

# Diversifying in the mountains: spatiotemporal diversification of frogs in the Western Ghats biodiversity hotspot

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## Abstract

Mountain ranges are hotspots of biodiversity. However, the mechanisms that generate biodiversity patterns in different mountainous regions and taxa are not apparent. The Western Ghats (WG) escarpment in India is a globally recognized biodiversity hotspot with high species richness and endemism. Most studies have either invoked paleoclimatic conditions or climatic stability in the southern WG refugium to explain this high diversity and endemism. However, the factors driving macroevolutionary change remain unexplored for most taxa. Here, we generated the most comprehensive dated phylogeny to date for ranoid frogs in the WG and tested the role of paleoclimatic events or climatic stability in influencing frog diversification. We found that the diversity of different ranoid frog clades in the WG either accumulated at a constant rate through time or underwent a decrease in speciation rates around 3–2.5 Ma during the Pleistocene glaciation cycles. We also find no significant difference in diversification rate estimates across elevational gradients and the three broad biogeographic zones in the WG (northern, central, and southern WG). However, time-for-speciation explained regional species richness within clades, wherein older lineages have more extant species diversity. Overall, we find that global paleoclimatic events have had little impact on WG frog diversification throughout most of its early history until the Quaternary and that the WG may have been climatically stable allowing lineages to accumulate and persist over evolutionary time.

**Keywords:** Ranoidea, escarpment, speciation, museum, cradle, macroevolution

## Introduction

Mountain ranges harbor high species diversity and endemism and are often considered biodiversity hotspots (Fjeldså et al., 2012; Hoorn et al., 2013; Rahbek, Borregaard, Colwell, et al., 2019). Despite occupying less than 25% of the Earth's land surface area, mountain regions harbor about 85% of the world's terrestrial vertebrates (Rahbek, Borregaard, Colwell, et al., 2019; Tenorio et al., 2020). Apart from mountain uplift creating several novel environments promoting speciation (Antonelli et al., 2018; Igea & Tanentzap, 2021), the complex topographic and environmental heterogeneity in mountain ranges can create barriers to gene flow and promote species divergence (e.g., Funk et al., 2016; Steinbauer et al., 2016). Climatic changes in mountain ranges over evolutionary time can also expand and contract species ranges (Thomas & Lennon, 1999) and influence lineage diversification (Hazzi et al., 2018; Kolář et al., 2016; Pepper et al., 2011). Although mountains are important “engines” of speciation, a clear understanding of the mechanisms that generate diversity patterns in mountains across taxa remains elusive.

Essentially, three main evolutionarily processes—speciation, extinction, and dispersal—determine regional species richness patterns (Ricklefs, 1987; Wiens & Donoghue, 2004). The relative role of each of these processes varies vastly based on the taxonomic group, biogeographic history, geomorphology, and geological history of an area (Rangel et al., 2018). For instance, it has been shown that the high diversity in the Neotropics is a result of different diversification scenarios and that Neotropical plant diversity has largely expanded through time while tetrapods accumulated at a slower rate or show recent rate declines (Meseguer et al., 2022; Vasconcelos et al., 2020). Over the years, several studies have examined richness patterns through these three processes and have proposed two main hypotheses to explain high species richness in mountains. First, mountains can be “cradles of speciation” where high species richness is a result of rapid speciation caused by mountain uplift or climatic oscillations; thus they act as “species pumps” leading to dispersals out of mountains to adjacent regions (Stebbins, 1974; Valentine, 1967). The second hypothesis is that mountains act as “museums of diversity”

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by providing refuge to specialized species and by reducing extinction rates leading to the persistence of old lineages (Rahbek, Borregaard, Antonelli, et al., 2019). Alternatively, some authors have also invoked the time-for-speciation effect (Stephens & Wiens, 2003) in the museum model wherein lineages colonize mountains early in their evolutionary history and have a longer time for species to accumulate (Hutter et al., 2013; Smith et al., 2007). There can also be considerable overlap between these two models wherein mountains accelerate speciation in some lineages, while also allowing the persistence of older lineages (Dagallier et al., 2020; Kennedy et al., 2022; McKenna & Farrell, 2006). More recently, mechanistic models and simulations of the processes shaping mountain biodiversity patterns suggest that some mountain regions can act as “graves” where extinction rates are unusually high (Rangel et al., 2018).

While multiple studies have supported the cradle and museum models (e.g., Esquerré et al., 2019; Igea & Tanentzap, 2021; Lagomarsino et al., 2016; Matos-Maraví et al., 2021; Sundaram et al., 2019), these simplistic models may have outlived their utility in understanding mountain diversification (Vasconcelos et al., 2022b), due to confusion in the mechanistic processes underlying such diversification patterns (Chazot et al., 2016). For instance, while Stebbins’ (1974) original definition of a “cradle” referred to regions with high environmental heterogeneity where range contraction, colonization, and speciation have led high speciation in clades (Vasconcelos et al., 2022b), regions with high dispersal rates into adjacent regions (Sedano & Burns, 2010; Esquerré et al., 2019) or having young endemic lineages (Dagallier et al., 2020) have also been considered cradles. Additionally, different factors such as topographic complexity and climatic stability can vary across mountainous regions and influence the diversification and dispersal dynamics of different groups of organisms in very different ways (Pontarp & Wiens, 2017; Rangel et al., 2018; Roy & Goldberg, 2007). Thus, elucidating the evolutionary drivers of mountain diversity requires an understanding of the factors affecting the diversification and dispersal dynamics of different groups across mountain regions (Meseguer et al., 2022). Some mountain regions such as the Andes, the European Alps, and the Himalayas have complex diversification histories and are largely influenced by multiple dispersal from surrounding regions (Antonelli et al., 2018; Ding et al., 2020; Hoorn et al., 2010; Kadereit, 2017; Xing & Ree, 2017; Yu et al., 2020). However, some mountain regions have remained in relative isolation harboring their own unique species that have predominantly diversified in situ after initial colonization (Muellner-Riehl et al., 2019; Xing & Ree, 2017). One such area is the Western Ghats in India where in situ diversification has led to the origin of several endemic groups of taxa (Bossuyt et al., 2004), making it an excellent model system to uncover patterns of species diversification in mountains.

The Western Ghats escarpment (hereafter WG) runs for about 1,600 km along the western coast of India and is recognized as one of the 10 most biodiverse hotspots due to its high species richness and endemism (Gunawardene et al., 2007). Three major gaps interrupt the WG and act as biogeographic barriers for several groups, broadly dividing the WG into the northern, central, and southern WG (Biswas & Karanth, 2021). There is also a clear south-to-north gradient in rainfall seasonality and vegetation structure across the WG, with the northern WG experiencing longer dry periods (Pascal, 1988)

and having shorter trees (Subramanyam & Nayar, 1974). This topographic and environmental complexity of the WG has dramatically influenced the diversification of many taxa (Robin et al., 2010, 2015; Vijayakumar et al., 2016). Recent studies have highlighted the role of paleoclimatic fluctuations during the Eocene-Oligocene transition (ca 30 Ma), late Miocene (ca. 11 Ma), and the Pleistocene glaciation events (ca. 2 Ma) in driving diversification patterns (Cyriac & Kodandaramaiah, 2017; Robin et al., 2010; Vijayakumar et al., 2016). Alternatively, it has been suggested that peninsular India has remained climatically stable and paleoclimate has had a relatively minor role in determining biogeographic patterns of peninsular Indian taxa until the Pleistocene glaciations (Mani, 1974). Moreover, the southern WG may have acted as a refugium for several specialized species to persist during periods of climatic fluctuations (Bharti et al., 2021; Bose et al., 2019; Prasad et al., 2009). However, how the WG has influenced speciation and extinction dynamics of different groups is not well understood.

