Title: Idiosyncrasies unveiled: examining the pace, patterns and predictors of biotic diversification in peninsular India

Short title: Diversification in peninsular India

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Abstract (197 words)

The Peninsular Indian Plate (PIP), an ancient Gondwanan landmass, the oldest region for diversification with complex geoclimatic history in Tropical Asia, harbours highly diverse and endemic biota with distinct biogeographic affinities. However, our understanding of the diversification dynamics of its biota in a quantitative framework is limited. Given this, we used time-calibrated molecular phylogenies and birth-death models to examine the diversification tempo, mode, and drivers across 34 well-studied endemic lineages (~670 species). Lineage identity and biogeographic affinity differentially influenced the diversification rates, where plants had the highest and soil arthropods had the lowest diversification rates. Also, younger Asian groups diversified faster than older Gondwanan taxa. The gradual accumulation was supported in 19 lineages, suggesting that the historical stability of their habitat was an important driver, although the region has had a dynamic geoclimatic past. Miocene aridification, monsoon intensification, changes in paleotemperature, and species diversity explained diversification patterns among the other 15 lineages. The diversification rates predicted the species diversity better than clade age across lineages. Our results highlight the role of regional biogeographic, geoclimatic processes, and phylogenetic history on diversification dynamics, which is critical for predicting how PIP biota may respond to global change amid significant anthropogenic threats.

Introduction

Diversification, a balance between speciation and extinction, is known to shape biodiversity patterns, and the tropical biome, the most species-rich terrestrial biome, has been central to diversification studies (Cardillo *et al.* 2005; Dagallier *et al.* 2020; Eiserhardt *et al.* 2017; Ricklefs 2007). Multiple hypotheses have been invoked to explain the high tropical diversity, including a long time for speciation, being the oldest biome (McPeek & Brown 2007), greater climatic stability (Dagallier *et al.* 2020) and habitat, and climatic heterogeneity (Willig *et al.* 2003). One of the recent studies from Neotropics showed that gradual expansion of the diversity was the most common scenario, irrespective of biogeographic subregions and that diversification rates differed substantially across clades (Meseguer *et al.* 2022). On the other hand, in Australia, aridification and biogeographic barriers were important drivers of diversification (Pepper & Keogh 2021). In Madagascar, a continental island, wet-forest-adapted species showed accelerated diversification (Crottini *et al.* 2012). In addition, tropical islands have highly endemic adaptive radiations primarily driven by niche dynamics and biogeographic processes (Losos & Ricklefs 2009; Wallace 1887). These studies across the tropical regions suggest that patterns and drivers of diversification depend on regional biogeographic and geoclimatic processes, geographic settings such as being an island or a continent, and vary across the Tree of Life. Therefore, there is a need to identify and characterise the processes responsible for generating differential species diversity among distinct geographical regions and clades for a nuanced understanding of the processes contributing to tropical diversity.

In this regard, the Peninsular India Plate (PIP) of tropical Asia remains relatively unexplored despite being one of the oldest regions for diversification in Tropical Asia (Karanth 2021; Mani 1974). PIP was part of the Gondwanaland supercontinent ~ 200 mya ago (Ali & Aitchison 2008; Chatterjee *et al.* 2013). Around 120 Mya Ago, it separated from the supercontinent along with Madagascar and started drifting northeastward (Chatterjee *et al.* 2013). On its northward journey, India was a continental island for ~ 50 mya until it collided with Asia and harboured a predominantly Gondwanan biota, as evident from fossils and molecular phylogenetic studies (Bonaparte 1999; Joshi & Karanth 2011; Prasad *et al.* 2009). During this journey, PIP experienced mass extinctions owing to immense volcanic activity during the K-Pg boundary (70-60 Mya) that led to the formation of the Deccan plateau (Prasad *et al.* 2009). Subsequently, as it approached

the equator, PIP experienced an expansion of dense perhumid forests, followed by its collision with Asia (Morley 2018). The collision is argued to have occurred at around ~35 Mya post multiple transient land connections with parts of Southeast Asia (SEA) during 55-35 Mya (Ali & Aitchison 2008). These land connections and the prevalence of wet rainforests in PIP and SEA facilitated substantial biotic exchange between Asia and PIP in similar niches (Klaus *et al.* 2016). The collision also led to the onset of the Himalayan-Tibetan Orogeny (HTO) (Chatterjee *et al.* 2013; Ding *et al.* 2017), which is thought to have induced seasonality in PIP, leading to the formation of evergreen rainforests (Morley 2018). Post 20 Mya, dispersal barriers between PIP and SEA were established due to the intensification of the HTO (19 - 15 Mya), the contraction of wet evergreen rainforests by intensified aridification (11-7 Mya) and the expansion of C4-plants across the peninsula (9 - 2.5 Mya) (Karanth 2015; Morley 2018). Thus, PIP has wet forests restricted to the western slopes of the Western Ghats, mountain tops in the Eastern Ghats, and dry forests and Savanna in the Deccan peninsula (Karanth 2003, 2015; Mani 1974).

Undoubtedly, this complex geo-climatic history of PIP has played an important role in generating this complex landscape and, in turn, influenced the diversification of flora and fauna in PIP and also in Tropical Asia (Deepak & Karanth 2018; Joshi & Edgecombe 2019; Lajmi & Karanth 2020; Mani 1974) (Table 1). Additionally, owing to its “voyage in isolation” for over 50 My and with support from decades of biogeographic research, parallels in diversity patterns can be drawn between PIP and island systems (Chatterjee *et al.* 2013; Karanth 2015, 2021). The biotic diversity in PIP is highly endemic, comprising lineages/radiations of varying taxonomic affinities (arthropods, molluscs, amphibians, reptiles, angiosperms) and distinct biogeographic origins (Gondwanan, South-East Asian or Eurasian) (Joshi *et al.* 2020; Karanth 2021; Surveswaran *et al.* 2021). Interestingly, irrespective of biogeographic origins, many clades have undergone extensive in-situ diversification in PIP in the Cenozoic, making PIP a distinct biogeographic sub-region within Tropical Asia (Karanth 2021). However, our understanding of diversification tempo, mode and their driver remains limited for the peninsular Indian biota (Agarwal & Ramakrishnan 2017; Cyriac *et al.* 2024; Lajmi & Karanth 2020). Like most tropical areas, PIP diversity and habitats are threatened by global change. Therefore, it is imperative to know the diversification dynamics to assess the evolutionary past and predict the future of peninsular India's highly diverse endemic biota.

Given this, we examine the relative roles of geoclimatic processes, biogeographic affinities, and species traits likely to have shaped the extant diversity in peninsular India in a comparative framework. We use state-of-the-art birth-death models to examine the temporal mode of *in-situ* diversification and their drivers for PIP endemic plants and animal lineages (Condamine *et al.* 2013; May *et al.* 2016; Morlon *et al.* 2010). We compiled a dataset for 34 floral and faunal lineages (clades) where data on species distribution, molecular phylogenetic relationships, and divergence time estimates is available. Most of these lineages are endemic to peninsular India and have undergone extensive in-situ diversification, making it ideal for examining diversification patterns and their ecological and evolutionary drivers in a comparative framework. They are distributed in terrestrial (wet or dry forest) and freshwater habitats with either Asian or Gondwanan biogeographic affinity (Fig. 1, Fig. S2, Table S1). We build on these detailed phylogenetic and biogeographic studies to infer diversification rates, patterns, and potential drivers for peninsular Indian biota. Importantly, we propose the diversification hypotheses with testable predictions for the diversification dynamics of the endemic peninsular Indian biota and their drivers (Fig. 1; Fig. S1).

Box 1

"**Predictions for the tempo of diversification in PIP.** Based on the role of the intrinsic factors, we predicted plants to have higher diversification rates than animals (Hernández-Hernández *et al.* 2021; Scholl & Wiens 2016). Most Gondwanan clades are distributed in wet forests, showing niche conservatism, compared to Asian clades in PIP, which occupy wider niches and have distributions in wet and dry habitats. Hence, we hypothesised that younger Asian clades could have higher diversification rates than ancient Gondwanan clades. In peninsular India, Miocene aridification has led to wet forest fragmentation (Karanth 2003; Morley 2018). It has been hypothesised that vicariance could be a major biogeographic mode of speciation among wet-forest dwelling lineages (Joshi *et al.* 2020; Joshi & Edgecombe 2019).

In contrast, dry habitats have been occupied through dispersal events (Lajmi & Karanth 2020). Also, it has been suggested that vicariance-mediated diversification could lead to lower diversification rates and higher dispersal rates, which are often associated with faster diversification (Moen & Morlon 2014; Suárez *et al.* 2022). Therefore, we predicted that clades

adapted to wet habitats would diversify at lower rates than those adapted to dry habitats (Fig. 1).

