10), strongly supported for *Draco* (2lnBF > 7), and positively supported for Pteromyini (2lnBF \approx 5). Further, the analyses on gliding frogs showed a strongly supported (2lnBF > 8), steep increase in speciation rates during the Pliocene (*ca* 4 Ma) followed immediately by a strongly supported (2lnBF = 6) mass extinction event (electronic supplementary material, figure S25A). The analyses run using empirical hyperpriors resulted in the same patterns for all gliding groups, with marginally lower, yet significant support for rate shifts (electronic supplementary material, figures S23B–S25B). However, the empirical hyperprior analysis on gliding frogs did not retrieve support for the Pliocene mass

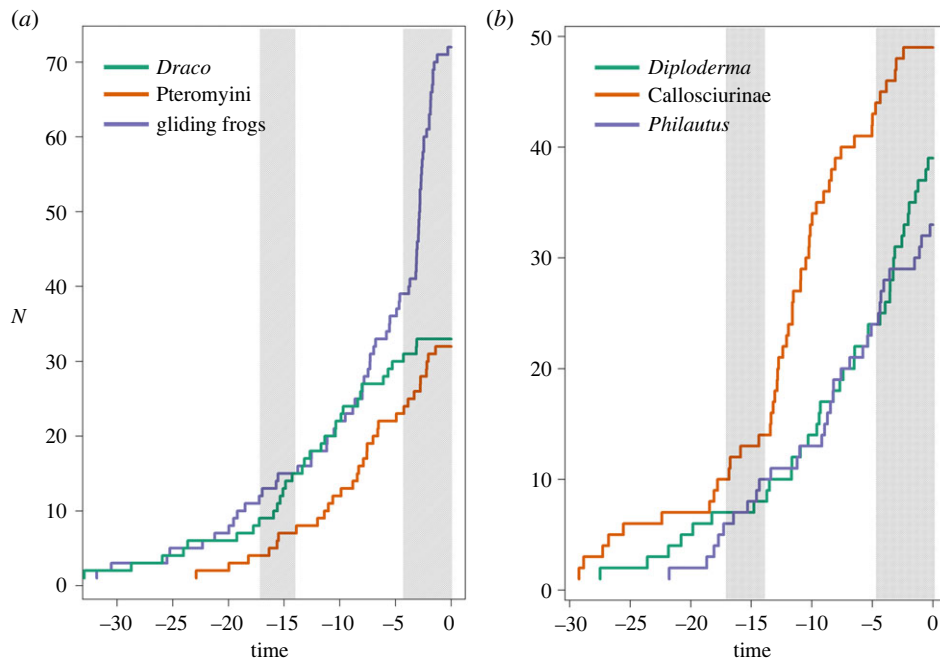


Figure 3. Lineages-through-time (LTT) curves of the (a) gliding vertebrates and (b) the ‘control’ groups, colour-coded cladewise. Shaded regions indicate the mid-Miocene climatic optimum (ca 17–14 Ma) and the Pliocene–Pleistocene (less than 5 Ma).

