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Accounting for extinction dynamics unifies the geological and biological histories of southeast Asia

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Abstract

Biogeographical reconstructions of Southeast Asia (SEA) have suggested recent spread across the Sunda and Sahul shelves of lineages with diverse origins. This is complementary with the geological scenario of recent tectonic uplift in the region. However, this story is challenged by new geological evidence suggesting that the Sunda shelf was never submerged prior to the Pliocene so that the recent uplift did not occur. Such mismatch between geological and biogeographical data may occur if previous biogeographic reconstructions when dynamics of extinct lineages are ignored. Here, we incorporate the modelling extinct lineages in reconstructing the historical biogeography of multiple SEA lineages previously used to infer the recent-uplift scenario. In contrast to their previous biogeographic reconstructions, we find that all of these clades, from plants to vertebrates, have a common and widespread geographic origin, and each has spread and colonized the entire region much earlier than previously thought. Our results describe how SEA biodiversity develops in deep time via sustained diversification and spread, which updates and unifies the geological and biological histories of SEA. Furthermore, we discuss that older biogeographical reconstructions may have biased our understanding of the geological processes impacting rates of diversification and connectivity across the globe.

Introduction

The surface of our planet has been greatly altered over time which has impacted the diversity of life at the highest level: many species are created and go extinct at the tempo of major geological events. Our ability to reconstruct the history of our planet is therefore only possible with the synergic view of geology and biogeography. A prime example of this is Southeast Asia (SEA) because its striking biodiversity that can only be understood by its geological dynamism (Carter et al., 2001; Zahirovic et al., 2014). The modelled geological history of SEA has critically influenced the biogeographic modelling of diverse clades (ranging from plants to vertebrates) and vice versa. However, new geological evidence has created a mismatch between biogeographic patterns and the connectivity of the landmasses in the region. Here, we aim to resolve this discrepancy by incorporating a key evolutionary process, species extinction, into biogeographic reconstructions.

The spatial configuration of islands and continental landmasses across SEA has changed considerably over geological timescales. There is a long-standing paradigm proposing that mainland Asia and Australasia were totally disconnected (at least) from 60 Ma (Lohman et al., 2011) to 10 Ma, when the appearance of the islands now forming the Indonesian archipelago and Wallacea region (Sumatra, Java, Borneo, Sulawesi, New Guinea and Philippines) could have served as stepping-stones for the dispersal of some clades. This geological hypothesis was supported by evolutionary studies conducted using modern geographic distributions and phylogenetic trees of extant species, which found constrained dispersal in ancient lineages across SEA, due to an extensive period of island non-connectivity. Both animal (Dong et al., 2018) and plant (Nauheimer et al., 2012; Williams et al., 2017) lineages arose as early as 40 Ma and according to those biogeographic reconstructions, they remained on the Sunda or Sahul continental shelves as small, low-diversity clades for over 20 Myr before dispersing elsewhere. Other taxonomic groups are documented to have originated in the Indochina peninsula, with a further dispersal eastward to colonize New Guinea (Atkins et al., 2020; Grudinski et al., 2014), whereas, the Philippines are thought to have been colonised relatively recently (Thomas et al., 2012). Other clades seem to have originated in the eastern part of the region followed by subsequent colonization events towards continental Asia (Bocek & Bocak, 2019). These spatial differences in origin and delayed colonization routes might reflect the composition of biotas in biogeographic provinces (e.g., the Sunda and Sahul provinces; Lohman et al., 2011) along with evolutionary dynamics at regional scales. Consistent with the idea of limited dispersal across the archipelago, widespread species are likely to form new species that become endemic to individual islands, the fundamental role of this mechanism is reflected in high rates of vicariance (i.e., geographically mediated speciation). Under this view, dispersal facilitation by the late appearance of island steppingstones is common to the biogeographical reconstructions of all the lineages.