Predictions for mode and drivers of diversification in PIP. Temporal modes of diversification can be broadly categorised into gradual, saturated, waxing and waning, and exponential accumulation (Meseguer *et al.* 2022; Morlon 2014; Morlon *et al.* 2010). These diversity accumulation profiles are combined outcomes of speciation and extinction rate dynamics. Gradual accumulation (Scenario 1 - SC1) is led by constancy in diversification rates over time and is attributed to prolonged environmental stability (Benson *et al.* 2016; Couvreur *et al.* 2011; Derryberry *et al.* 2011). Within PIP, the southern parts of the WG and the mountaintops of the EG have remained stable through evolutionary time. They could have served as refugia and, thus, could be the abode of lineages exhibiting gradual accumulation (Das & Chanda 1998; Gower *et al.* 2016; Joshi & Karanth 2013; Prasad *et al.* 2009). Alternatively, lineages can show time-varying changes in diversification rates (Morlon *et al.* 2010). One outcome could be an early increase in diversification followed by saturation (SC2) due to ecological limits/diversity-dependence or drastic geoclimatic perturbations (Condamine *et al.* 2019; Moen & Morlon 2014; Rabosky 2009, 2013; Wiens 2011). Also, species diversity can decline following bouts of increase, ultimately leading to a loss in diversity (SC3) (Condamine *et al.* 2019; Meseguer *et al.* 2022; Moen & Morlon 2014). Such "waxing and waning" diversification patterns are attributed to the inability of lineages to cope with a changing environment and associated decrease in available niches (Condamine *et al.* 2019; Moen & Morlon 2014). PIP has undergone drastic climate changes (e.g., Deccan volcanism and monsoon intensification) through the Cenozoic era, so waxing and waning dynamics might be relevant for many lineages (Chatterjee *et al.* 2013; Morley 2018). Lastly, lineages can exhibit an exponential increase of diversity towards the present (SC4) and are primarily attributed to geoclimatic perturbations and suitable environmental conditions promoting adaptive radiations (Meseguer *et al.* 2022; Morlon *et al.* 2010). Some of the critical geoclimatic events, like the Mid-Miocene aridification, monsoon intensification and expansion of C4-plants in peninsular India, could explain exponential accumulation (Agarwal & Ramakrishnan 2017; Deepak & Karanth 2018). Furthermore, the lineages may also experience episodic shifts in diversification rates, attributed to abrupt geoclimatic events that can cause rapid increase and/or decrease in diversification rates

(Kopperud *et al.* 2023; May *et al.* 2016). Species diversity within a lineage is expected to show fluctuations from general trends, as seen for SC1-4 at time periods relevant to such episodic rate shifts."

Materials and Methods

Data compilation: endemic lineages from peninsular India

We reviewed the published molecular phylogenetic studies on PIP biota on Google Scholar, where phylogenetic trees published till December 2022 were examined. We identified well-sampled dated phylogenetic trees for the PIP lineages where at least 65% of the species were endemic. We found 42 time-calibrated phylogenetic trees, of which 34 lineages had at least four species. We collected data on the biogeographic origin, distribution, crown age and species richness of these 34 peninsular Indian endemic lineages of animals (including arthropods, amphibians, reptiles, and birds) and plants representing 669 species, of which 633 species are endemic to PIP. We requested and obtained time-calibrated tree files (maximum clade credibility trees) from respective authors (Table S1). N*ewick* species trees were manually written based on median node ages from published time trees for the remaining lineages.

They encompass 669 species, of which 94% (633 species) are endemic to PIP, including 50 species of soil arthropods (centipedes and scorpions), three freshwater molluscs (22 species - mussels), eight amphibians (153 species - frogs and caecilians), 12 reptiles (304 species - turtles, geckos, agamids, skinks, lacertids and snakes), one bird (4 species), and five plants (136 species - angiosperms). They are distributed in terrestrial (30 lineages) and freshwater habitats (four lineages). Among terrestrial lineages, 18 are restricted to the wet zones of the Western Ghats, Eastern Ghats, and Sri-Lankan Forests, and 12 are distributed across both wet and dry zones in Peninsular India and/or Sri Lanka. Of these 34 lineages, 21 have Asian and 13 Gondwanan biogeographic affinity. Among terrestrial lineages, 18 are restricted to the wet zones of the Western Ghats, Eastern Ghats, and Sri Lankan Forests, and 12 are distributed across both wet and dry zones in Peninsular India and/or Sri Lanka (Fig. 1; Fig. S2; Table S1).

These lineages do not necessarily pertain to one specific taxonomic rank (ranges from species groups to family level). This was done to compare lineages based on their ages and not of specific taxonomic ranks (like genus), as time (clade age) is thought to be one of the significant

drivers of diversification (McPeek & Brown 2007). Taxa of different taxonomic ranks can have similar ages, and taxonomic ranks are arbitrary (Scholl & Wiens 2016).

Assessing the tempo and mode of species accumulation within each of the lineages

The tempo of diversification - The net diversification rates were calculated to assess the relative pace of diversification for each lineage. The rates were measured in three approaches - 1) by fitting a constant-birth death model from the R package *RPANDA*, 2) by taking the mean speciation and extinction rates from the posterior distribution of the CoMET (Compound Poisson processes on Mass Extinction Times) analysis (in the R package *TESS)* for each time bin, and, 3) by taking the mean speciation and extinction rates at all nodes and tips constituting distinct clades of interest, estimated in the ClaDS analysis using the Julia package *PANDA* (Höhna *et al.* 2016; Maliet & Morlon 2022; Morlon *et al.* 2016). Next, the Wilcoxon test was performed using the *stat_compare_means()* function from the *ggplot2* package (Wickham 2011) in R to check if the tempo of diversification varied across different taxonomic groups, biogeographic affinities and habitat preferences for the lineages.

Assessing mode of diversification - The mode of diversification was evaluated to understand the temporal dynamics of diversification rates in lineages. Firstly, we fitted homogenous birth-death models (constant-rate and time-varying) to all 34 lineages. Constant-rate models included constant-rate pure birth (CB - only a constant speciation rate, no extinction) and constant-rate birth and death models (CBD - constant and finite speciation and extinction rates). Time-varying models included combinations of linearly ($\lambda(t) = \lambda_0 + \alpha \cdot t$, $\mu(t) = \mu_o + \beta \cdot t$) or exponentially ($\lambda = \lambda_0 \cdot e^{\alpha \cdot t}$, $\mu = \mu_o \cdot e^{\beta \cdot t}$) varying (with time - t) birth (λ) and death (μ) rates (λ_0 and μ_o are the expected speciation and extinction rates at t=0, α and β are the coefficients of gain or decay in the functions and time, here, is interpreted as time from the present) (Condamine *et al.* 2019; Morlon *et al.* 2010). These combinations also included constant-rate models for scenarios where one rate (birth or death) varies with time, and the other remains constant. In the models above, the absolute values of speciation and extinction rates are considered even when the models infer negative values. The negative values for speciation and extinction rates are not biologically informative but are feasible mathematically. Therefore, we followed the approach Morlon *et al.* (2020) described to include a set of models with the same mathematical formulations where we

take a value of 0 in cases where rates become negative and refer to them as "non-negative models". These functions capture the broad trends in diversification mode within a lineage.

Additionally, to model the possibility of symmetrical local peaks and dips (sharp increase followed by a decrease in diversification rates or *vice versa*) in diversification rate in time, we developed a continuous time-varying mathematical function to model symmetrical local peaks in diversification and to perform model fitting in the same framework. This function follows the "Witch of Agnesi" curve, where the diversification rates diverge from a baseline constant rate: $\lambda(t) = \lambda_0 + \frac{\alpha\omega}{p} \cdot \left(\frac{t}{(t-p)^2 + \omega}\right)$, where λ_0 represents a baseline rate of speciation, α represents the intensity of the peak (or dip), ω represents the spread of the peak or dip, and p represents the position of the peak (or dip) in My (Spencer 1940). Similar rate shifts in extinction were also modelled. This helped examine the prevalence of symmetrical local peaks (or dips) in diversification. Additionally, using this function, we qualitatively assessed the role of specific geoclimatic events (Table 1) on the diversification of lineages corresponding to the time of occurrence of a peak (or dip). We called this model the "symmetrical local shift"/"symmetrical episodic shift" model and implemented it in the *RPANDA* model-fitting framework. Model fitting using constant-rate and time-varying birth-death models was executed in *RPANDA* using the *fit_bd()* function to determine the diversification pattern of each lineage (Morlon *et al.* 2016).

Best-fitting models were selected based on AICc scores to account for over-fitting. ΔAICc scores were calculated as absolute differences in the AICc scores between each model and the model with the lowest AICc score. The models with ΔAICc scores lesser than two were chosen for each lineage. If multiple models showed ΔAICc below two, i.e., all models were equally likely, then the model with the least parameter complexity was chosen as the best-fitting model. If multiple models of similar AICc and the same complexity existed, the model with the least AICc was selected as the best-fitting model. However, if CB or CBD were found along with other models to be equally likely, the corresponding constant-rate model was considered the best-fitting model for a lineage, as the simplest model could not be rejected. We used the parameter values (λ_0, α, λ_o and ω) of the selected diversification models to evaluate the scenarios mentioned in Table S2 and Fig. 1, Fig. S1.