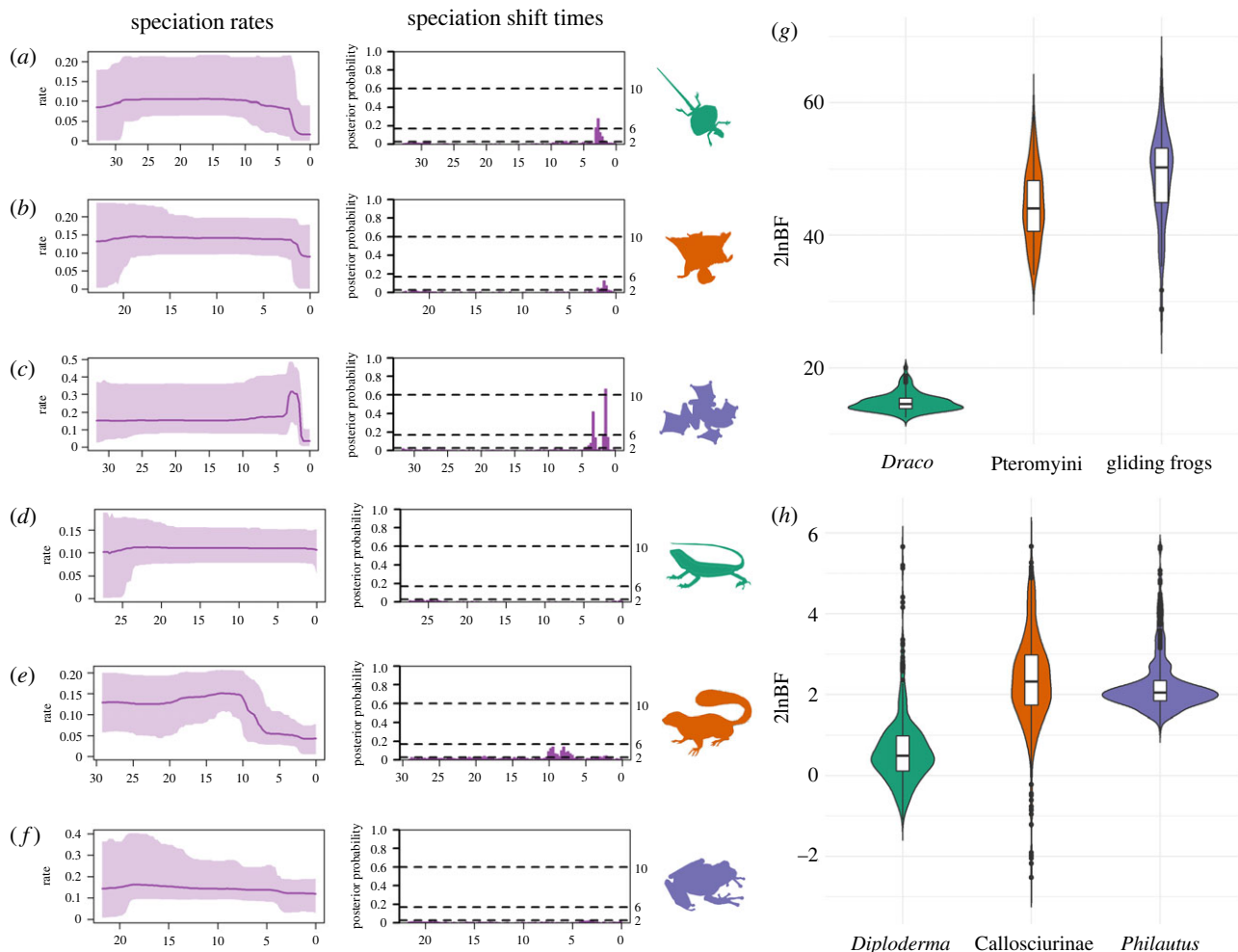


Figure 4. Speciation rates inferred using CoMET with *a priori* hyperpriors, conducted on the chronograms of the focal groups (a) *Draco*, (b) *Pteromyini* and (c) gliding frogs and ‘control’ groups (d) *Diploderma*, (e) *Callosiurinae* and (f) *Philautus*. Bayes factors (2lnBF) support for models simulating an episodic decline in rates during the Pliocene–Pleistocene over constant birth–death models, applied on 100 empirical trees each for (g) gliding vertebrates and (h) non-gliding ‘control’ groups, colour-coded clade-wise. Note the difference in scale in the Y-axis between the gliding (g) and non-gliding (h) groups.

extinction event (electronic supplementary material, figure S25B). Extinction rates were largely constant in all groups in the analyses using empirical hyperpriors. The results

obtained from the TreePar method for all groups were highly consistent with results from the *a priori* CoMET analyses (table 3).

Table 3. Results of the TreePar analyses conducted on the focal and non-gliding, ‘control’ groups. The two most likely scenarios (M_0 and M_1) in each analysis are compared. r, rates; st, shift times.

clade	M_0	M_1	$-\log \text{lik} (M_0)$	$-\log \text{lik} (M_1)$	χ^2	r1	r2	r3	st1	st2
Dipterocarpoidea	1 shift	2 shifts	112.4	111.9	0.98	0.04	0.02	0.0001	2	1
<i>Draco</i>	0 shifts	1 shift	114.2	107.4	0.99	0.09	0.0001	—	3	—
Pteromyini	0 shifts	1 shift	97.6	94.7	0.90	0.14	0.02	—	2	—
gliding frogs	1 shift	2 shifts	215.4	212.1	0.91	0.009	0.02	0.01	4	1
<i>Diploderma</i>	0 shifts	1 shift	120.9	120.1	0.32	0.10	—	—	—	—
Callosciurinae	0 shifts	1 shift	167.2	156.8	0.99	0.1	0.03	—	8	—
<i>Philautus</i>	0 shifts	1 shift	101.8	99.5	0.80	0.12	—	—	—	—

The RevBayes analyses for *Draco* and Pteromyini did not indicate a steep drop in speciation rates during the Pliocene–Pleistocene (electronic supplementary material, figures S26 and S27). However, they showed a significant increase in extinction rates during this time, adversely affecting net-diversification rates for these groups. The diversification patterns for gliding frogs were similar in both the RevBayes and the *a priori* CoMET analyses (electronic supplementary material, figure S28).