Here, we explore how the WG has affected frog diversification through an extensive sampling of the extant ranoid frogs in the WG. We model species diversification rates through time to better understand the roles of paleoclimate, geography, and time-for-speciation in giving rise to the WG’s incredible biodiversity. Ranoidea is a superfamily of frogs with 17 different families distributed across the world and makes up the vast majority of the diversity of frogs in the WG (including Families Microhylidae, Micrixaliadae, Nyctibatrachidae, Ranixalidae, Dicroglossidae, Ranidae, and Rhacophoridae). These frogs are a particularly attractive group to test the role of the WG escarpment on species diversification as they show high levels of diversity and endemism within WG (Dahanukar & Molur, 2020) and show a diverse array of reproductive strategies, ecology, and natural history. For instance, nyctibatrachids and micrixalids occupy torrential streams; ranixalids are primarily terrestrial frogs; rhacophorids are predominantly arboreal; while microhylids and dicroglossids have species that are terrestrial, aquatic or burrowing. Ranoids also consist of several clades that have predominantly evolved in situ in the WG (Biju, Garg, Gururaja, et al., 2014; Ramesh et al., 2020; Van Bocxlaer et al., 2012; Vijayakumar et al., 2016), resulting in entire families or genera being endemic to the mountain range (e.g., Micrixalidae, *Nyctibatrachus*, Ranixalidae) or genera where a majority of extant taxa are endemic to the WG with a few dispersals to other regions (e.g., *Raorchestes*, *Indosylvirana*, and *Uperodon*).

In this study, we reconstruct the most comprehensive dated phylogeny of ranoid frogs in the WG thus far and test the role of the climate and topography of the WG in species diversification. Specifically, by modeling the temporal diversification patterns within selected clades, we tested whether the diversification of ranoid frog families in the WG shows deviations from a constant rate associated with global paleoclimatic events or has been driven by constant rates of species accumulation as predicted by museum models. We then estimated diversification rates across frog lineages in the WG and examined spatial differences in diversification rates. Specifically, we tested whether lineages in the southern WG have higher net diversification rates than the central and northern WG, as would be expected if the southern WG was a refugium for lineages to accumulate and persist during periods of climatic fluctuations. We also tested whether lineages at higher elevations diversify faster as expected by the cradle model. Finally,

we asked if regional species richness among different clades of WG frogs is explained by differences in diversification rates or evolutionary time.

## Methods

### Taxon sampling

Extensive field sampling for frogs was carried out by KPD, VT, and SPV across the WG between 2008 and 2015 as an attempt to resolve the prevailing Linnean and Wallacean shortfalls in the Western Ghats (WG) amphibians. Our sampling across 13 of the 14 major massifs in the WG accounted for topographic, climatic, and geological heterogeneity to increase the detection of possible allopatric and parapatric lineages for fine-scale analyses of distribution, diversification, and systematics (see Vijayakumar et al., 2016 for details). For this study, we generated 247 sequences of combinations of three mitochondrial (16S rRNA, Cytb, and ND1) and three nuclear genes (TYR, BDNF, and RAG1) for 93 species of four families of ranoid frogs in the WG (Supplementary File 1). We also included sequences for potentially new lineages sampled by us from the Western Ghats. We then compiled available sequences for these six genes in addition to two mitochondrial (12S rRNA and COX1) and one nuclear (RHOD) gene from GenBank for other ranoid frogs (including those in the WG). For families such as Microhylidae, Dicroglossidae, and Rhacophoridae, wherein there have been multiple dispersal events into the WG, we included sequences of closely related species not restricted to the WG. We additionally included representative sequences from all other families within the larger Ranoidea clade to build a phylogenetic hypothesis for WG amphibians. In cases where sequences from the same individual sample were unavailable for genetic markers of our interest, we substituted them with sequences from other individuals of the same species to obtain a more complete dataset. While such chimeric sequence datasets could potentially affect phylogenetic inferences (Koonin, 2005), it has been shown that even highly heterozygous sequences have minimal impact on phylogenetic reconstructions (Kates et al., 2018). In total, we compiled a nine-gene dataset for 457 species within the large superfamily Ranoidea, covering an average of ~4.54 loci per species. Our dataset also included a near-complete sampling of the families Nyctibatrachidae, Micrixalidae, Ranixalidae, Ranidae, and Rhacophoridae in the WG, while sampling ca. 88% of Microhylidae and ca. 78% of Dicroglossidae in the WG; in total, we sampled ca. 80%–90% of all the ranoid frogs in the WG (see Supplementary File 1).

### Phylogenetic reconstruction and divergence dating

Sequences of each genetic marker were aligned separately using the MUSCLE algorithm in MEGA 11 (Tamura et al., 2021), checked visually and concatenated. The final nine-gene dataset contained 7,956 bp of data from 460 taxa (including three outgroups). We partitioned the dataset by genes for the nonprotein-coding genes and by codon position for the protein-coding genes. We performed Maximum Likelihood analyses in IQ-TREE v 2.0.6 (Minh et al., 2020) using a GTR+G4+I+F nucleotide substitution model with 1,000 ultrafast bootstrap (UBF) replicates to assess branch support. Since ML tree topologies have low reproducibility (Shen et al., 2020), we performed ten independent tree searches in IQ-TREE and compared the tree topologies from these 10 runs to check for reproducibility (see Supplementary File 4:

Methods S1 and Table S1 for details). We then selected the tree topology with the highest likelihood as the input tree for the dating analysis.

We estimated divergence times using the MCMCTree program (Yang & Rannala, 2006) implemented in PAML v.4.9f (Yang, 2007). MCMCTree allows the Bayesian estimation of species divergence times on a priori fixed tree topology using soft fossil constraints (Yang & Rannala, 2006). In order to partition the alignment for the MCMCTree analysis, we used the relative evolutionary rates for each position in the sequence alignment from TIGER (Cummins & McInerney, 2011) to generate three candidate partition schemes using RatePartitions (Rota et al., 2018). TIGER is a tree-independent method that scores similarity within homologous characters in a multiple sequence alignment as a proxy for evolutionary rate (Cummins & McInerney, 2011). These similarity scores can then be used to group characters with similar rates into user-defined bins or partitions (Rota et al., 2018). We then identified the best-fit partition scheme using PartitionFinder2 v2.1.1 (Lanfear et al., 2017) (Supplementary File 4: Table S2). We used the tree topology obtained from ML analyses and set the root age to 140 Ma based on the known estimated stem age of Ranoidea (Hime et al., 2021). We then estimated the mean substitution rate for the seven partitions using the baseml program in PAML to parameterize the diffuse gamma Dirichlet prior and set the birth–death speciation prior (see Supplementary Methods S1 for details). We used the partitioned alignment and the ML tree with seven fossil calibrations, five secondary calibrations, and one geographic calibration as input for the analyses (Supplementary File 4: Table S3). We applied these eight temporal calibrations with varying distributions (see Supplementary Methods S1 for details) following Feng et al. (2017), albeit with some differences in the position of the calibration points (Supplementary File 4: Table S3). We implemented three independent MCMC chains with a 2,000,000 burn-in, after which we ran one million generations sampling every 100 generations under an independent lognormal clock model and HKY85+Γ5 substitution model. We checked the three chains for convergence and summarized the three trees.