Many studies have applied standard biogeographic reconstruction methods and weaved biogeographical hypotheses consistent with this geological hypothesis. However, this understanding of the geological history of SEA has recently been challenged by geomorphological evidence pointing to the presence of ancient land bridges between mainland Asia and the Indonesian islands (Husson et al., 2020; Salles et al., 2021; Sarr et al., 2019). For instance, Sundaland (i.e., western part of

the archipelago) was permanently continental at least until 6 Ma (Husson et al., 2020), which predates the previous hypothesis for the onset of regional connectivity by tens of million years (Hall, 2013). This radical change in understanding of regional geological history may require us to reconsider the evolutionary dynamics that gave rise to the contemporary biota. Clades that evolved during the period when land bridges connected the major SEA landmasses would have similar evolutionary histories and provide little evidence for ancient dispersal-limitation in driving contemporary patterns. This hypothesis conflicts with the patterns seen in current reconstructions of biogeography for the region (Atkins et al., 2020; Dong et al., 2018; Su & Saunders, 2009). There is thus a mismatch between our best current geological understanding and our best current biological understanding of the region's history.

One potential explanation for this disparity between geological and biological histories is that inferring the true biogeographic histories of clades is complicated by unrecorded species extinctions. Extinction inevitably removes the evidence of geographic distributions of extinct species in reconstructed phylogenetic trees. Studies based on methods of biogeographic reconstruction that do not account for extinctions are incomplete and may be compromised. It has recently been demonstrated that two clades with the same history of speciation and rates of range evolution (i.e., colonization and local extirpation), will erroneously be inferred to have different origins and historical biogeographical dispersal events if they differ in background rates of lineage extinction (Herrera-Alsina et al., 2022). Thus, radically different biogeographical reconstructions of regional biotas can be inferred when extinct lineages and their distributions are modelled explicitly. The amount of historical extinction in SEA is unknown but is likely to be high (Louys et al., 2007). We thus hypothesise that the discordance between current geological understanding of the region's history and our best biological understanding arises due to lineages' extinctions having not been accounted for in previous biogeographic inferences.

To test this hypothesis, in this paper we revisited the biogeographic history of clades previously used to characterize the patterns of speciation and dispersal in SEA. These clades differ in dispersal capacities, life histories, distribute entirely in SEA, and have high-quality phylogenetic trees as well as well-known geographic distributions. We collated eight clades of organisms ranging from plants to vertebrates (breadfruit *Artocarpus*, orchids *Paphiopedilum*, treelets *Pseuduvaria*, taros *Alocasia*, crabs *Parathelphusa*, crickets *Cardiodactylus*, parachuting frogs *Rhacophorus*, and trees *Cyrtandra*) that have diversified across SEA over the last 45 million years. We explicitly model the geographic distribution of extinct lineages and compare our findings to those of original publications which applied approaches that assume zero extinction through lineage evolution.

Results

By explicitly accounting for lineage extinctions, we obtain substantially different geographic origins and patterns of species distributions on the biogeographical histories of clades in South East Asia to that inferred from previous research which assumes zero extinction. When extinction is included, we find much greater concordance between the clades' geographic origins (Fig. 1), we infer much earlier spread across the region for all clades (Fig. 2) and we find that in-situ speciation becomes more important relative to vicariant speciation in generating the contemporary biodiversity of the region (Table 1).

Under the extinction free methods, all eight clades had geographic-restricted origins, and these were divided between locations, supporting the dispersal-limitation hypothesis. However, when extinction is modelled, seven clades in fact had widespread origins, encompassing both Borneo and mainland SEA, suggesting no ancestral dispersal limitation (Fig. 1). When we set our model to assume zero extinction, we recovered the same geographic origins as those reported in the original studies, suggesting that discrepancies between our results and previous efforts are due to an effect of species extinction rather than other differences in modelling or data handling. For all eight clades, the inferred geographic origin of a common ancestor changes when extinction is included, however the extent of the change varies across clades. For *Pseuduvaria* treelets, the change in inference is the smallest; while extinction-free inference points towards the original ancestral range including continental SEA and New Guinea, when extinction is included, these regions form the ancestral range alongside Borneo. Across all seven other clades we also infer a greater number of regions comprising the ancestral range of the common ancestor when extinction is accounted for, and, similar to the *Pseuduvaria*, we find that these regions are in addition to the ones identified with the extinction-free methods.