In addition, we performed the CoMET (CPP on Mass-Extinction Times) analysis using the R package *TESS* (Höhna *et al.* 2016; May *et al.* 2016) to detect times of significant rate shifts in a lineage's history and generate rates-through-time (RTT) plots. The CoMET analysis involves binning the history of a clade into 100-time points at equal intervals. We initially estimated empirical hyperpriors and ran the analysis by setting 1000 MCMC generations. Post the analysis, we checked the Effective Sample Size (ESS) for each time bin in both speciation and extinction rates. If the ESS had not reached 200 for at least one time category, then the analysis was re-run with five times the previous number of generations. This action was looped until all the time bins showed a minimum ESS of 200 for speciation and extinction rates. For each lineage, we extracted the Bayes Factor (BF) supports for rate shifts at these 100-time points and chose the ones where 2 * ln(BF) scores were substantially higher than constant rates (≥4.6 (Hohna *et al.* 2015; Jeffreys 1998)).

To summarise, diversification scenarios were inferred from the results of these two analyses - *RPANDA* models and CoMET.

Determining drivers of diversification rates and diversity

<u>Assessing drivers of diversification patterns:</u> We evaluated the role of important climatic variables on the diversification patterns of biota from PIP, mainly temperature, changes in seasonality patterns and Miocene aridification. We obtained paleoclimate data for temperature (Zachos *et al.* 2008), reconstructed Himalayan elevations (Ding *et al.* 2017) (as a proxy for the onset of seasonality patterns) and pedogenic carbon content, as a proxy for aridification and expansion of C4 plants (Clift & Webb 2019; Quade *et al.* 1989) from the Potwar plateau. The curves for all the paleo-climatic data were smoothened through spline interpolation using the *ss()* function from the *npreg* package (Helwig 2020) in R. Subsequently, we used the same combinations for rate-dependencies (birth and death) as on time (except the episodic local shift model), on temperature, paleo-elevation of the Himalayas and the pedogenic Carbon content and fitted these models using the *fit_env()* function from *RPANDA* package in R. Additionally, we included the functions ($\lambda(T) = \lambda_0 \cdot e^{-\alpha/T}$, $\mu(T) = \mu_0 \cdot e^{-\alpha/T}$) inspired by the metabolic theory of biodiversity as provided in a recent study (Condamine *et al.* 2019) for temperature-dependence (TD) (Brown *et al.* 2004). Among biotic drivers of diversification, we checked for diversity-

dependence (DD) on speciation and extinction rates, incorporating both linear and exponential dependencies (Condamine *et al.* 2019; Etienne *et al.* 2023). The code for calculating AICc for all DDD models referred to relevant sections of source codes for *fit_bd()* and *fit_env()* functions from *RPANDA* (Morlon *et al.* 2016).

Furthermore, a factor analysis of mixed data (FAMD) was performed to assess the correlations among different ecological and evolutionary drivers and to explain the patterns of species diversity (or richness) and diversification across lineages (Pagès 2004). This reduced ecological-evolutionary framework was further used to assess the spread and clustering of lineages. Both quantitative and qualitative (categorical) variables were used in this analysis. We also performed the permutational multivariate analysis of variance (PERMANOVA), utilising the dissimilarities (Gower's distance) between lineages calculated from FAMD coordinates of each lineage to assess the statistical significance of clustering (Anderson 2017). All the analyses were performed using functions from the R packages - *FactoMineR* and *factoextra* (Irnawati *et al.* 2021; Lê *et al.* 2008).

Assessing congruent classes of diversification models

A recent study by Louca and Pennell highlighted the unreliability of temporal diversification patterns (Louca & Pennell 2020). They showed that there could be an infinite class of congruent birth-death functions with similar likelihoods of fitting a phylogeny. Hence, besides the canonical diversification rates (CDR), we assessed and summarised the trends in pulled diversification rates (PDR) using two approaches.

Firstly, we fitted PDR models present in the *castor* package in R (Stilianos Louca 2017). Specifically, we used the *fit_hbd_pdr_on_grid()* with a NULL value for the age_grid parameter to find the likelihood, AIC and BIC of fitting a model where the birth-death rates have remained "time-independent" (Louca & Pennell 2020). Following this, we used the *fit_hbd_pdr_on_best_grid_size()* to assess the best number of time grids (between 1 to 5) that the evolutionary time (clade age) of a lineage can be split into, in each of which rates can vary linearly or exponentially (i.e. rates are piecewise time-dependent) (Louca & Pennell 2020). The AIC and BIC of this time-varying model were then compared with that of the time-independent model to assess the dynamicity in the diversification rates.

Secondly, we performed the CRABS ("Congruent Rate Analyses in Birth–-death Scenarios") test to account for the unreliability of the CoMET estimates for times of episodic rate shifts and the overall dynamicity of diversification rates (Höhna *et al.* 2022). We used the rate (i.e., canonical rate) through time estimates from the CoMET analysis for each lineage, specified alternate extinction rate functions through time, and computed the corresponding speciation rate functions to construct a set of congruent classes. These extinction rate functions were defined for each time bin, and they could remain constant or vary linearly, exponentially and sigmoidally with time (i.e., piecewise time or binned time). Additionally, different values were taken for the parameters (such as slope) that govern the rate of change in those functions to span a wide range of hypotheses. The temporal trends across the congruent classes were then visually assessed. Custom code for this test was written, modifying the relevant code from a recent study (Cyriac *et al.* 2024).

Results

Mode and tempo of species accumulation within each lineage

Tempo of diversification - The tempo of diversification across the 34 lineages was measured in terms of the mean speciation, extinction, and net diversification rates. We found a significant disparity in the diversification rates among the different taxonomic groups examined in our dataset ($p < 0.05$ for comparisons by the Wilcoxon test), where arthropods showed significantly low diversification rates, and plants had significantly higher diversification rates than other taxonomic groups ($p < 0.05$, Fig. 2.a.i, b.i, c.i). Within different habitat types, lineages distributed in the freshwater habitats (n=4) showed a slower pace of diversification than lineages in terrestrial habitats (n=30) ($p < 0.05$ - Fig. 2.a.ii, b.ii c.ii); however, diversification rates did not vary across terrestrial habitat types. Furthermore, the diversification rates were significantly lower among the Gondwanan than in Asian lineages ($p < 0.05$, Fig. 2.a.iii, b.iii, c.iii). Differences in speciation rates mainly contributed to disparities in net-diversification rates because extinction rates across groups are low (Fig. S3a, S3b).

Mode of diversification - Constant and time-varying models of canonical diversification rates (CDR) were fitted to all lineages. We found that 19 lineages supported the constant-rate birth (CB) model, which leads to gradual expansion (SC1), and 15 supported time-varying birth-death models that leads to diversification slowdowns (SC2) and Waxing and Waning (SC3) (Table 2;

Table S1, Fig. S4). These 19 lineages were spread across taxonomic groups, biogeographic origins and habitat types (Fig. S4). Among 15 lineages which supported time-varying birth-death models, 13 also showed episodic shifts in the diversification rates and two lineages (*Hemidactylus* lizards and *Pseudophilautus* frogs) showed saturated accumulation (SC2) without any episodic rate shifts. Among the 13 lineages with episodic rate shifts, one lineage showed slowdown (SC2), four lineages with waxed and waned (SC3), and eight lineages showed episodic rate shifts. Episodic rate shifts were inferred by CoMET and the symmetrical shift model in *RPANDA* in 9 and 8 lineages, respectively, out of which both methods concordantly inferred four (Fig. 3). However, none of the lineages favoured exponential accumulation (SC4). Parameter estimates of birth-death model-fitting (*RPANDA*) and CoMET analysis are provided in Table S3.

Pulled Diversification Rates (PDR) suggested temporal non-uniformity (best age grid size >= 2) of diversification rates in 9 lineages and constancy of rates through time in 13 lineages. The remaining 12 clades were depauperate, and PDR functions could not be successfully fitted (Table 2, Table S1). We also performed the CRABS test to assess the trends of congruent classes across the evolutionary time of each lineage. We found a high prevalence of constancy in rates through time for 14 lineages, conclusive recent rate shifts in 16 lineages, and a decreasing trend in multiple time bins in one lineage (*Pseudophilautus*). The remaining three clades showed ambiguous trends across congruence classes across their evolutionary times (Table 2, Table S1).

Abiotic and biotic drivers of diversification patterns

There was no association between the diversification scenarios and taxonomic groups, habitat types or biogeographic origins (Fig. 3, 5; Fig. S4), except in molluscs, where all three lineages supported the gradual accumulation scenario (SC1). The time-varying diversification rates were primarily associated with paleo-temperature and existing diversity through time (Table 2; Table S1 and S4; Fig. 3, 5). Of 15 lineages that supported time-varying models and/or shifts over constant rates, 10 showed temperature dependence (TD). Among these 10 TD lineages, three lineages equally supported (ΔAICc ≤ 2) diversity-dependence (DD) (Fig. 3; Table 2, S1, S4). Furthermore, two of these lineages supported Himalayan-orogeny-dependence, and none supported C4-plant-expansion-dependence (Fig. 3, Table S4).