### Diversification within clades

Since the WG frogs are not a monophyletic group (see Results), we evaluated temporal diversification patterns in six clades by pruning them from the ranoid time tree (*Nyctibatrachus* [family Nyctibatrachidae], *Micrixalidae*, *Ranixalidae*, *Raorchestes* [family Rhacophoridae], WG *Ranidae*, and *Uperedon* [family Microhylidae]). These six clades are predominantly in situ radiations in the WG (Biju, Garg, Gururaja, et al., 2014; Biju, Garg, Mahony, et al., 2014; Garg et al., 2018; Ramesh et al., 2020; Van Bocxlaer et al., 2012; Vijayakumar et al., 2016). A few species within *Raorchestes*, WG *Ranidae*, and *Uperedon* are distributed outside the WG (i.e., Sri Lanka, South-east Asia), thus, we also pruned these species before analyses. We first tested for episodic shifts in diversification rates associated with key global paleoclimatic events by using a stepping-stone algorithm to estimate marginal likelihoods for different diversification models implemented in the R package TESS v.2.1.2 (Höhna et al., 2016). We estimated marginal likelihoods for a set of seven models with episodic rate shifts and compared them with a constant birth–death model. For the episodic rate-shift models, we specified rate shifts at 30 Ma marking the Eocene-Oligocene transition (Bosboom et al., 2014; Sun



& Windley, 2015; Wang et al., 2016), at 12 Ma when the monsoons intensified (Sarr et al., 2022), and at 2 Ma marking the timing of the Pleistocene glaciation events (Zachos et al., 2001). We evaluated the fit of these models through a pairwise Bayes Factor comparison wherein  $BF > 3.2$  were considered substantial and  $BF > 10$  was strong support for model  $M_0$  over  $M_1$  (Jeffreys, 1961).

We then tested for variation in diversification rates using a Maximum likelihood framework for each of the six clades. We fit 11 diversification models which included one constant birth–death model, three time-varying, three temperature-dependent, and four diversity-dependent models (Supplementary File 4: Table S4) accounting for incomplete taxon sampling within the WG. Models were built by varying the dependency of speciation and extinction events with time (for time-varying models) using the `fit_bd` function, and with paleotemperature (for temperature-dependent models) using the `fit_env` function in the R package RPANDA v 1.4 (Morlon et al., 2016). We fitted density (for density-dependent models) with an exponential and/or linear function using the `dd_ML` function in the R package DDD v 5.0 (Etienne et al., 2012). Since linear diversification dependencies produced negative speciation rate estimates in some cases, we avoided fitting linear functions for the time-varying and temperature-dependent models (see Gamisch, 2020). We compared these models by evaluating the second derivative of the Akaike information criterion (AICc) values. We used  $\Delta AICc$  values to select the best-fit model and estimated the speciation ( $\lambda_0$ ) and extinction ( $\mu_0$ ) rate at present (or at temperature 0 °C for the temperature-dependent model) and the rate of change of speciation ( $\alpha$ ) and extinction rates ( $\beta$ ) with time (or temperature for the temperature-dependent model). A positive value of  $\alpha$  or  $\beta$  in the time-varying models indicates a slowdown of rates towards the present, while a negative value indicates an increase in rates towards the present.

Temporal diversification models may not always be reliable because there are infinite speciation and extinction scenarios with the same likelihood (congruent classes) that can generate a given timetree (Louca & Pennell, 2020). Thus, we accounted for the problem of identifiability of diversification models by examining the trends within congruent classes constructed under alternative hypotheses for all the six frog clades using the R package CRABS v 1.1.0 (Höhna et al., 2022). CRABS allows sampling alternative rate functions within congruent classes and can be used to identify common features shared among these congruent classes (Höhna et al., 2022). To assess congruent classes, we first estimated time-varying diversification rates using the CoMET model implemented in TESS. CoMET models the timing of rate-shift events by considering speciation and extinction rate shifts as compound Poisson processes (May et al., 2016). We ran the CoMET analyses using empirical hyper priors and setting the estimated number of rate shifts as two for 1,000,000 MCMC generations. We discarded the first 25% of the samples as burn-in and ensured the ESS values were greater than 300. We then estimated the pulled diversification rate and constructed alternate congruent classes by specifying alternative extinction rate functions and computing the matching speciation rate function using the R package CRABS v. 1.1.0. We set these alternate extinction rate functions by assuming constant extinction rates, linearly increasing and decreasing rates, exponentially increasing and decreasing rates, and abrupt or sudden increase or decrease in rates. For each of these alternate hypotheses, we set varying

rate parameters to represent a wide range of extinction scenarios and visualized trends in the speciation rates.

### Diversification across clades

To test for heterogeneity in diversification rates across different families of ranoid frogs in the Western Ghats, we used Missing State Speciation and Extinction (MiSSE), a state-dependent approach that estimates branch-specific diversification rates (Vasconcelos et al., 2022a). We used the entire ranoid time tree which included 457 species of the ca. 719 known species and implemented MiSSE using the R package *hisse* v 2.1.9 (Beaulieu & O’Meara, 2016). We implemented the MiSSE analysis by setting the `stop.deltaAICc` parameter to 4 and the `chunk.size` to 10. We used the `GetModelAveRates` function in *hisse* to estimate the tip speciation, extinction, and net diversification rates for each species by averaging models based on their AICc weights. We tested for differences in the species-specific speciation, extinction and net diversification across different frog families in the WG using a Kruskal–Wallis test. Additionally, we also performed cladogenetic diversification rate shift analysis (ClADS) (Maliot et al., 2019) and Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky, 2014), which estimates lineage-specific diversification rates across the tree. ClADS estimates small and large shifts in diversification rates and can detect gradual changes in diversification rates across lineages (Maliot et al., 2019). We used the data augmentation approach developed for the cladogenetic diversification rate shift model (ClADS2) implemented in the “jPANDA” package in Julia (Maliot & Morlon, 2022) to estimate speciation rates across lineages using default priors. We ran the MCMC chains discarding the first 25% as burn-in. We ensured convergence by estimating the Gelman statistic (Gelman et al., 2014) every 1,000 generations and stopped the analysis when Gelman statistic was below 1.05, following Maliot & Morlon (2022). The BAMM analyses was implemented in BAMM v. 2.5.0 (Rabosky, 2014). We ran BAMM for 100 million generations using a rate-shift prior of 1 and rate priors estimated by the function `setBAMMpriors` in the R package BAMMtools v 2.1.9 (Rabosky et al., 2014). We also accounted for incomplete sampling of tips by specifying the sampling probability of each family within the ranoid tree. We checked the run for convergence by examining the trace plots and the effective sample size using the R package *coda* v 0.19-4 (Plummer et al., 2006). We extracted the tip rates from the BAMM posterior distribution to obtain species-specific speciation and net diversification rates and compared them across frog families in the WG using a Kruskal–Wallis test.