We estimated substantially earlier dates at which clades arrived onto different landmasses when lineage extinction is included in the biogeographic reconstruction for the region. For example, according to our new results, the breadfruit (*Artocarpus*) clade colonized the Philippines earlier in its evolution (22 Mya versus 10 Mya as previously estimated) and also gained species richness rapidly (Figures S1-S3) in models accounting for species' extinctions; for taros, Sulawesi is estimated to have been colonized much earlier in models assuming intermediate/high extinction rates (35 Ma), than in models with zero extinction (7 Ma). For *Cyrtandra* trees, the expansion out of Borneo is estimated to have occurred at least 2 million years earlier than previously thought - Sumatra, for instance, is estimated to have been part of the geographic range of *Cyrtandra* for the last 10.5 million years but models with zero extinction infer colonization of Sumatra only 6 Mya. For SEA, we found that Sulawesi was richer in *Paphiopedilum* orchid species at 10 Mya than it is at the present. Because we modelled extirpation to be constant over time, the reduction in orchid species in Sulawesi is not associated with increased extirpation. Instead, the decreasing orchid richness is caused by [global] processes that led to lineage extinction (Wilting et al., 2012). Taken together, these new reconstructions of the biogeographic histories of the eight clades provides a substantially altered picture of much earlier accumulation of species diversity and richness across SEA and much less certainty on the inference that these taxa had spatially disparate origins (Fig. 2).

188 We find that the relative contribution of vicariance (geographically mediated
189 divergence resulting in allopatry) and in-situ speciation also depends on the
190 assumed extinction rate, and this varies across taxonomic groups. The contribution
191 of in-situ speciation increases with the assumed rate of lineage extinction. When
192 lineage extinction is assumed to be low, vicariance is estimated to be higher than in-
193 situ speciation except in breadfruits and parachuting frogs where in-situ speciation is
194 the main mechanism of speciation. By increasing extinction to an intermediate level,
195 our analysis shows that also in *Pseuduvaria* and taros, diversification is in-situ
196 dominated (Table 1). For the models assuming high rates of extinction, in-situ
197 speciation is the main mechanism behind diversification in all groups.

198

Taxon	Reference	Low extinction			Intermediate extinction			High extinction		
		In-situ speciation	Vicariance	Range evolution	In-situ speciation	Vicariance	Range evolution	In-situ speciation	Vicariance	Range evolution
Breadfruit	Williams et al. 2017	0.04	0.0023	0.017	0.067	0.001	0.018	0.45	0.001	0.074
Orchids	Tsai et al. 2020	0.37	1.05	0.69	0.59	1.18	0.08	4.74	0.001	0.017
Treelets										
Pseuduvaria	Su and Saunders 2009	0.21	0.299	0.012	0.33	0.22	0.013	2.3	0.001	0.021
Taros	Nauheimer et al 2012	0.08	0.59	0.008	0.173	0.062	0.009	1.6	0.001	0.018
Crabs	Klaus et al. 2013	0.7	2.5	0.03	1.71	4.4	0.03	1.52	0.001	0.047
Crickets	Dong et al. 2018	0.043	0.409	0.003	0.07	0.35	0.003	0.53	0.001	0.004
Parachuting frogs	O'Connell et al. 2018	0.054	0.016	0.006	0.083	0.014	0.008	0.54	0.001	0.013
Trees	Atkins et al. 2022	0.182	1.59	0.009	0.299	1.46	0.01	2.15	0.177	0.012

Table 1. Rates of range evolution (colonization and extirpation), in-situ and vicariant speciation estimated during the reconstruction of ancestral geographic distribution for eight clades. For each dataset, we modelled three different scenarios that assume low, intermediate and high rates of lineage extinction.