(iv) Non-gliding ‘control’ groups

Diversification analyses conducted using all three methods did not yield any support for rate shifts or mass extinction events in the history of *Diploderma* and *Philautus* (figure 4d,f; table 3; electronic supplementary material, figures S29, S30, S33, S34) and all methods supported a largely constant birth–death model. Further, the results of the CoMET analysis conducted on *Diploderma* did not change with varying sampling probability (ρ ; electronic supplementary material, figure S35). However, the RevBayes analyses suggested a marginal increase in extinction rates during the Pliocene for both genera, but this did not affect their net-diversification rates (electronic supplementary material, figures S30 and S34).

For Callosciurinae squirrels, the CoMET analyses using *a priori* and empirical hyperpriors indicated shifts in speciation rates immediately after 10 Ma (figure 4e; electronic supplementary material, figures S31A and S31B). The TreePar analysis corroborated this, with support for a decline in rates *ca* 8 Ma (table 3). However, RevBayes analysis suggested a much earlier decline in rates (*ca* 14 Ma; electronic supplementary material, figure S32), immediately after the mid-Miocene climatic optimum. Further, the RevBayes analysis did not show any increase in extinction rates for Callosciurinae post the Miocene (electronic supplementary material, figure S32). None of the methods supported a Pliocene–Pleistocene decline as observed in the Callosciurinae LTT plot (figure 3b).

(c) Accounting for phylogenetic uncertainty

The model-fitting exercise conducted on 100 trees sampled from the post-burn-in treespace generated from the divergence dating analyses for the gliding vertebrates yielded decisive support for an episodic rate-shift over a constant birth–death process ($2\ln\text{BF} > 10$ for *Draco*; > 28 for Pteromyini; > 22 for gliding frogs) during the Pliocene–Pleistocene (figure 4g). All

100 sampled trees in these groups supported the episodic rate-shift model over the constant birth–death model.

Since none of the diversification analyses (CoMET, RevBayes or TreePar) conducted on the ‘control’ groups supported an episodic shift during the Pliocene–Pleistocene, we explicitly tested the likelihood of a rate shift in these groups later than 5 Ma, by varying the timing of such an event across this time period (5–1 Ma, in intervals of 1 Ma) for all 100 trees. The model-fitting analyses yielded low support ($2\ln\text{BF} < 3$) for a rate shift in over 90% of the sampled trees for all ‘control’ groups, indicating that the occurrence of such an event in their history during the Pliocene–Pleistocene was highly unlikely (figure 4h).

4. Discussion

(a) Diversification patterns in context of Asian palaeoclimate and the fossil record

We detected strong signals for a precipitous drop in diversification rates of Asian gliding vertebrates, concomitant with the pattern seen in dipterocarp trees during the Pleistocene, but not in the non-gliding ‘control’ groups. Callosciurinae showed an earlier decline in diversification rates during the Miocene (*ca* 8 Ma), which is unlikely to have been caused by the same processes that affected the dipterocarps and the gliding groups. The non-gliding groups *Philautus* and *Diploderma* followed a constant birth–death model with no rate shifts in their evolutionary history. These results suggest that the fates of gliding vertebrates may be strongly linked with dipterocarps, which are crucial for their survival and proliferation. However, it may be argued that climate change during the Pliocene–Pleistocene could have exclusively and independently affected the diversification of the gliding vertebrates. Chaitanya & Meiri [29] quantitatively showed that the Indian gliding lizard *Draco dussumieri* is unable to disperse into regions devoid of dipterocarps, despite climatic suitability. This suggests most gliding vertebrates may require the presence of dipterocarps even in regions where climate is suitable for their persistence. This can further explain why gliding vertebrates are most speciose in regions with dipterocarp forests. Therefore, we infer that while the disjunct distributions (figure 1a) and decay in diversification (figure 2b) of dipterocarps were likely precipitated by the step-wise increase in aridity in Asia, these events concomitantly induced the remarkably similar patterns of

biogeography (figure 1*b–d*) and diversification (figure 4*a–c*) seen in the gliding vertebrates.

After the mid-Miocene climatic optimum (17–14 Ma), the Indian subcontinent and southern China (excluding southwestern China that has remained tropical) saw a protracted shift from humid to arid regimes caused by the uplifts of the Himalayas, and the Tibetan plateau, respectively [58–60]. By the Pliocene–Pleistocene, these regions had undergone profound aridification followed by acute climatic fluctuations during the Quaternary glacial cycles [61]. Through this time, the rest of Southeast Asia remained largely evergreen, acting as a refugium for wet-adapted organisms [61–63].