### Diversification across regions in the Western Ghats

To test for diversification across regions in the WG and across elevational gradients, we used the tip speciation and net diversification rates estimated using MiSSE and ClADS. We relied on the MiSSE and ClADS estimates because these methods can pick up varying diversification rates at each tip, while BAMM rates are inferred from discrete rate shifts on the tree, and tips after the rate shift inherit similar rates (Rabosky, 2014; Vasconcelos et al., 2022a). We compiled species distribution ranges from published articles and our own extensive surveys spanning the entire latitudinal and elevational extent of the WG. In total, we gathered 3,740 occurrence records of 203 species in the WG (Supplementary File 2) and extracted the latitude from all occurrences for each species and categorized

species as being in the southern, central, and northern WG or shared between these regions. The division of the WG into the north, central, and southern WG is based on two geographic gaps (the Palghat gap and the Goa gap) that have been shown to determine phylogenetic patterns in many taxa (e.g., Robin et al., 2010; Van Bocxlaer et al., 2012; Vijayakumar et al., 2016). We considered regions below the Palghat gap as the southern WG, between the Palghat and the Goa gap as the central WG and regions above the Goa gap as the northern WG. We then tested for differences in the tip diversification rates of species distributed across the three regions using a Kruskal–Wallis test.

Additionally, we obtained the elevation of each record from the ASTER Digital Elevation Model (Abrams et al., 2020) with a spatial resolution of 1 arc-second (ca. 30 m) using the “extract” function in the R package *raster v3.5* (Hijmans et al., 2015) and extracted the median latitude and elevation across all occurrences of a species. Next, we tested the relationship of tip net diversification rate with median latitude and median elevation. We used the “TipCorrelation” function in the R package *bisse v 2.1.9* that performs a regression analysis with zero intercepts on the positized phylogenetic independent contrasts of tip rates and the continuous trait (Vasconcelos et al., 2022a). Since sister species tips may inherit similar rate values and may constitute pseudoreplicates (Vasconcelos et al., 2022a), we performed the regression both with and without sister tips. Additionally, we tested for latitude and elevation-dependent speciation using ES-sim, a simulation-based test that uses the log-transformed ES measure (DR statistic), a tip-specific metric of speciation rate that performs better than other tip rate measures and model-based test of trait-dependent diversification (Harvey & Rabosky, 2018). We implemented ES-sim using the R script provided by Harvey & Rabosky (2018) (available at <https://github.com/mgharvey/ES-sim>) for the six frog clades analyzed in the temporal diversification section.

### Diversification and species richness

Finally, we tested the relationship of diversification rates and evolutionary time with species richness. First, we estimated the regional species richness (including potential undescribed species) within the WG for all genera that mainly radiated in situ in the WG based on published literature and our analyses. We then extracted the divergence dates for each of these clades and estimated the mean net diversification rates from the tip rates obtained from the MiSSE analysis (Supplementary File 4: Table S15). We considered the crown ages for each of these clades as the timing of the first colonization into the WG. We then used linear regression to test for relationships between log-transformed regional species richness and evolutionary time as well as log-transformed regional species richness and diversification rates following (Rabosky, 2012).

## Results

### Phylogenetic reconstruction and divergence dating

Phylogenetic analysis of the 457 taxa within Ranoidea based on 9 genes was largely well-supported and congruent with other large-scale phylogenetic trees. We recovered Ranoidea to be monophyletic with strong support, with Afrobatrachia sister to Microhylidae, which together were sister to the rest of the Natatanura (Supplementary File 2). Among the WG frogs, we recovered six well-supported monophyletic groups

including Micrixalidae, Nyctibatrachinae, Ranixalidae, *Raorchestes*, *Indosylvyrana*, and *Uperodon*. We recovered a well-supported sister relationship between Micrixalidae and a clade with Nyctibatrachidae, *Astrobatrachus*, and the African family Ptychadenidae (99 UBF). Interestingly, the sole member of the genus *Astrobatrachus* was sister to Ptychadenidae with strong support but it is currently classified in the family Nyctibatrachidae. The WG family Ranixalidae was recovered as a sister to the clade containing sub-Saharan African families (Pyxicephalidae, Odontobatrachidae, Phrynobatrachidae, Conrauidae, and Petropedetidae), albeit with low support (85 UBF). We recovered Ranidae to be sister to a clade with Mantellidae and Rhacophoridae (90 UBF), and this clade was sister to the Dicroglossidae (90 UBF). The mean divergence dates obtained from the time-calibrated phylogeny were also broadly consistent with previous hypotheses. Our analysis indicated that Micrixalidae, Nyctibatrachidae, and Ranixalidae were among the oldest WG lineages with mean estimated age of 63, 59, and 53 Ma, respectively, while all the other WG clades were less than or around 40 Ma (see Supplementary File 3).

### Diversification within clades

Diversification patterns of the six clades representing WG in situ radiations indicated no support for episodic shifts in diversification rates. A pairwise comparison of the marginal likelihood of the episodic shift models indicated that a rate constant birth–death model was the best-fit model (2ln BF > 10) (Supplementary File 4: Table S5). Testing the fit of different time-varying, temperature-dependent, and diversity-dependent models revealed different diversification patterns in the six clades (Supplementary File 4: Tables S6–S8). We found that a density-dependent model with linear dependence on speciation and extinction rates was the best-fit model for *Nyctibatrachus* and *Raorchestes* with moderate to strong support compared to most other models ( $\Delta\text{AICc} > 2$ ). However, there was no strong support against a density-dependent model with constant speciation and a linear or exponential dependence on extinction for *Nyctibatrachus* ( $\Delta\text{AICc} = 1.46\text{--}1.64$ ). A temperature-dependent model with constant speciation and an exponential dependence on extinction best-fit the diversification pattern in Micrixalidae with moderate support compared to most other models ( $\Delta\text{AICc} > 2$ ). However, this model was not supported against a constant birth–death model ( $\Delta\text{AICc} = 1.97$ ) and a time-varying model with constant speciation and exponentially varying extinction ( $\Delta\text{AICc} = 1.61$ ). For Ranixalidae, Ranidae, and *Uperodon*, the best-fit model was a constant birth–death model. However, for Ranixalidae, this model was not supported against two time-varying models, two temperature-dependent models and a diversity-dependent model with linear dependence on both speciation and extinction ( $\Delta\text{AICc} < 2$ ) (Supplementary File 4: Table S9). Parameter estimates of the best-fit model for *Nyctibatrachus* and *Raorchestes* indicate a constant high rate of speciation and very low extinction rates compared to other frog groups (Table 1). However, the estimated carrying capacity ( $K$ ) (*Nyctibatrachus* = 86.19; *Raorchestes* = 93.38) indicated that current levels of species diversity in these two genera are yet to saturate. The best-fit model for Micrixalidae indicated a positive association between extinction rate and paleotemperature (Table 1) with extinction rates decreasing towards the present. Parameter estimates of the best-fit model for Ranixalidae, Ranidae, and

**Table 1.** Parameter estimates for the best-fit diversification model for the five ranoid frog groups in the WG. The best-fit models include a constant birth–death (CBD), temperature-dependent (TD) and diversity-dependent (DD) models. The parameters estimated are the speciation rate or initial speciation rate ( $\lambda$ ), extinction rate or initial extinction rate ( $\mu$ ), the rate of change of extinction rate ( $\beta$ ), and the carrying capacity ( $K$ ). Note that  $\lambda$  for the TD model indicates the speciation rate when the temperature is 0.