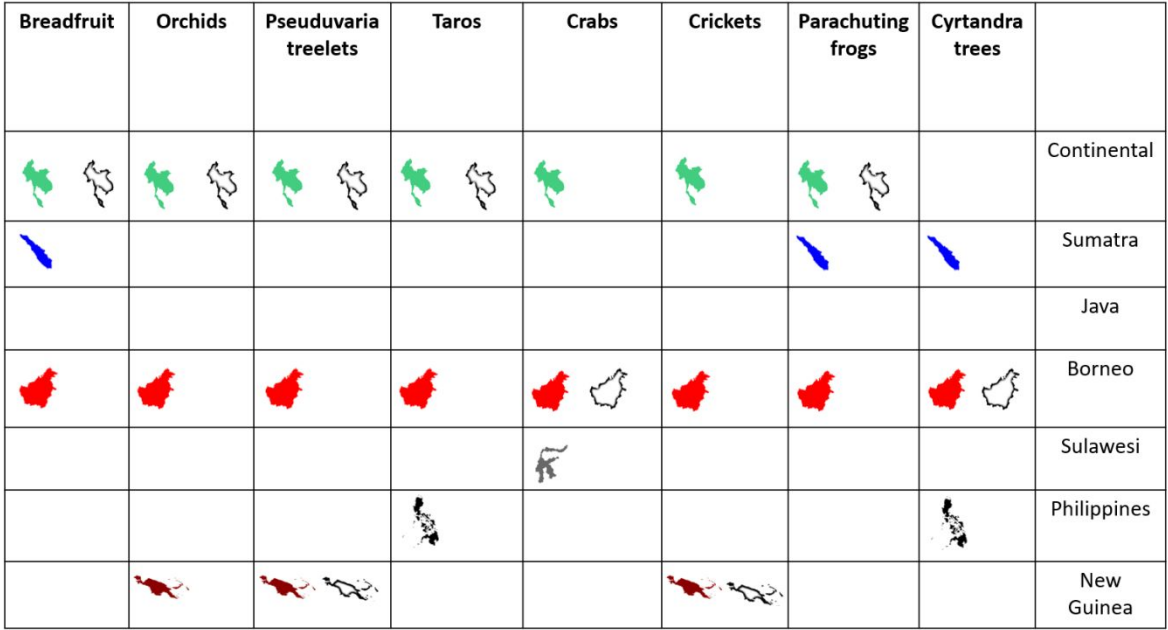


Figure 1. Geographic origins of eight clades in southeast Asia. For each dataset, we reconstruct the distribution (shown as solid islands) of the clade’s common ancestor while assuming intermediate/high rates of lineage extinction. Islands silhouettes show geographic origins when lineage extinction is not considered in the reconstruction (as original papers and also when using our method with extinction = 0).

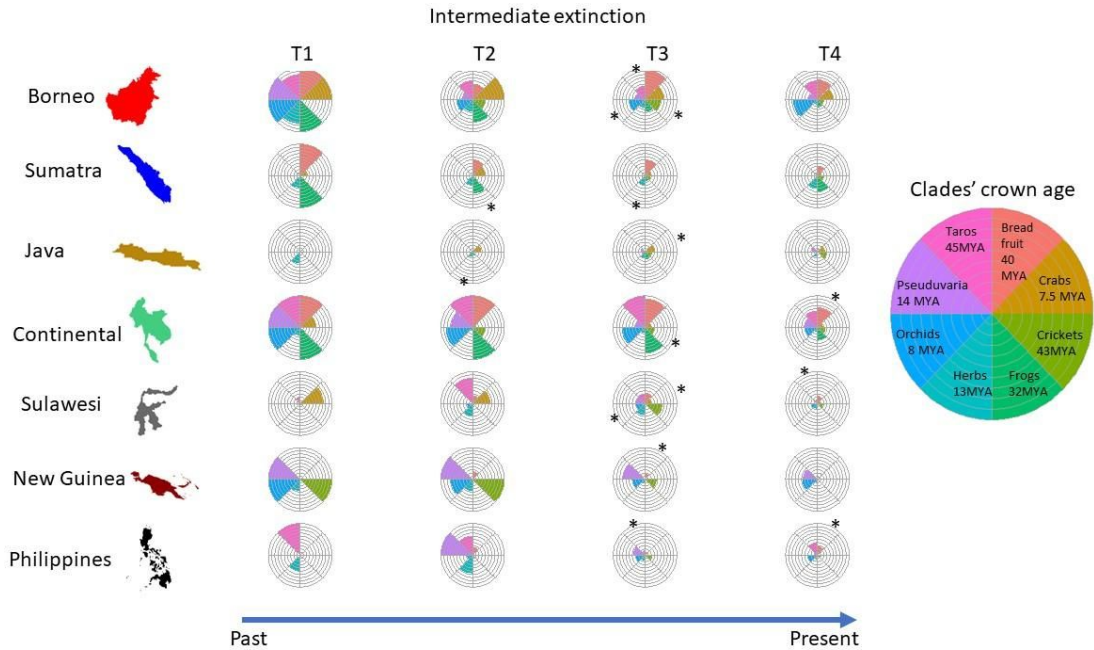


Figure 2. Reconstructed species richness over time across SEA under intermediate rates of extinction scenario. Using four time windows in each clade’s history (from past to present T1-T4), radial charts show the relative number of species inhabiting each location at each time point. Notice that widespread ancestors contribute to the

species richness of several locations. Asterisks show when in time a location was firstly colonized according to previous studies that assume zero extinction. Similar figures but assuming low and high rates of extinction can be found in Supplementary Material.