Diversification rate shifts were inferred for 13 lineages, and 12 of them were found to occur in Neogene, as shown in Fig. 3. Also, nine lineages among the 12 lineages above showed diversification rate shifts within the geological period that experienced a mid-Miocene intensification of aridification, and monsoons and expansion of C4-plants in PIP. Four lineages showed rate shifts younger than 3 Mya, and two showed rate shifts in the late Neogene. Sharp declines in global temperatures from around 2 Mya to the present are concurrent with these recent rate shifts in these lineages, all of which are also declines in diversification rates (Fig. 3, 4).

In the FAMD analysis, the first two dimensions explained ~37% (Fig. 5 - Axis 1: 17.9%, Axis 2: 18.9%) of the total variation (Fig 5). Majorly, diversification scenarios, species richness, temperature-dependence and diversity-dependence contributed to dimension one and biogeographic origins, taxonomic groups and clade ages contributed to dimension two (Fig S7a). Additionally, species richness and net diversification rates were associated. However, clade ages did not show strong relationship with species richness (Fig. 5, Fig. S7b).

Boxplots and the Wilcoxon test reconfirmed the association between TD, DD, species richness and net diversification as the lineages showing Temperature-dependent and Diversity-dependent diversification had significantly higher species richness and net-diversification rates (Fig. S7c). Additionally, among diversification scenarios, gradual accumulation favoured lower species richness and net-diversification rates (Fig. S7c), reconfirming the association between scenarios, species richness and net-diversification rates, as indicated by the FAMD.

Convex hulls around clusters of diversification scenarios illustrating time-varying diversification were predominantly concordant with temperature- and diversity-dependence. Also, clusters of lineages of different biogeographic origins showed minimal overlap in the multidimensional space. Additionally, all arthropod (n=5) and mollusc (n=3) lineages were found to form distinct clusters, with no overlap with clusters composed of amphibians, reptiles and plants (Fig. 5b). *P-values* of PERMANOVA tests, indicating the significance of overlaps between clusters on each categorical variable, have been provided in Table S5.

Discussion

Understanding the tempo and mode of diversification and its consequences for tropical biodiversity remains a key challenge as different clades and regions exemplify distinct patterns and processes. Our meta-analyses demonstrate that regional-level biogeographic and climatic processes, phylogenetic history, species traits, and contemporary habitat heterogeneity shaped the diversification of the endemic biota in PIP.

Disparities in the tempo of diversification in PIP biota: The taxonomic, biogeographic, and habitat affinities have driven disparities in diversification rates among PI biota. The taxonomic identity, a proxy for clade-specific traits, such as range size, dispersal abilities, and ecological niches, is thought to influence net diversification rates (Scholl & Wiens 2016). As predicted, angiosperms (flowering plants) had the highest diversification rates, which could be because they typically have larger clade-level range sizes (Hernández-Hernández *et al.* 2021), polyploidy (Heslop-Harrison *et al.* 2023) and higher dispersal ability (Suárez *et al.* 2022). It means that angiosperms can occupy a wide range of ecological niches and are more likely to colonise new areas, promoting their diversification. In contrast, centipedes and scorpions had the lowest net diversification rates (Fig. 2). These soil arthropods are among the top predators in soil ecosystems and tend to show specialisation for ecological niches, i.e., being both fossorial (burrowing) and predators may limit their opportunities for speciation. They also have relatively low dispersal abilities (Bharti *et al.* 2023; Joshi *et al.* 2020; Loria & Prendini 2020), which could further restrict their ability to colonise new areas and diversify (Wiens 2004). Shieldtails, another group of burrowing predators, have been shown to have similar patterns (Cyriac & Kodandaramaiah 2018).

Peninsular Indian biota has lineages with an ancient Gondwanan or young Asian biogeographic affinity, which have undergone in-situ speciation (Karanth 2021). This offered us a unique opportunity to explore the role of distinct biogeographic affinities in diversification rates. As mentioned, Gondwanan lineages show a high degree of ecological specialisation and retention of their ancestral niches through niche conservatism. For example, many of the lineages occur only in wet forests and are fossorial, e.g., soil arthropods, blind snakes and caecilians, and preference for freshwater habitat by molluscs . Additionally, many Gondwanan lineages show

less dispersal and more vicariance-mediated diversification than Asian lineages. Therefore, ecological specialisations and biogeographic processes may limit diversification rates, leading to lower diversification rates among Gondwanan lineages (Cyriac & Kodandaramaiah 2018; Da Silva *et al.* 2020; Wiens 2004).

On the other hand, many Asian lineages occupy diverse ecological and climatic niches, contributing to higher diversification rates. For example, lizards (e.g. - *Hemidactylus*, *Geckoella*, *Ophisops*) occupy wet and dry forests and multiple niches like rocky outcrops, forest floor and leaf litter, and arboreal. However, the preference for forest type, distinct in their climatic conditions, didn't influence the diversification rates (Fig. 2) (Karanth 2003; Mani 1974). The freshwater lineages (n=4) showed significantly lower diversification rates than terrestrial lineages. Hence, we speculate that species traits could have influenced the diversification rate more than habitat preference. However, a larger sample size is required to strengthen this claim.

It is important to note that speciation rates majorly drove the diversification in PIP lineages, as extinction rates remained low across lineages (Fig. S3b). Most of these lineages have diversified in the Cenozoic, post-Deccan Volcanism, which led to massive extinctions. Hence, the signature of extinction may not have been captured in the current analyses. Also, low extinctions could be statistical artefacts of the employed methods owing to the fewer tips in the phylogenies. Old relictual fauna with high diversity, like millipedes, would be appropriate to check signatures of clade-wide mass extinctions. Furthermore, old Gondwanan clades distributed throughout Asia (e.g. Dipterocarpeceae) can be better candidates to capture such signatures of high extinction (Bansal *et al.* 2022).

Climatic stability, paleotemperature, and ecological limits: More than half of the lineages (approximately 56%) supported the constant-rate pure-birth model, indicating a gradual accumulation of diversity over time. This gradual increase in diversity is attributed to the stable climate in regions of diversity expansion (Couvreur *et al.* 2011; Derryberry *et al.* 2011; Meseguer *et al.* 2022), especially in tropical biomes like the tropical forests of peninsular India. This is an intriguing pattern given that the PIP has experienced significant climatic changes throughout the Cenozoic era, going from perhumid to seasonal wet, monsoon intensification and aridification,

during which diversity has accumulated (Bansal *et al.* 2022; Chatterjee *et al.* 2013; Morley 2018). Therefore, we suspect some regions in peninsular India may have served as refugia like it was indicated in the biogeographic studies that SWG was refugia during volcanic activity in the Cretaceous and later in the mid-Miocene (Joshi & Karanth 2013; Prasad *et al.* 2009). Future studies should conduct spatially explicit diversification analyses to examine how diversification rates vary across space in peninsular India. Like PIP, 50–67% of endemic plant and tetrapod lineages in the Neotropics supported gradual diversity expansions (Meseguer *et al.* 2022). This suggests that stable climate refugia supporting diversity accumulation is not unique to peninsular India but may have global relevance in tropical regions. A focus on identifying and characterising these past climatic refugia across tropical landscapes and understanding their potential to sustain tropical diversity in changing climates would be helpful across tropical regions.

Alternately, the constant rates of diversity accumulation among PIP lineages also suggest that the habitat/ecosystem could have been stable. The forests in PIP, home to endemic lineages, are majorly constituted by angiosperm lineages that have not been stable, as indicated by pollen fossil records (Bansal *et al.* 2022; Prasad *et al.* 2009). Specifically, the angiosperm fossil record suggests the presence of diverse Gondwanan flora in PIP until at least the late Paleocene, which now has extant relatives in Southeast Asia and therefore, PIP is referred to as an "evolutionary graveyard" (Bacon *et al.* 2022; Bansal *et al.* 2022; Prasad *et al.* 2009; Wheeler *et al.* 2017). Both extinct Gondwanan and current Asian floral lineages occupy similar climatic niches, where the current flora in PIP is a result of the dispersal events from SEA rather than the retention of Gondwanan relics (Klaus *et al.* 2016). Therefore, a rapid turnover of the forest ecosystems where ecologically similar species of Asian origins replace Gondwanan lineages could have provided habitat stability, indicating that realised habitats of the lineages have been stable despite the landscape not being stable. A recent global study on angiosperms also inferred the prevalence of rapid turnover at lower taxonomic levels following high extinctions (i.e. similar species took over the niches of extinct species very rapidly) during the Cretaceous-Paleogene (K-Pg), using both paleobotanical records and molecular-phylogeny-based diversification analyses (Thompson & Ramírez-Barahona 2023).