Datasets	Best-fit model			$\lambda$	$\mu$	$\beta$	$K$
	Model	Parameters	Dependency				
<i>Nyctibatrachus</i>	DD	Speciation	Linear	0.106	1.9e-14	—	86.186
		Extinction	Linear				
Micrixalidae	TD	Speciation	constant	0.056	-4.6e-06	0.2	—
		Extinction	Exponential				
Ranixalidae	CBD	Speciation	Constant	0.054	8.6e-08	—	—
		Extinction	Constant				
<i>Raorchestes</i>	DD	Speciation	Constant	0.138	1.2e-13	—	93.383
		Extinction	Linear				
WG Ranidae	CBD	Speciation	Constant	0.086	1.9e-07	—	—
		Extinction	Constant				
<i>Uperodon</i>	CBD	Speciation	Constant	0.064	-2.5e-07	—	—
		Extinction	Constant				

*Uperodon* indicated considerably low speciation rates and very low extinction rates (Table 1).

The CoMET model indicated that the speciation rates estimates were relatively constant in deep time but showed a sharp decline at ca. 3–2.5 Ma in *Nyctibatrachus*, Micrixalidae, Ranixalidae, and *Raorchestes* (Supplementary File 4: Figures S1 and S2). However, speciation rate estimates remained relatively constant through time for Ranidae and *Uperodon* except for a minor decline at ca. 2.5 Ma in Ranidae (Supplementary File 4: Figure S2). Extinction rates estimated for all six clades were relatively constant through time (Supplementary File 4: Figure S1–S2). Exploring directional trends in speciation rates among congruent models in the CRABS analyses indicated that the rate decline identified for *Nyctibatrachus*, Micrixalidae, Ranixalidae, and *Raorchestes* in the CoMET model was represented in all their corresponding congruent models (Supplementary File 4: Figures S1 and S2). However, we found no consistent directional trends in speciation rates across congruent models for Ranidae and *Uperodon* (Supplementary File 4: Figure S2) suggesting that speciation rate change is relatively constant or shallow.

### Diversification across families

Tip net diversification rates estimated from the MiSSE analysis indicated significant differences across families ( $\chi^2 = 85.349$ ,  $df = 6$ ,  $P < 0.001$ ) (Figures 1 and 2A; Supplementary File 4: Table S10). Pairwise comparisons indicated that Micrixalidae and Ranixalidae had significantly lower net diversification rates compared to all other frog families in the WG ( $p < .05$ ) (Figure 2A). The WG Ranidae had significantly higher net diversification ( $p < .05$ ) compared to all other frog families except Nyctibatrachidae and Microhylidae. Net diversification was not significantly different across Nyctibatrachidae, Dicroglossidae, Rhacophoridae, and Microhylidae. The ClaDS2 analysis also indicated a significant difference in speciation rates estimated across different families ( $\chi^2 = 85.9$ ,  $df = 6$ ,  $p < .001$ ). The difference across families was largely consistent with that from the MiSSE estimates except that

speciation rates were significantly lower in Nyctibatrachidae compared to Rhacophoridae. There was no significant difference in the rates in Ranidae when compared with Dicroglossidae and Rhacophoridae, and between Micrixalidae and Ranixalidae (Supplementary File 4: Table S11; Figure S3). Tip net diversification estimated from the BAMB analysis incorporating family-specific sampling fraction also indicated significant difference across families ( $\chi^2 = 2471.9$ ,  $df = 6$ ,  $p < .001$ ). All pairwise comparisons indicated significant difference in net diversification across all families except between Nyctibatrachidae and Micrixalidae, and between Dicroglossidae and Rhacophoridae with Ranidae and Microhylidae showing higher net diversification than all other families (Supplementary File 4: Table S11; Figure S4).

### Diversification across regions of the Western Ghats

We compared diversification rates across the northern, central, and southern WG. Tip rates estimated by MiSSE and ClaDS2 indicated no significant differences in rates across the three biogeographic regions in the WG (Figure 2B; Supplementary File 4: Table S12; Figures S3 and S5). However, BAMB indicated no significant difference in net diversification across the central and southern WG but indicated significantly lower rates in the northern WG compared to the central and southern WG (Supplementary File 4: Table S12; Figure S6A). Further, we find no relationship between the latitudinal midpoint of each species and tip diversification rates estimated by MiSSE ( $R^2 = 0.0002$ ,  $p = .87$ ) (Figure 2C) and ClaDS2 ( $R^2 = 0.0005$ ,  $p = .79$ ) (Supplementary File 4: Table S13; Figure S3C). We also found no strong association between diversification rates and the elevational midpoint of each species (MiSSE:  $R^2 = 0.011$ ,  $p = .21$ ; ClaDS2:  $R^2 = 0.003$ ,  $p = .479$ ) (Figure 2C; Supplementary File 4: Table S13, Figure S3D, Figure S7). These patterns were similar even when we tested for relationships of the log ES measure with median latitude and median elevation of species within the six clades (median latitude:  $\rho = -0.209$ – $0.234$ ,  $p = 0.187$ – $0.961$ ; median elevation:  $\rho = -0.243$ – $0.355$ ,  $p = .295$ – $.933$ ) (Supplementary File 4: Table S14, Figure S8).

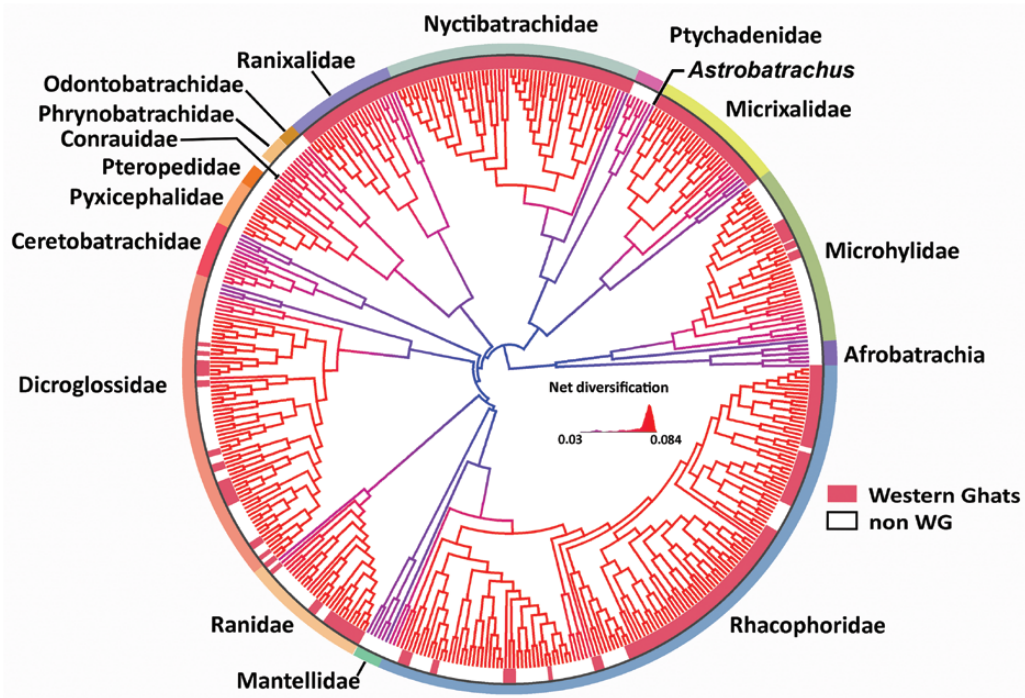
### Diversification and species richness

We found no significant relationship between the regional species richness of each clade in the WG and mean net diversification rates of the clade obtained from the tip rates estimated from the MiSSE analysis ( $R^2 = 0.003$ ,  $p = .84$ ) (Figure 3). Removing an outlier produced the same result, with no significant relationship between the regional species richness and mean net diversification rates ( $R^2 = 0.185$ ,  $p = .162$ ) (Supplementary File 4: Figure S9). However, we found a strong positive correlation between regional species richness of each clade in the WG and its clade age ( $R^2 = 0.77$ ,  $p < .0001$ ) (Figure 3).