Discussion

Our results suggest that biological radiations in Southeast Asia (SEA) are characterized by early and widespread dispersal which results in a reconstructed widespread distribution of the common ancestor. We found that all clades were present in all the modern islands far earlier than was previously thought. The geographic expansion of SEA region after the rise of a taxonomic group happened relatively fast. As we included groups with large differences in dispersal capacities and evolutionary age, our results suggest that 1) the movement of species throughout the region was not strongly constrained and 2) a large part of SEA was formerly fully connected forming a rather continuous unit for an extended period over the past 45My at least. Importantly, accounting for species extinction during lineage evolution was required to uncover this pattern. Our work challenges the idea that islands or island-like conditions are required for diversification and supports the new geological evidence that the Sunda shelf was never submerged prior to the Pliocene (Husson et al., 2020; Sarr et al., 2019). Under this scenario, vicariance processes are less likely to explain diversification, instead, speciation events take place within islands.

Our models consistently selected Borneo and continental SEA (plus occasionally New Guinea) as the geographic origin of the clades we revisited when assuming non-zero rates of extinction. The modelled taxonomic groups do not only differ in life history traits but also greatly vary in their evolutionary age, which suggests that the former landmass represented by these territories has consistently played an important role in shaping the biota of SEA (De Bruyn et al., 2014). Sundaland has been the cradle of entire taxonomic groups and also the stage of many speciation events, reinforcing its role as an evolutionary source of biodiversity, rather than the destination (De Bruyn et al., 2014; Grismer et al., 2016). For instance, the common ancestor of *Cardiodactylus* crickets which was previously thought to be of Sahul origin is reconstructed to be also present in Sundaland according to our results. When intermediate and high rates of extinction were assumed, our models suggest that continental SEA and Borneo were occupied by all eight clades throughout their history. The exceptions were *Pseuduvaria* treelets and taros that re-colonized after a brief absence.

We find that the estimates of in-situ and vicariant speciation change in their relative contributions when varying the assumed extinction rate. Our models featuring high extinction on average estimate in-situ speciation to be higher than vicariance and there are two reasons for this. On the one hand, vicariance can take place only when species are geographically widespread i.e., species present in more than one region. With high extinction, many lineages are likely to disappear soon after they arise, causing lineages not to have enough time to expand their geographic range. Accordingly, our rates of range expansion are estimated relatively low. This precludes the existence of widespread lineages and decreases the opportunity for vicariant speciation. On the other hand, during an in-situ speciation event, local diversity increases by one which makes areas resistant to being completely depleted of species in the presence of high extinction. For example, lineage X occurring at areas AB can [in-situ] speciate to produce lineage Y present in A while still being present in AB. If extinction removes X, the area A is not empty, since Y remains. Models with high rates of species extinction will be associated with high rates of in-situ speciation as this results in islands unlikely to become devoid of all species,

which would otherwise be at odds with likelihood computation. If extinction is ignored, this process would appear to represent a range contraction of lineage X, which according to our estimates, takes place at low rate.

Our analysis assuming extinction rate = 0 reconstructed the same geographic origin than in the original studies which suggests that, in the absence of species extinction, both frameworks are equivalent. In all clades with intermediate or high levels of species extinction, our model estimates more widespread lineages than zero-extinction scenarios. We argue that this is not an artefact but a real pattern. On the one hand, our model does not always reconstruct widespread ancestors (see Supplementary Material and Herrera-Alsina et al. 2022) neither in recent nor basal nodes. On the other hand, when varying the assumed rates of extinction, the model does not compensate for changes in ancestral distributions by fitting high rates of range evolution. Instead, the estimated rates of range evolution are similar across different extinction rates which demonstrates that our model successfully disentangles species extinction from extirpation (i.e., local extinctions).

Integrating extinction dynamics into ancestral reconstructions is crucial to reconcile evolutionary processes shaping the modern patterns of species diversity and geological history; our study is not the first one to highlight this. For instance, when assuming non-zero rates of extinction, the common ancestor of hummingbird species was reconstructed to have lived in North America (Herrera-Alsina et al., 2022) which is consistent with fossil record but could not be supported with previous (extinction-free) biogeographic methods (McGuire et al., 2014; McGuire et al., 2007). Our results encourage the use of interdisciplinary views and complementary approaches to address questions that cannot, otherwise, be properly answered.