On the other hand, lineages with time-varying diversification rates show a complex interplay between climatic events, episodic rate shifts, and species traits. The Neogene period, especially during the mid-Miocene, witnessed intensified aridification and seasonality in the Indian subcontinent, which is believed to have significantly impacted diversification, particularly among lizards (Agarwal & Ramakrishnan 2017; Deepak & Karanth 2018). While previous studies suggested a connection between climatic events and diversification, a robust statistical framework to test these hypotheses was limited. Of the 14 lineages with episodic rate shifts, 12 occurred during the Neogene (23–2.6 Mya), and three occurred more recently, younger than 3 Mya. These shifts involve an overall decline in diversification rates due to ecological limits or symmetrical episodic shifts (SES), indicating alternating periods of increased and decreased diversification. Nine of these lineages showed rate shifts that consistently overlapped with the temporal range climatic events, suggesting a potential link between climatic changes and diversification in these lineages. We also reported strict declines in diversification rates in four lineages, which appear to be concurrent with drastic declines in global temperatures during the late Neogene and throughout the Quaternary (Fig. 3, 4).

Another important diversification pattern observed among multiple taxa globally and in tropical regions is the slowdowns in diversification rates . A global study assessing the drivers of slowdowns inferred the role of diversity-dependence (or ecological limits) and declining global paleotemperature (Condamine *et al.* 2019; Moen & Morlon 2014). In PIP, diversification slowdown and diversity dependence were observed in *Hemidactylus* geckos. Additionally, we found slowdowns in two more lineages of scorpions (Heterometrinae) and bush frogs (*Pseudophilautus*). These patterns were also linked to diversity dependence and temperature dependence, suggesting that changes in species diversity and temperature fluctuations play an important role in diversification rates. In four lineages, waxing and waning (diversity declines) were detected and influenced by temperature fluctuations, and only two of these lineages showed equal support for diversity dependence. Again, variation in speciation rates contributed to diversity declines in these lineages, except in one where the extinction rate was relatively high (*Ophisops*) (Fig. S3b, Table S1).

Mid-Miocene intensification of aridification and monsoons have also been hypothesised to drive exponential species accumulation in PIP (SC4 - Fig. 1, S1) (Agarwal & Ramakrishnan 2017;

Deepak & Karanth 2018). However, none of the lineages in our dataset supported a recent rise or exponential accumulation. Also, the role of Himalayan orogeny and the expansion of C4 plants in explaining diversification among PIP biota remained limited. Only a few lineages depended on these factors, and their influence may have been episodic and inconsistent throughout lineage history. Hence, derivative curves of these factors, highlighting periods of instability, can be utilised to check the dependence on diversification. Other factors, such as paleo-temperature, could have played a more significant role in diversification. Analytical methods to determine the dependence of diversification in specific time intervals (piecewise dependence) on factors like paleo-climate and existing diversity can be useful in these scenarios.

Understanding diversification in tropical areas: limitations and the way forward

There has been tremendous growth in methods that allow to infer the diversification tempo and mode using time-calibrated phylogenies (Helmstetter *et al.* 2023; Martínez-Gómez *et al.* 2024; May *et al.* 2016; Morlon *et al.* 2010). However, one of the limiting factors to applying these across taxa and regions has been the requirement of large datasets, where the number of tips analysed in each lineage should be high. Many clades studied in our study and other areas are inherently species-poor. To overcome this, we used birth-death models implemented in different frameworks like homogeneous birth-death models of specific mathematical constructs in *RPANDA*, and episodically varying models in CoMET, and we used mean branch rates inferred from the ClaDS model that estimates lineage-specific diversification rates. After performing a meticulous review to verify the sampling of the species in each clade, we assigned a sampling fraction of 1 to all the analyses across all lineages. However, with the ever-increasing usage of integrative taxonomy, more species are being described, and species boundaries are being redefined (Joshi & Agarwal 2021). Thus, we acknowledge that a sampling fraction of 1 might contribute to erroneous assessments in diversification models, especially in slowdowns when incompletely sampled taxa. Hence, we could use precise sampling fractions for each lineage in future studies. Nevertheless, simulations through our parameter estimates were able to recover the branching patterns and the number of tips of the empirical phylogenies (Fig. S9).

Our dataset comprising 633 endemic peninsular Indian species is strongly biassed towards small vertebrates (~70 %), and birds, freshwater biota and soil arthropods are among the most

underrepresented groups. However, it is worth noting that the endemicity among birds (~5%) and mammals (~15%) itself is low in peninsular India (IUCN maps) as compared to the soil arthropods (~ 90%), small vertebrates (~ 52% - amphibians and reptiles) and flowering plants (~ 26%) (Bharti *et al.* 2021; International Union for Conservation of Nature (IUCN) 2022; Loria & Prendini 2020). This could be because bird and mammal assemblages in PIP are mainly dispersal-driven and haven't undergone in-situ speciation. Therefore, focusing on herpetofauna, arthropods, and plants will be more insightful in understanding the drivers of diversification processes in landscapes like PIP.

Furthermore, speciation rates drove diversification rates among peninsular Indian taxa, as extinction rates remained low across peninsular Indian lineages. Given the current peninsular India biota primarily comprises groups which have evolved post the K/T mass extinction event (ca. 66 Mya), we do not find the signature of extinctions in our dataset (Keller *et al.* 2009; Prasad *et al.* 2009). The current diversity estimates could also be underestimated for soil arthropods, herpetofauna and freshwater biota, as many new species are still being described (Joshi & Agarwal 2021). Also, many studies have explicitly focused on the Western Ghats, the known biodiversity hotspots, and other regions of peninsular India, including the savanna, which remains unexplored and understudied. Even in global datasets, soil and freshwater habitats are poorly represented, urging us to focus on unexplored taxa and habitats for a holistic understanding of the tempo and mode of diversification across tropical forests. Additionally, phylogenetic reconstructions using more sophisticated tree priors like the fossilised birth-death (FBD) may influence the estimates for the diversification dynamics and need to be integrated into future studies.

We show that diversification in Peninsular India has a signature of historical ecosystem stability, paleotemperature, Miocene aridification and intensification, and existing diversity, the known global drivers of diversification. The complex tempo and mode of diversification shown in our results suggest that regional biogeographic, geoclimatic and phylogenetic history are critical to understanding the origins of tropical diversity and need to be examined across tropical regions. Furthermore, exploring spatially structured and trait-based cladogenesis among endemic lineages, using heterogeneous birth-death models and SSE models, could shed light on the bioregionalisation within PIP and other biomes (Helmstetter *et al.* 2023; Martínez-Gómez *et al.*

2024). Studies like this, where multi-taxa comparisons are carried out from different tropical areas, are critical for gaining insights into the evolution of biodiversity in a tropical biome and predicting how these groups may respond to changing climatic conditions.

Box 2 - What explains the species richness in PIP endemic biota?

Species richness patterns are arguably influenced by the inherent diversification rates (intrinsic tempo) and the age (temporal scope) of clades. These drivers of species richness are non-exclusive and have been debated for the last two decades across the globe, particularly for the tropical biome, which is old and diverse (Hedges *et al.* 2015; McPeek & Brown 2007; Rabosky *et al.* 2012; Scholl & Wiens 2016). The clade-age hypothesis suggests that older clades would be more species-rich, owing to their longer evolutionary time for speciation. Alternatively, the diversification-rate hypothesis suggests that clades with faster diversification rates can result in being more speciose, irrespective of their clade ages. Owing to the remarkable disparities in the clade ages and the species richness of endemic PIP lineages, we found it imperative to test the influence of both these factors on the current species richness of these endemic clades. We performed pairwise PGLS in all combinations among clade age, species richness, and net-diversification rate for all the lineages to test the relative roles of the predictors (check the details in figure captions of Fig. S8). Species richness and net-diversification rates were significantly associated across lineages and biogeographic and habitat affinities (Fig. 6c, S8b, S8c). The strong relationship between the diversification rates and species richness has been suggested in clade-specific studies (e.g., plant family Annonaceae) as well as across the Tree of Life (Scholl & Wiens 2016; Xue *et al.* 2020).