The Pliocene–Pleistocene fossil record from the Indian peninsula attests to the extirpation of most dipterocarp flora from modern-day arid regions (see [64] and references therein) [31,65–69]. This aridification relegated dipterocarps to the wet rainforests of the Western Ghats and Sri Lanka, forging the disjunct distribution seen today (figure 1*a*) [21,31,70]. Similarly, the presence of dipterocarps in southern China during the mid-Miocene [71–73], and their conspicuous absence thereafter, is indicative of the change in climatic regimes in the region. Most of the early Pteromyini (flying squirrel) fossils (early Miocene up to the Pliocene) are from Europe, suggesting that many lineages went extinct there [14]. Our analyses of Pteromyini diversification do not detect this signal, presumably because of the dominance of Southeast Asian taxa, and the absence of extinct lineages from our crown group. Nevertheless, the Pleistocene Pteromyini record is dominated by fossils from south and southeast China [14,74] indicating large-scale extirpations from this region.

The disjunct extant distributions shared by Asian gliding vertebrates and dipterocarps were likely shaped by these palaeoclimatic processes. This vicariance drove the evolution of allopatric species pairs in South and Southeast Asian dipterocarps within the genera *Hopea*, *Shorea* and *Dipterocarpus* [21,31], much like the patterns seen in Pteromyini, gliding frogs, and *Chrysopelea* snakes [15,39,75] (electronic supplementary material, figures S13–S14). However, our *Draco* phylogeny indicates an early split between the sole Indian species (*Draco dussumieri*) and the Southeast Asian lineages (electronic supplementary material, figure S11). One explanation for this scenario is that, while *D. dussumieri* may have found refuge in the evergreen forests of the Western Ghats, other Indian *Draco* species, more closely related with Southeast Asian congeners, have gone extinct due to the aridification of the peninsula.

(b) Remarks on the methods used

While we assembled the most comprehensive datasets possible for each of these groups based on available literature, we cannot rule out either taxonomic incompleteness due to undescribed cryptic lineages, or reticulations between tip nodes due to suboptimal methods of species delimitation. Therefore, we must caution that future revisions with major taxonomic changes of the groups we test may affect the results presented herein.

Further, the reliability of diversification estimates that are based solely on extant timetrees has been hotly debated (e.g. [76]). Louca & Pennell [34] showed that, for any diversification scenario that explains the extant timetree presented, there exist an infinite number of alternative scenarios that are equally likely. Therefore, they argue that a reliable inference of diversification history is not possible based solely on

a timetree of extant species and must be supported conclusively by other information such as palaeontological data. Our results support models that indicate a steep decline in net-diversification rates during the Pliocene–Pleistocene by either a marked decrease in speciation rates (CoMET, TreePar) or an increase in background extinction rates (RevBayes) for dipterocarps as well as three independently evolving lineages of gliding vertebrates. These results are supported for dipterocarps and Pteromyini by an extensive Pliocene–Pleistocene fossil record and by previous studies on Asian palaeoclimate in the context of these taxa that converge on similar conclusions [14,21,30,31]. However, there are no known fossils of either *Draco* or the gliding frogs that can either corroborate or refute this scenario. Nonetheless, the similarity of the results across taxa, the dissimilarity of patterns for the non-gliding groups, and the close agreement with the fossil records in the two groups for which fossils are known support the veracity of our conclusions.

The CoMET algorithm has also been criticized for producing spurious signals, especially pronounced terminal (<5 Ma) declines in diversification rates even when taxonomic coverage is near-complete [49]. However, the CoMET analyses conducted on the non-gliding ‘control’ groups either do not produce this pattern (*Diploderma*, *Philautus*) or recover a much older decline in rates (Callosciurinae). Further, several studies that used CoMET, with varied clade sizes, crown ages, and sampling probabilities (ρ), do not show terminal declines in speciation rates (e.g. [77–81]). We therefore have confidence in the CoMET results, which are further substantiated by the other methods employed here.

(c) Conclusions and future work

The patterns of distribution and diversification in the Asian gliding clades that we analysed are remarkably similar, and are distinct from those of the non-gliding groups. We postulate that these patterns were forged by the diversification and biogeography of the dipterocarps, which in turn were shaped by palaeoclimatic processes. Consequently, we caution that the degeneration of Asian dipterocarp forests due to climate change or deforestation may adversely affect the fates of the region’s gliding vertebrates.

An interesting follow-up study could test if the evolution of gliding was triggered by the dominance of tall trees in other regions of the world, i.e. the gliding marsupial lineages (flying phalangiers, feathertail gliders and greater gliders [82]) that occur in regions with dipterocarps (New Guinea) and tall eucalypt trees (eastern Australia), or the ancient anomalures of Africa that occur in sympatry with the African dipterocarps [83]. Gliding is known to have evolved at least thirty times in phylogenetically unrelated extinct and modern vertebrate lineages. Applying this hypothesis across time and space to test if each of these instances was triggered by tall trees will make for a compelling study, and greatly improve our understanding of the evolution of gliding in vertebrates.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data are provided in electronic supplementary material [84].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. R.C.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft;

J.A.M.: data curation, validation, writing—review and editing; P.K.: data curation, writing—review and editing; S.M.: supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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