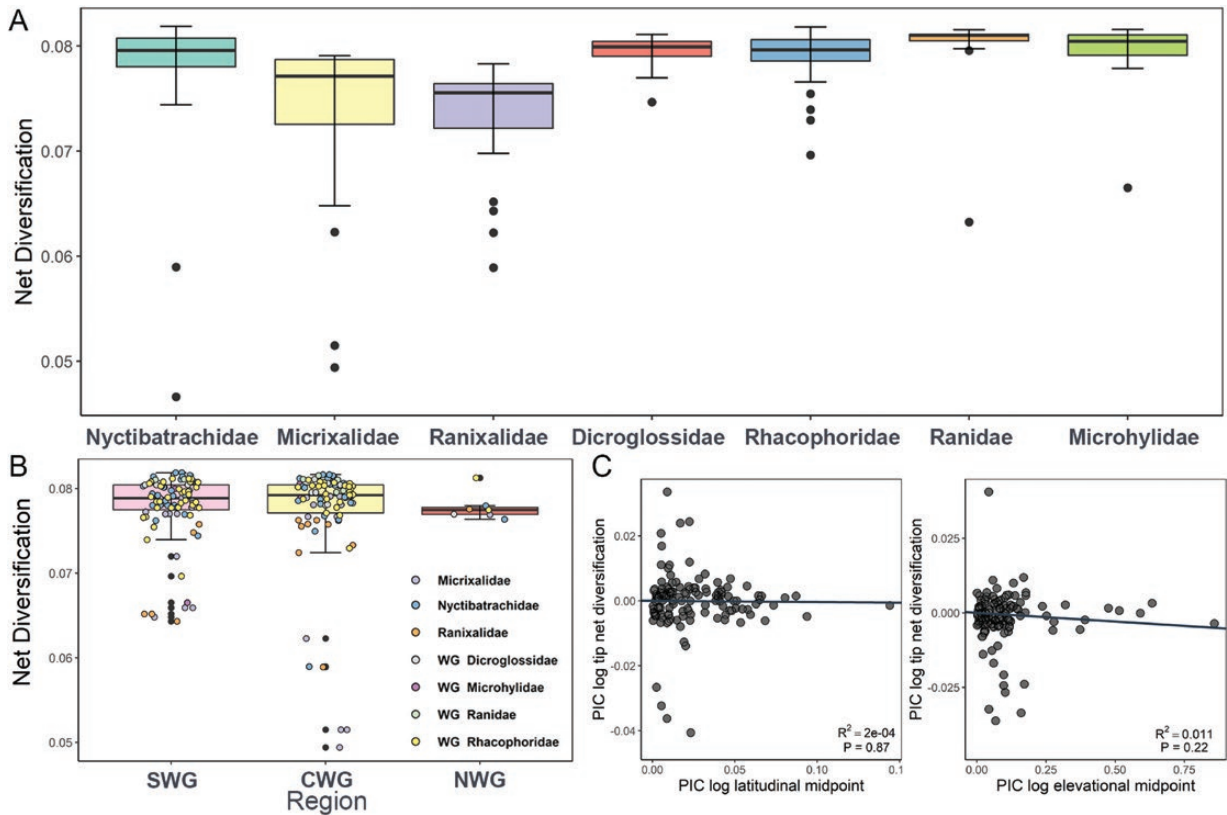
## Discussion

The Western Ghats is exceptionally diverse and is one of the major biodiversity hotspots in the world. However, the mechanisms that have generated this diversity remain poorly explored. While some studies have invoked the role of paleoclimate in driving diversification patterns (Cyriac & Kodandaramaiah, 2017; Robin et al., 2010, 2015; Vijayakumar et al., 2016), others have suggested that stable climatic conditions, particularly in the southern WG, may

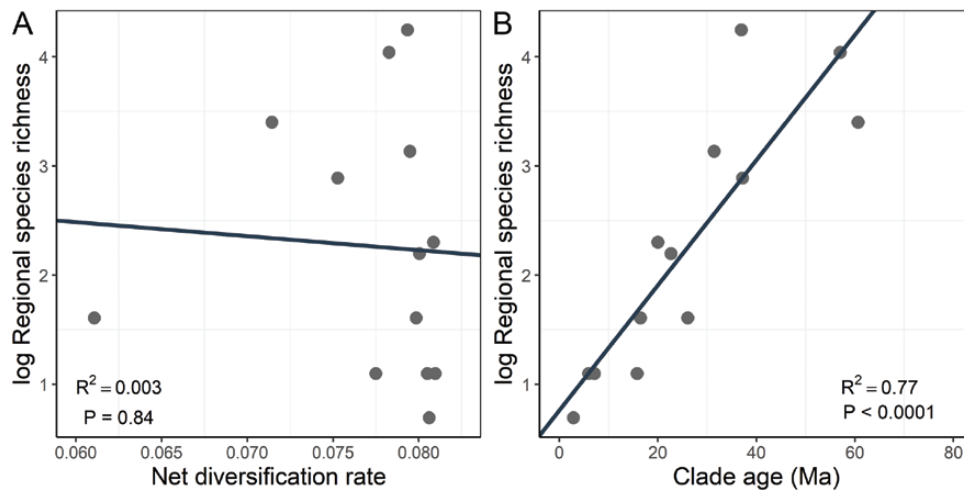




**Figure 1.** Phylogenetic relationship among ranoid frogs based on a maximum likelihood analysis of nine genes with branches colored by net diversification rates estimated from the MiSSE analysis. The inner coloured circle indicated the distribution in the Western Ghats and the outer coloured circle represents the different ranoid frog families.



**Figure 2.** Variation in diversification rates across clades and region. (A) Tip net diversification rates across different families of Ranoidea frogs in the Western Ghats (WG) estimated from the MiSSE analysis. (B) MiSSE tip net diversification rates across the southern WG (SWG), central WG (CWG), and northern WG (NWG). (C) Regression through origin of PIC of net diversification rate with PIC of median latitude and median elevation of species after removing sister pairs.



**Figure 3.** Relationship of the log species richness of WG frog clades with (A) average net diversification estimated by MiSSE and (B) the clade age.

have allowed species to persist and accumulate over evolutionary time (Bharti et al., 2021; Bose et al., 2019; Mani, 1974; Prasad et al., 2009). Here, by substantially increasing the sampling of species and genetic markers, we generated the most comprehensive time tree to date for ranoid frogs in the WG. Using this tree, we infer the spatial and temporal diversification patterns within and across WG frog clades. Using multiple time-dependent and lineage-dependent diversification analyses, we provide evidence that global paleoclimatic events have had little impact on the diversification of frogs in the WG except for the Pleistocene glaciation events ca. 2.5 Ma, and that the WG may have been climatically stable allowing lineages to accumulate and persist over evolutionary time. We outline the results of our phylogenetic and diversification analyses to provide insights into the diversification patterns of WG frogs.