Older lineages, persisting in a region for long, are expected to have limited ecological niches to diversify further. In peninsular India, old lineages of Gondwanan origins are expected to show diversity-dependent diversification. However, only six out of 34 lineages showed strong evidence for diversity-dependence, of which only three had Gondwanan (total n=13) affinity, indicating that other factors are also at play in shaping diversification patterns. Interestingly, a negative relationship was observed between net diversification rates and clade ages across lineages with a high phylogenetic signal (Fig. 5.c, S8b, S8c). Phylogenetic niche conservatism (PNC) could explain low diversification rates among older lineages of Gondwanan affinity

compared to the younger Asian clades. In PIP, young (geckos, frogs and plants) and old (centipedes and scorpions) lineages share biogeographic and ecological similarities in terms of climatic niche, range, dispersal ability, and trophic levels. Ecology and evolutionary history of biota are strongly tied in peninsular India, which may pose ecological constraints on diversification, contributing to disparities in diversification rates. It is also likely that the biomes and ranges that comprise the old lineages constitute museums of biodiversity, whereas the ones composed of young lineages constitute cradles of biodiversity. A recent study on endemic woody plants suggests that the Western Ghats is both a museum and a cradle of diversity (Gopal *et al.* 2023). Given many endemic lineages (e.g. - centipedes, scorpions, geckos) found in the WG are not restricted to the biodiversity hotspot but have pan-PIP distributions, the entirety of PIP may potentially be a museum and a cradle of biodiversity. The old lineages studied here follow the museum model, with low diversification rates, longer persistence times and constant diversification. In contrast, younger lineages show characteristics of the cradle model of more dynamic and higher diversification rates. This could explain the negative relationship between diversification rates and clade ages (Fig. 6c, S7b, S8b). It would be worth exploring this further to validate this relationship with more lineages with distinct ages, richness patterns and ecologies across tropical regions.

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Figures and Tables

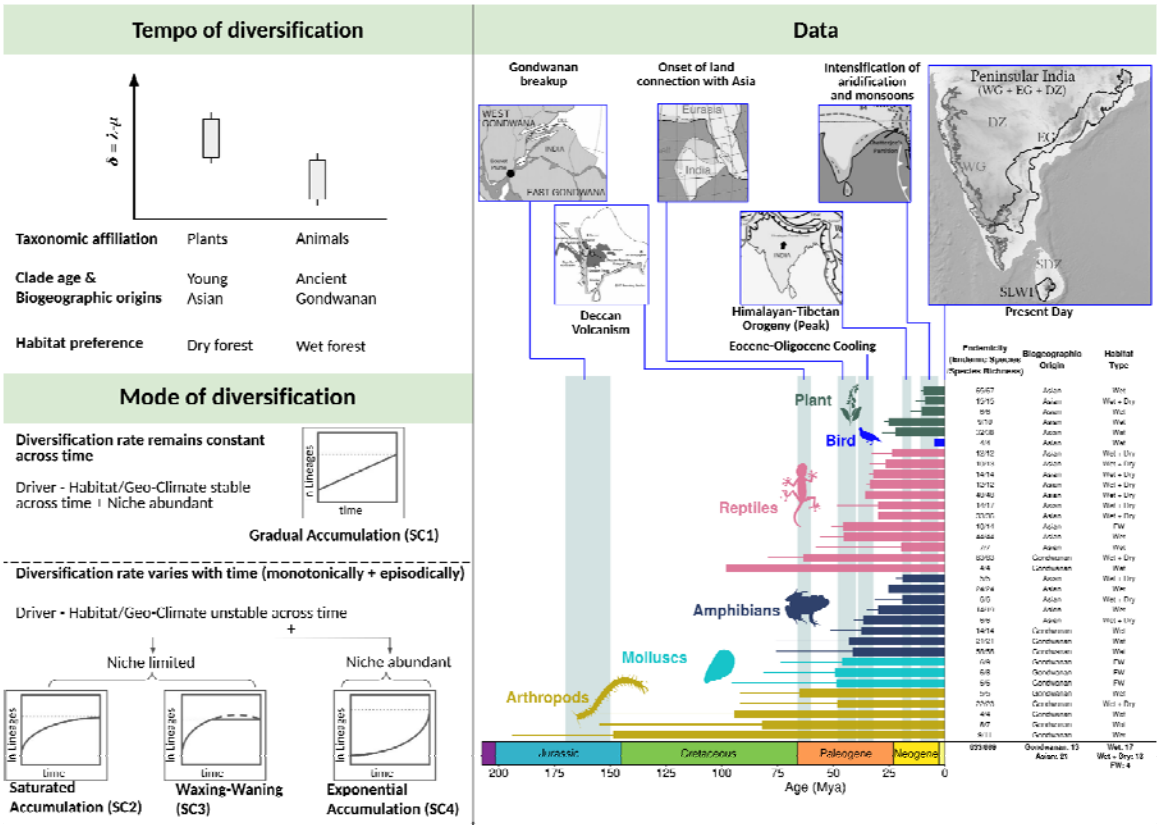

Fig. 1. Predictions for the tempo and mode of diversification and the data used in the study. (Left panel) Mean diversification rates (i.e. tempo) of PIP lineages can be influenced by taxonomic affiliations, clade age, biogeographic origins and habitat preference. A cartoon box plot representation illustrating the disparities in the tempo with various predictors has been illustrated (see Box 1 for details). The mode of diversification in PIP lineages can follow multiple scenarios, and the broad patterns are illustrated here. These patterns/scenarios of diversity accumulation can result from various combinations of speciation and extinction rate dynamics (see Fig S1 for details). (Right panel) Our dataset comprises 34 endemic lineages from peninsular India. They are of varying clade ages, number of species, endemicity, biogeographic, and habitat affinities, and these disparities are illustrated here. Key geological events (Table 1) are highlighted by grey vertical bars. Maps used in the figure have been extracted and edited from multiple studies, and the map for the present day has been generated using QGIS (Ali & Aitchison 2008; Chatterjee *et al.* 2013; Morley 2018).

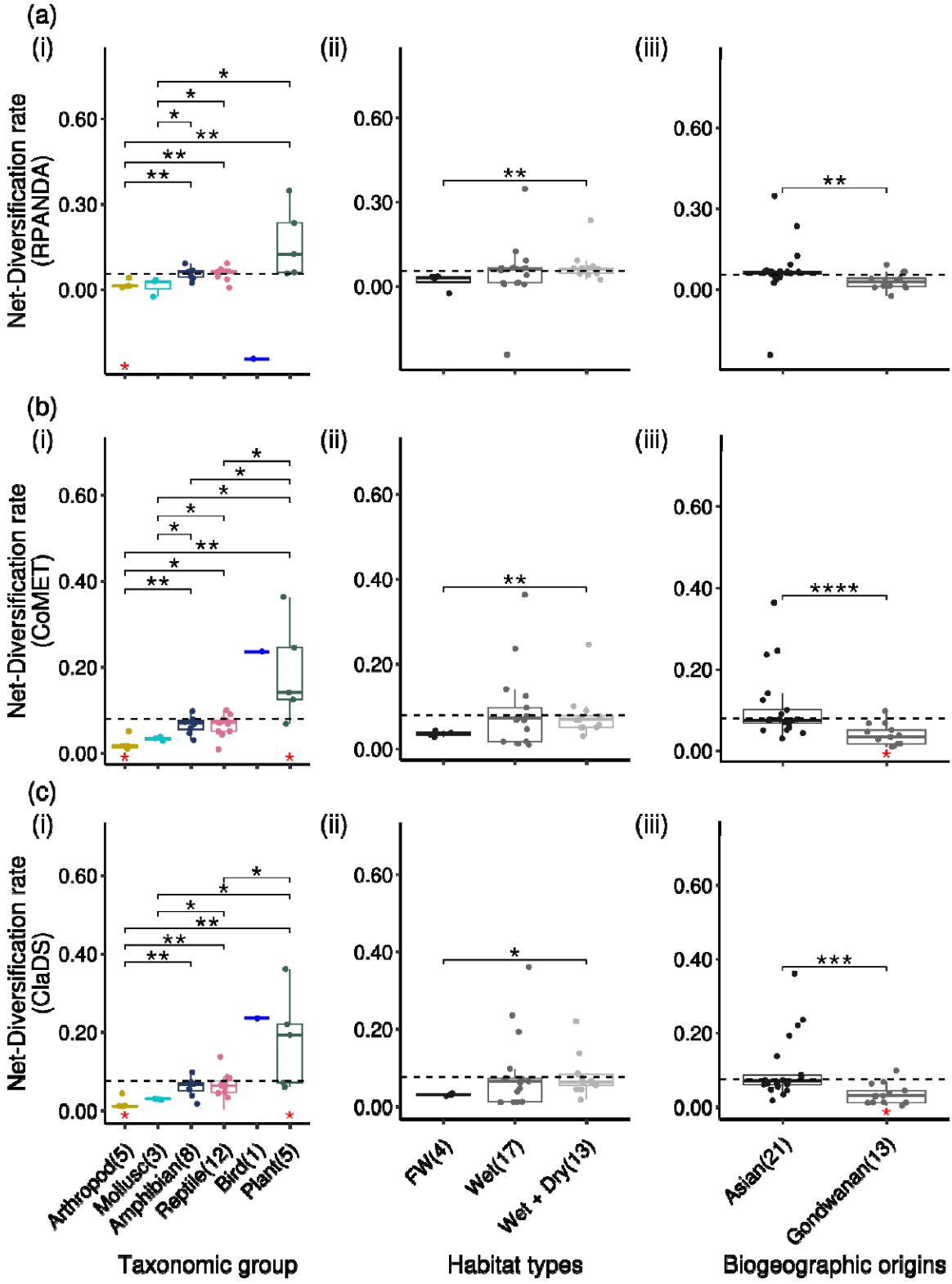

Fig. 2. The tempo of diversification. The tempo of diversification was measured in three approaches - (a) by model fitting in RPANDA, and (b) by taking the mean rates through time estimated in the CoMET

analysis and (c) by using the ClaDS model. Boxplots in the figure represent the disparities in the tempo of diversification across taxonomic groups (a.i, b.i, c.i), habitat types (a.ii, b.ii, c.ii) and biogeographic affinities (a.iii, b.iii, c.iii). Black asterisks on top of the boxplots indicate statistical significance in comparisons (* - $p < 0.05$, ** - $p < 0.01$, non-significant comparisons haven't been highlighted), and numbers in the x-axis labels indicate sample size within each category. The dotted line indicates the overall mean rate of speciation or extinction, and the red asterisks at the top indicate that the rates of the corresponding categories are significantly different from the overall mean.