Methods

We collated published papers that reconstructed the biogeographic history of clades in southeast Asia and selected those whose area delimitation had slight or no departure from the following geographic localities: Borneo, Sulawesi, Sumatra, Java, Philippines, New Guinea and Continental SE Asia. The taxonomic scope of the studies we managed to collect ranged from plants to vertebrates: breadfruit (*Artocarpus*; Williams et al., 2017), orchids (*Paphiopedilum*; Tsai et al., 2020), treelets (*Pseuduvaria*; (Su & Saunders, 2009), taros (*Alocasia*; Nauheimer et al., 2012), crabs (*Parathelphusa*; Klaus et al., 2013), crickets (*Cardiodactylus*; Dong et al., 2018), parachuting frogs (*Rhacophorus*; O'Connell et al., 2018), and trees (*Cyrtandra*; Atkins et al., 2020). Those studies applied DEC (Ree & Smith, 2008) or DIVA (Matzke, 2014; Ronquist, 1997) models for the historical reconstruction. The authors kindly provided phylogenetic trees and geographic information used for their analyses.

To revisit the geographic distribution of the ancestors in those groups, we used LEMAD (Lineage Extinction Model of Ancestral Distribution), a framework that, unlike previous methods, explicitly models the distribution of extinct lineages in geographic reconstruction (Herrera-Alsina et al., 2022). LEMAD generalizes the likelihood described in GeoSSE (Goldberg et al., 2011) for any number of areas and under several sets of geographic assumptions that facilitates its use in ancestral distribution estimation. Consider that lineage Z can have any of three distributions

(area A, area B or being present in both AB), LEMAD uses an equation for the probability of lineage Z being present in A coupled with an equation that reflects the possibility of an extinct lineage which was present in A. The same computation is carried out for area B and AB. The assumed extinction rate is setup by the user. These equations are numerically integrated along all the tree branches from the tree tips (using the geographic information of extant lineages) rootward. Once the likelihood is optimized, these probabilities are retrieved at each node along with the rate estimates for dispersal/extirpation (local extinction), in-situ and vicariant speciation (geographically mediated divergence resulting in allopatry, i.e., complementary ranges).

Vicariant and in-situ speciation can be modelled in mainly two different ways. On one hand, the DEC model (Ree & Smith, 2008) assumes that during vicariance, one of the daughter lineages will be present only at one single region (e.g., ABCD species splits in A-BCD or B-ACD; narrow vicariance); for in-situ speciation, it allows that a population from a widespread species diverges to form a new species which co-occurs with the parental one (i.e., in-situ subset). On the other hand, DIVA model (Ronquist, 1997) assumes that widespread species can split their ranges with no restriction in the number of areas where daughter lineages inhabit as long as they form complementary distributions (e.g., a species presents in region A, B, C and D can split in AB-CD or A-BCD; widespread vicariance). In DIVA, the in-situ subset mode is not assumed. In a LEMAD framework, DEC and DIVA are different versions of the same model (LEMAD_{DIVA} and LEMAD_{DEC}); they differ in the arrangement of parameters, thus their likelihoods are comparable. We fit LEMAD_{DIVA} and LEMAD_{DEC} to the revisited datasets. Because the current distribution of most species across revisited studies is restricted to one or two areas and to be in line with the original analyses, the maximum number of areas where ancestors could have inhabited was set to three.

For each dataset, we ran four models that differed in the assumed rates of lineage extinction (hereafter extinction). We fit a standard birth-death model to each phylogenetic tree and used the estimated speciation rate as the assumed rate of extinction for the first model. Next, we divided this rate by 10 for the second model and multiplied by 10 for the third model. Note that during LEMAD likelihood optimization, speciation and range evolution rates are adjusted accordingly to the assumed extinction rate (i.e., speciation rate is in all cases higher than extinction). We let the rates of in-situ and vicariant speciation and range evolution (i.e., colonization, and local extinction -hereafter extirpation-) be free parameters of the model. Finally, we fit models assuming zero extinction. We found that LEMAD_{DEC} models had better likelihood than LEMAD_{DIVA}, so we report results of the former.

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