### Phylogenetic reconstruction and divergence dating

The phylogenetic reconstruction and divergence time estimation from this study is largely consistent with other large-scale phylogenetic studies (Jetz & Pyron, 2018; Pyron & Wiens, 2011). However, there are a few notable discrepancies in the placement of a few taxonomic groups compared to studies using large genomic data. For example, Afrobatrachia is sister to the Natanurans in genomic trees (Feng et al., 2017; Hime et al., 2021; Yuan et al., 2018), but our analysis places Afrobatrachia sister to Microhylidae with strong support similar to other large-scale phylogenetic analyses (Jetz & Pyron, 2018). Our tree topology indicates that Ranoidea in the WG are not monophyletic and have likely originated from multiple dispersal events into India supporting earlier studies suggesting that India acted as a “biotic ark” for multiple dispersals between Africa, India, and Asia (Yuan et al., 2018). The mean divergence dates obtained from our dating analysis were also broadly comparable with previous findings (Feng et al., 2017; Hime et al., 2021; Pyron & Wiens, 2013) except for larger confidence intervals in many of the nodes in our analysis. Some studies have raised concerns about the effect of topological and age uncertainty on estimating diversification rates and biogeographic inferences (Magalhaes et al., 2021; Peña & Espeland, 2015). It has also been shown that phylogenetic uncertainty does not drastically impact diversification rate estimates (Wertheim & Sanderson, 2011).

Our phylogenetic reconstruction of Ranoidea shows some discrepancies in the topology and age estimates compared to previously published phylogenetic trees. However, most relationships inferred among species within the different WG frog families were consistent with previously published genus-level phylogenies (Biju, Garg, Gururaja, et al., 2014; Biju, Garg, Mahony, et al., 2014; Garg et al., 2017, 2018; Ramesh et al., 2020; Vijayakumar et al., 2016). Thus, it is unlikely that the differences observed in our tree reconstructions impacted the outcome of our diversification analyses, especially while examining temporal diversification patterns within the WG clades.

### Diversification rates and paleoclimate

Temporal diversification patterns of the WG ranoid frogs suggest a complex diversification history across different groups. Different methods (“RPANDA,” “DDD” and “TESS”) also showed contrasting patterns and varying support for different diversification scenarios. The “RPANDA” and “DDD” analyses indicated a constant birth–death process in two frog groups (WG Ranidae and Microhylidae [genus *Uperodon*]). In Nyctibatrachidae (genus *Nyctibatrachus*) and Rhacophoridae (genus *Raorchestes*), which are the two most diverse groups of frogs in the WG, the analyses supported a diversity-dependent diversification pattern. In contrast, the diversification patterns in Micrixalidae, a group of stream-dwelling torrential frogs, and Ranixalidae, a group of forest leaf-litter dwelling frogs, indicated no clear trend with different models being equally supported (i.e.,  $\Delta AICc < 2$ ). Surprisingly, the episodic birth–death shift models fit using “TESS” indicated no shifts in diversification rates across all six frog clades. However, the CoMET model indicated a constant rate of extinction in all frog groups and a sharp decline in speciation rates at ca. 3–2.5 Ma in *Nyctibatrachus*, Micrixalidae, Ranixalidae, and *Raorchestes*, while showing only a shallow decline in Ranidae and a constant rate in *Uperodon*.

Recent studies have shown that there are infinite combinations of speciation and extinction scenarios (or congruent classes) that can give rise to a particular diversification history (Louca & Pennell, 2020), and have raised concerns about the reliability of time-dependent birth–death models in distinguishing between different congruent sets of diversification scenarios (Louca & Pennell, 2020, 2021; Pannetier et



al., 2021). Nonetheless, fitting diversification models within a hypotheses testing framework and identifying shared patterns within congruent sets of alternate diversification scenarios can still provide significant information about past diversification (Kopperud et al., 2023; Morlon et al., 2022). Our analyses of congruent sets of alternate diversification scenarios consistently indicated a speciation rate decline across all congruent models between 3 and 2.5 Ma in the predominantly wet-forest endemic clades, *Nyctibatrachus*, Micrixalidae, Ranixalidae, and *Raorchestes*. However, there were no consistent directional trends in speciation rates across congruent models for Ranidae and *Uperodon*. Such inconsistent directional trends in diversification rates across congruent classes generally suggest relatively constant or minor changes in rates over time.

Globally, the Cenozoic has witnessed several dramatic climatic fluctuations (Zachos et al., 2001), and these have been associated with the temporal diversification patterns of many groups (e.g., insects [Condamine & Hines, 2015; Condamine et al., 2016], mammals [Stadler, 2011], birds [Claramunt & Cracraft, 2015; Jetz et al., 2012], fish [Near et al., 2012], amphibians [Roelants et al., 2007]; and squamates [Pie et al., 2017]). Studies on dry-adapted peninsular Indian taxa have also invoked paleoclimatic events such as the Eocene-Oligocene cooling (ca. 33 Mya) and the late Miocene acidification (ca. 11–5 Mya) in driving divergence patterns (Agarwal & Ramakrishnan, 2017; Deepak & Karanth, 2018; Lajmi & Karanth, 2020). However, diversification dynamics of the few wet-forest adapted groups studied in peninsular India have shown contrasting patterns. While global Cenozoic climatic fluctuations have been associated with high extinctions in fossorial uropeltid snakes (Cyriac & Kodandaramaiah, 2017), paleoclimate has had no discernible effect on diversification of WG pseudoscorpions (Johnson et al., 2022). Our analyses also indicate that, although the WG frogs have had a long evolutionary history, the diversification dynamics of most WG ranoids have either remained constant through time or show a decline in diversification rates at around 3–2.5 Ma. These results suggest that global paleoclimate events have not significantly impacted frog diversification in the WG during the Tertiary period (66–2.5 MA), but have had a notable effect during the Quaternary glaciation events (ca. 2.5 Ma).

### Diversification across the Western Ghats

Tip diversification rates estimated by all three methods showed significant differences across the WG frog families. Although there were also considerable differences in the tip rates estimated by MiSSE, ClaDS2, and BMM, the MiSSE and ClaDS2 rates were more comparable. For instance, MiSSE and ClaDS2 estimated low net diversification (or speciation) rates for Micrixalidae and Ranixalidae, while these rates were not significantly different between the WG Ranidae and WG Microhylidae or between WG Microhylidae and Nyctibatrachidae. In contrast, the BMM analysis, accounting for within family sampling fraction, estimated very low tip net diversification rates for Micrixalidae and Nyctibatrachidae, while net diversification was highest in WG Ranidae and WG Microhylidae. Interestingly, MiSSE and ClaDS2 found no significant difference in net diversification or speciation rates across different regions in the WG. However, while BMM indicated no significant difference in net diversification across the central and southern WG, rates were significantly lower in northern WG. BMM also

indicated a significant difference in speciation rates across the three regions in the WG.

Such discrepancies could arise because we used clade-specific sampling fractions in BMM while MiSSE and ClaDS2 use a global sampling fraction to account for incomplete taxon sampling (Vasconcelos et al., 2022a). While using clade-specific sampling fraction to account for incomplete taxon sampling seems appropriate, it has been shown that it may lead to incorrect likelihood estimations (Beaulieu, 2020). Alternatively, the significantly lower frog diversity in the northern WG compared to the central and southern WG (Daniels, 1992) may well be a result of differences in diversification patterns, but this may have been obscured by reduced sampling in this region. Different lineage-dependent diversification methods can produce significantly different rate estimates due to differences in the parameterizations of extinction rates, thus, calling for the use of multiple methods in making macroevolutionary inferences (Martínez-Gómez et al., 2023). Our analyses suggest that, across methods, there was no significant difference in net diversification rates between the central and southern WG, while indicating a potential difference in the northern WG. Furthermore, we also detected no significant association of diversification rates estimated by MiSSE, ClaDS2, and DR statistic with the median latitude or elevation of species. Although comparing the median latitude and elevations may not be informative in capturing the complexities in a species' distribution range, most endemic frog species in the WG show very narrow distribution ranges within specific elevational bands (e.g., Vijayakumar et al., 2016), and thus provide a fair estimate of their spatial position in the WG.