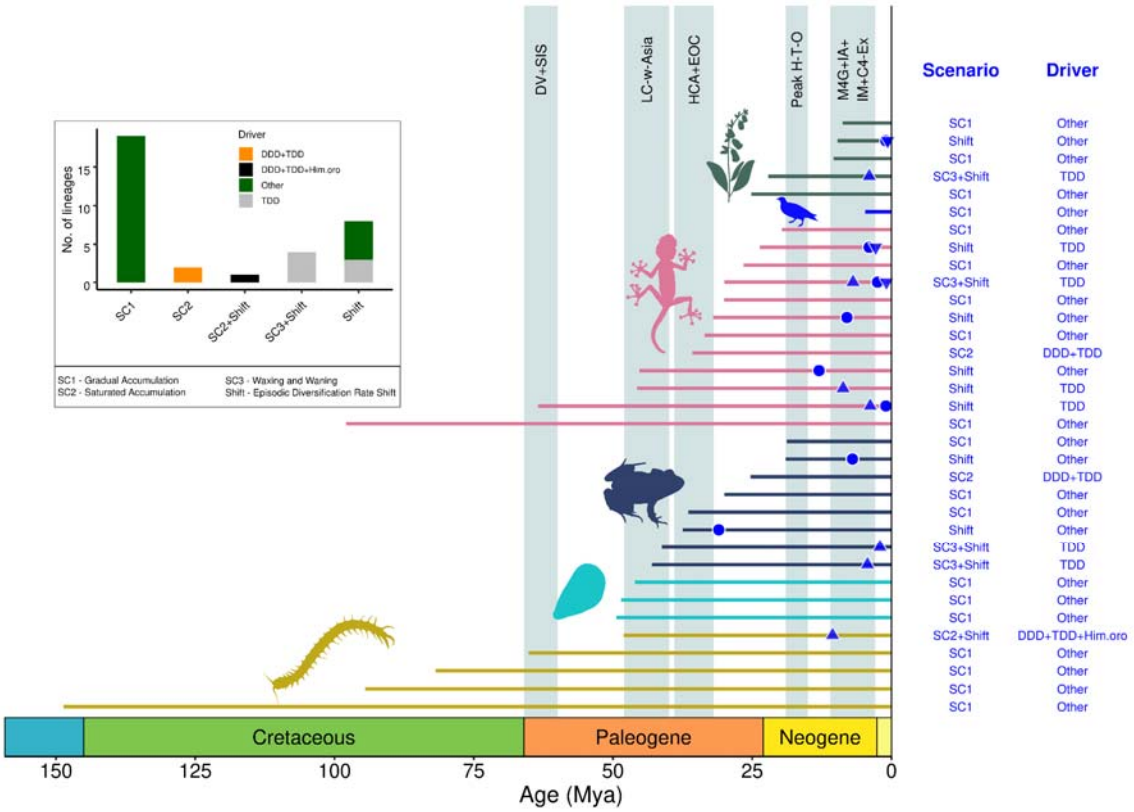

Fig. 3. Diversification patterns and drivers. Horizontal bar plots indicate clade-ages (crown ages) of 34 lineages, circles indicate symmetrical rate shifts, triangles represent one-way episodic rate shifts, and their positions indicate their time of occurrence. Multiple opposing one-way rate shifts (sudden increase followed by a sudden decrease or sudden decrease followed by sudden increase) within a lineage, inferred by the CoMET analysis, are indicated by multiple oppositely faced triangles. Text in blue indicates the diversification scenario favoured by a lineage, followed by the prevalence of temperature (TDD) and/or diversity-dependence (DDD) in the lineage. Key geological events (Table 1) are highlighted by grey vertical bars. **(inset)** Vertical Bar plot indicates the prevalence of different diversification scenarios in PIP lineages, SC1 - gradual accumulation, SC2 - slowdowns, SC3 - Waxing and Waning and Episodic Rate Shifts and the drivers.

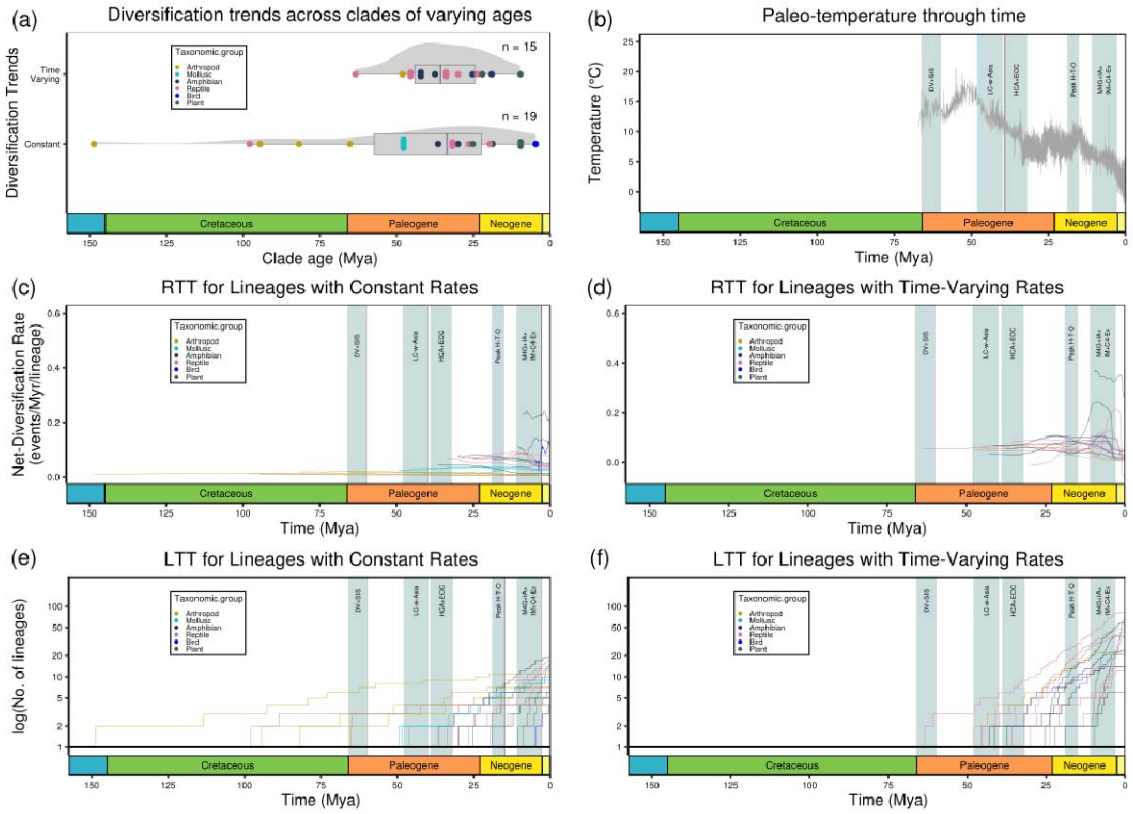

Fig 4. Paleotemperature, diversification trends, rates and diversity through time. (a) PIP biota show idiosyncratic patterns of diversification where 19 lineages show diversification with constant rates of speciation and extinction, and 15 lineages show time-varying rates of speciation and extinction. The patterns do not vary with the age of the lineages. (b) Paleotemperature since the Cretaceous has been relevant to diversification in Peninsular Indian biota, and 10 out of 15 lineages with time-varying diversification rates show strong support for dependence on paleotemperature. (c, d) Canonical Diversification Rates calculated in the CoMET analysis have been plotted through time to visualise the diversification dynamics. (e, f) As a consequence of these dynamics, lineages have accumulated diversity in varying patterns and the empirical LTT (Lineage through time) curve from their respective phylogenies has been plotted to visualise diversity accumulation profiles.