Several studies have noted a northward decrease in species diversity and endemism in the WG (Barboni et al., 2003; Davidar et al., 2007; Gimaret-Carpentier et al., 2003), attributed to climatic stability and refugia in the southern WG (Prasad et al., 2009). Some studies have lent support to the refugia hypothesis by showing that phylogenetic diversity of ancient lineages of plants and centipedes decreases from south to north (Bharti et al., 2021; Bose et al., 2019). Additionally, some ancient lineages of centipedes show multiple dispersal events from the southern WG to other biogeographic zones in the WG suggesting that the southern WG may have acted as a refugium in some groups (Joshi & Karanth, 2013). While we would expect higher net diversification rates as a result of low extinction rates in the southern WG refugia, our analyses show that diversification rates are largely similar across regions in the WG, except for potentially lower net diversification in the northern WG as indicated by BMM.

### Reconciling diversification patterns in Western Ghats frogs

While it has been suggested that mountains act as species pumps for amphibian diversification (García-Rodríguez et al., 2021a), other studies have suggested that mountains are museums of amphibian diversification with evolutionary time and climatic stability explaining species richness patterns (García-Rodríguez et al., 2021b). Although we found diversification rates varied across frog families in the WG, we found no significant difference in rates across elevational range. The regional species richness in WG frog clades was significantly associated with clade age rather than diversification rates. The time-for-speciation hypothesis has received overwhelming support from multiple studies (Hutter et al., 2013; Pyron & Wiens, 2013; Stephens & Wiens, 2003; Wiens et al., 2007),

suggesting that the high species richness in mountain regions may be mainly driven by the antiquity of wet tropical forests (Tietje et al., 2022). However, the relationship between clade age and species richness can be a result of different models of diversification (Rabosky & Benson, 2021), and a correlation between clade age and species richness cannot reject a diversity-dependent model of species accumulation (Rabosky & Hurlbert, 2015). Nonetheless, the temporal diversification patterns inferred for the WG frog clades suggest that that speciation rates have remained largely constant through time until as recently as 3–2.5 Ma. While we cannot completely eliminate the possibility of diversity dependence in determining WG frog diversity, our results support the “tropical conservatism hypothesis” wherein the high frog diversity in the WG is mainly a result of gradual species accumulation in the relatively stable environments of the WG.

The few exceptions to speciose groups of frogs within Ranoidea in the WG are the family Nasikabatrachidae, genus *Astrobatrachus* (Nyctibatrachidae), *Melanobatrachus* and *Mysticellus* (Microhylidae), and *Beddomixalus* and *Mercurana* (Rhacophoridae). While these depauperate taxa may have had diverse pasts (Billaud et al., 2020), reconstructing their diversification histories remains difficult since these lineages are known from just one or two species. Interestingly, most of these lineages are adapted to fossorial/leaf-litter microhabitats, a specialization that can negatively influence diversification rates (Cyriac & Kodandaramaiah, 2018; Moen & Wiens, 2017). Testing the role of microhabitats may provide further insights into the diversification dynamics of WG frogs.

Recent studies have indicated that WG may have been climatically relatively stable across evolutionary time. Several palynological studies have suggested that wet tropical forests existed across different parts of peninsular India and the WG during the Eocene and Mid-Miocene (Kern et al., 2013; Kumar, 1990; Mandaokar & Mukherjee, 2012; Rao et al., 2013; Shukla & Mehrotra, 2014; Shukla et al., 2018). Additionally, evidence from fossilized trees and fossil-based climate reconstructions suggest the presence of wet evergreen forests across western India from the Early Eocene up to the Plio-Pleistocene (Bande, 1991; Guleria, 1991; Shukla et al., 2013; Srivastava et al., 2014, 2016), and that grassland expansion may have been more recent (Dunlea et al., 2020; Riedel et al., 2021). This supports the long-standing assertion that the WG escarpment has remained climatically relatively stable and has served as a rainforest refuge for several groups of taxa (Mani, 1974).

While we have assembled the most comprehensive dataset to date for ranoid frogs of the WG to explore diversification patterns, recent studies have questioned the reliability of many of the current diversification analyses to uncover the evolutionary history of taxa (Louca & Pennell, 2020, 2021; Pannetier et al., 2021; Rabosky & Benson, 2021). Although these studies have also suggested ways to examine the reliability of these inferred diversification models by examining common trends across congruent models (Kopperud et al., 2023; Louca & Pennell, 2020), they also suggest that diversification inferences cannot be made solely on extant time trees but should be supported by fossil evidence (Louca & Pennell, 2020, 2021). Although the fossil record is extensive for some taxa in peninsular India (e.g., Bande, 1991; Čerňanský et al., 2022; Kern et al., 2013; Shukla et al., 2013; Srivastava et al., 2016), there are no known fossils for most of the Indian frog

clades (except for *Indorana prasadi*, a rhacophorid frog from the early Eocene of Gujarat: Folie et al., 2012) that corroborate their diversification scenarios. Nonetheless, the shared patterns across different frog groups, and the concordance with the fossil record of other groups, support our conclusions that global paleoclimatic fluctuations may have had little impact on frog diversification until the Quaternary glaciation events.

Overall, we find that ranoid frogs in the Western Ghats have experienced varied diversification histories and a simplistic dichotomous cradle and museum model may not completely reflect diversification patterns. Notably, the diversification patterns for range-restricted, wet-forest clades (Nyctibatrachus, Micrixalidae, Ranixalidae, and Raorchestes) was different from the relatively more wide-spread groups (Ranidae and *Uperodon*). However, contrary to recent studies on the diversification of WG taxa, we find that diversification patterns of frogs in the WG have not been significantly influenced by global paleoclimatic events except during the Quaternary glaciation events. Moreover, our results suggest that most of the WG may have been climatically stable throughout the Tertiary period allowing the accumulation and persistence of frog lineages over evolutionary time.

## Supplementary material

Supplementary material is available online at *Evolution*.

## Data availability

The GenBank accession numbers of the sequences used to generate the dated phylogenetic tree are provided in [Supplementary File 1](#). The final trees and the R script used in our analyses are accessible through Dryad: <https://doi.org/10.5061/dryad.8kpr4xv4>. The phylogenetic trees generated were uploaded to TreeBase and can be accessed through the link (<http://purl.org/phylo/treebase/phyloids/study/TB2:S30411>). All other data are provided in Supplementary Material.

## Author contributions

Conceptualization: V.P.C., K.S.; investigation: V.P.C., A.V.M., K.P.D., S.P.V., K.S.; field sampling: S.P.V., K.P.D., V.T.; genetic data: V.T., A.J., P.S.; data compilation: V.P.C., A.V.M.; analyses: V.P.C.; figures and tables: V.P.C., writing original draft: V.P.C.; manuscript editing: V.P.C., A.V.M., S.P.V., K.S.

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*Conflict of interest:* The authors declare no conflict of interest.

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