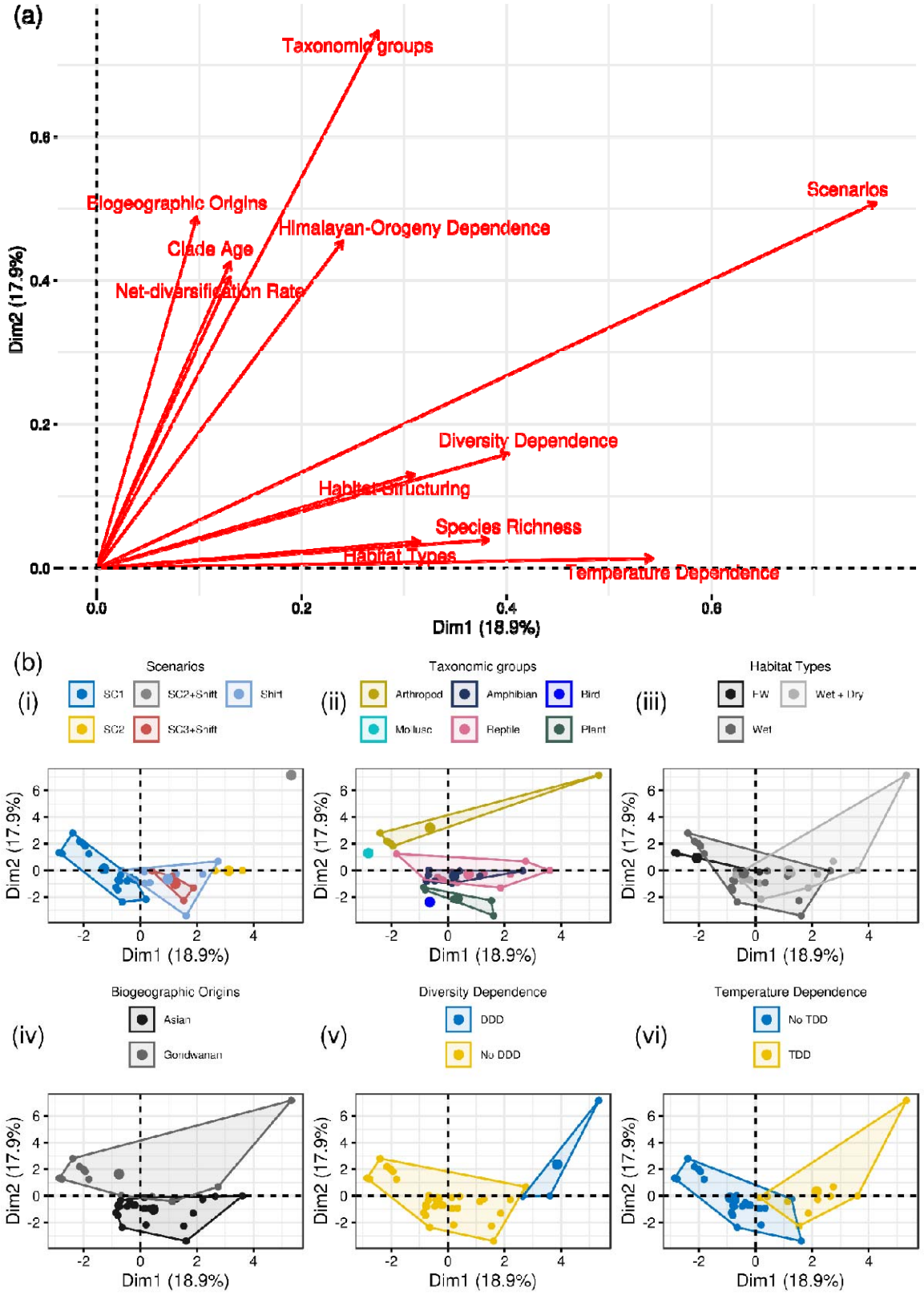
(a)
Taxonomic groups
Scenarios
Biogeographic Origins
Himalayan-Orogeny Dependence
Clade Age
Net-diversification Rate
Diversity Dependence
Habitat Structuring
Species Richness
Habitat Types
Temperature Dependence
Dim2 (17.9%)
Dim1 (18.9%)
(b)
(i)
Scenarios
SC1
SC2+Shift
Shift
SC2
SC3+Shift
(ii)
Taxonomic groups
Arthropod
Amphibian
Bird
Mollusc
Reptile
Plant
(iii)
Habitat Types
FW
Wet + Dry
Wet
(iv)
Biogeographic Origins
Asian
Gondwanan
(v)
Diversity Dependence
DDD
No DDD
(vi)
Temperature Dependence
No TDD
TDD

Fig. 5. Factor Analysis of Mixed Data ordination plots made using 13 relevant ecological and evolutionary parameters for 34 lineages. a) The first two dimensions of the ordination analysis explain that the variables positioned in the space represent their relative contribution to the relevant axes. The positions of the variables relative to each other represent the strength of their associations. Dimension 1 is majorly explained by variables relevant to lineage identity (Taxonomic group, Biogeographic Origin and Clade age) and Dimension 2 is majorly explained by diversification and diversity dynamics (Species richness, Diversification Scenarios, etc.), **b)** Each panel represents a categorical variable, and the clusters within them represent the categories. Clusters relevant to diversification scenarios are largely congruent with diversity-dependence and temperature-dependence. Check SI Table 5 for information relevant to PERMANOVA tests for inferring significantly distinct clusters within each categorical variable.

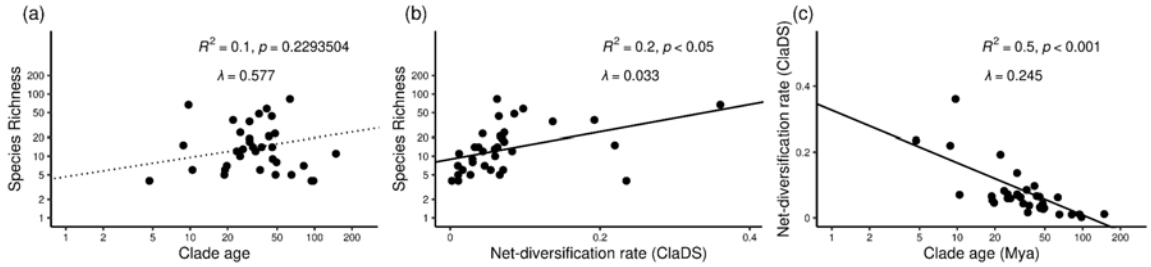

Fig. 6. Drivers of species richness. Phylogenetically corrected linear regression analysis of species richness (log-transformed) versus clade-age (log-transformed) and diversification-rates (n=34 for all three plots). Each point is relevant to one lineage, R^2 values indicate the goodness of fit of the regression lines, *p*-value indicates the significance of the regression, and λ indicates the degree of phylogenetic non-independence of the correlation (i.e. the phylogenetic signal in the correlation). Solid and dotted lines indicate statistically significant and non-significant linear models (significance level - $p < 0.05$), respectively.

Table 1: Major geoclimatic events relevant to peninsular India and their estimated periods of occurrence (Ali & Aitchison 2008; Chatterjee *et al.* 2013; Ding *et al.* 2017; Morley 2018)

Geological event	**Code used in further analysis**	**Period of occurrence (Mya)**
Gondwanan split (GS)	"GS"	Between 170 and 150
Deccan volcanism and Seychelles-India separation	"DV+SIS"	Between 67 and 60
Transient land connection with Southeast Asia	"LC-w-SEA"	Between 48 and 40
Hard collision with Asia and Eocene-Oligocene cooling	"HCA+EOC"	Between 39 and 32
Peak Himalayan-Tibetan Orogeny	"Peak H-T-O"	Between 19 and 15
Mi-2 glaciation, Intensified aridification, Intensification of monsoons, Expansion of C4 plants	"M4G+IA+IM+C4-Ex"	Between 11 and 3 (overlapping ranges of events, hence clubbed together)

Table 2. Patterns and drivers of diversification. Numbers indicate the number of lineages favouring each canonical diversification scenario, pulled diversification trends and diversification-dependence on paleo-temperature, existing diversity, Himalayan orogeny and expansion of C4-plants.

Diversification Trends	Trends in CDR (*RPANDA* and CoMET)	No. of lineages (CDR)	Temperature-Dependence on CDR	Diversity-Dependence on CDR	Himalayan-Orogeny-Dependence on CDR	Trends in PDR	No. of lineages (PDR)	Trends in CRABS	No. of lineages (CRABS)
Constant rates	Gradual Accumulation (SC1)	19	0	0	0	Constant rates	13	Constant rates throughout	14
Time-Varying	Saturated accumulation (SC2)	2	2	2	0	Rates not constant	9	Rate shift in recent time; constant in the past	9
	Saturated accumulation + Episodic rate Shift (SC2+Shift)	1	1	1	1			Rate shift(s) in recent time; ambiguous in the past	7
	Waxing-waning + Episodic rate Shift (SC3+Shift)	4	4	2	0			Decreasing-rate trend in multiple time bins	1
	Only Episodic rate Shift (Shift)	8	3	0	0				
Ambiguous	-	-	-	-	-	Ambiguous	12	Ambiguous throughout	3