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Accounting for extinction dynamics unifies the geological and biological histories of Indo-Australian Archipelago

Abstract

Biogeographical reconstructions of the Indo-Australian Archipelago (IAA) have suggested recent spread across the Sunda and Sahul shelves of lineages with diverse origins, which appears to be congruent with a geological history of recent tectonic uplift in the region. However, this scenario is challenged by new geological evidence suggesting that the Sunda shelf was never submerged prior to the Pliocene, casting doubt on the interpretation of recent uplift and the correspondence of evidence from biogeography and geology. A mismatch between geological and biogeographical data may occur if analyses ignore the dynamics of extinct lineages, because this may add uncertainty to timing and origin of clades in biogeographical reconstructions. We revisit the historical biogeography of multiple IAA taxa and explicitly allow for the possibility of lineage extinction. In contrast to models assuming zero extinction, we find that all of these clades, including plants, invertebrates and vertebrates, have a common and widespread geographic origin, and each has spread and colonized the region much earlier than previously thought. The results for the eight clades re-examined in this paper suggest that they diversified and spread during the early Eocene, which helps to unify the geological and biological histories of IAA.

Introduction

The surface of our planet has been altered greatly on geological timescales, 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 evolution of global biodiversity can therefore be achieved only by combining evidence from geology and biogeography. The Indo-Australian Archipelago (IAA) provides a prime example of this principle, because its striking biodiversity can only be understood by its geological dynamism (Carter et al., 2001; Zahirovic et al., 2014). The modelled geological history of IAA 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 paradox by modelling and incorporating a key evolutionary process, species extinction, into biogeographic reconstructions.

The spatial configuration of islands and continental landmasses across IAA has changed considerably over geological timescales. There is a long-standing paradigm proposing that the Malay peninsula and Greater Sunda islands were totally disconnected from (at least) 60 Ma (Lohman et al., 2011) to 10 Ma, when the appearance of the islands now forming the Indonesian archipelago and Wallacea region 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 appeared to find constrained dispersal in ancient lineages across IAA, due to an extensive period when islands were not connected. Both animal (Dong et al., 2018) and plant (Nauheimer et al., 2012; Williams et al., 2017) lineages that arose as early as 40 Ma underwent limited dispersal within but not between their centres of origin on either the Sunda or Sahul continental shelf, 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), while 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).Consistent with the idea of limited dispersal across the archipelago, widespread species are likely to form new species that become endemic to individual islands (Simaiakis et al., 2012). The fundamental role of this mechanism is reflected in high rates of vicariance (i.e., speciation due to differentiation between two populations which that different islands). Under this view, dispersal facilitation by the late appearance of island steppingstones is common to the biogeographical reconstructions of all the lineages that have been examined in recent studies (Atkins et al., 2020; Thomas et al., 2012).

Many studies have applied standard biogeographic reconstruction methods and weaved biogeographical hypotheses that are consistent with this geological hypothesis. However, this understanding of the geological history of IAA 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, it is hypothesized that Sundaland (i.e., the western part of the archipelago) was permanently continental

until at least 6 Ma (Husson et al., 2020), which pre-dates the onset of regional connectivity by tens of millions of years (Hall, 2013). 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 interpretations of the region's history from the perspectives of geological and biological evidence.

One potential explanation for this disparity 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. Traditional biogeographic approaches model only *local* extinction (also known as extirpation), which is different from lineage/species extinction. Recent work has demonstrated that two clades with the same history of speciation and rates of range evolution (i.e., colonization and local extirpation), can be inferred erroneously 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 IAA is unknown but is likely to be high (Louys et al., 2007). A discordance between current geological understanding of the region's history and our best biological understanding might arise because lineage extinctions have not been accounted for in previous biogeographic inferences.

Specifically, we hypothesize that clades used land bridges connecting the major IAA landmasses since their origin. If that is the case, we expect to find evidence against limitation in ancient dispersal, wider ancient geographic distributions and early colonization of the entire archipelago (compared to zero-extinction models). Furthermore, we expect that high connectivity among landmasses limits geographic isolation, which in turn decreases the likelihood of differentiation among allopatric populations (i.e., inhabiting different islands) leading to vicariant speciation, compared to in-situ speciation (i.e., speciation within an island or location through any potential mechanism including fine-scale geographic isolation).

To test this hypothesis, we revisited the biogeographic history of clades that had been used previously to characterize the patterns of speciation and dispersal in IAA. These clades differ in their dispersal capacities and life histories, possess high-quality phylogenetic trees and well-known geographic distributions. We collated data used to reconstruct the phylogenies and biogeographic histories of eight clades representing plants, invertebrates and vertebrates (the breadfruits *Artocarpus,* orchids *Paphiopedilum*, treelets *Pseuduvaria,* taros *Alocasia,* crabs *Parathelphusa,* crickets *Cardiodactylus,* parachuting frogs *Rhacophorus,* and herbs *Cyrtandra*) that have diversified across IAA over the last 45 million years. We considered the influence of extinction on the biogeographic reconstructions by explicitly modelling both the missing branches (due to extinction) on a phylogenetic tree and the geographic distribution of those extinct lineages. Our approach uses contemporary species distributions and does not require paleogeographic information. We applied a likelihood framework where tree branches are used to compute the change in probability of a lineage (extant) being present at a given location. This probability

also considers that a lineage could have existed at any point along a branch, could have changed across locations, and went extinct before the present.

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 the Indo-Australian Archipelago to that inferred from models assuming 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 (Fig. 3).

A cradle for clades

When we set our models to assume zero extinction, we recovered the same geographic origins as those reported in the original studies. Models with zero extinction showed that all eight clades had narrow geographic origins that, in general, included either continental Asia or New Guinea. We found that the inferred geographic origin of the common ancestor of a clade changed when extinction rates higher than zero were assumed in the models. For instance, in *Cardiodactylus* crickets, a model assuming zero extinction reconstructs New Guinea as the original ancestral range, but when extinction was allowed, Borneo and continental Asia were inferred to be the centre of origin. In all cases apart from *Cyrtandra* herbs we found that Borneo and continental Asia were included within the centre of origin when extinction was explicitly incorporated into models (Fig. 1).

Dispersal and early land connectivity in IAA

We estimated substantially earlier dates at which clades arrived onto different landmasses when models assumed lineage extinction rates higher than zero than when extinction was neglected (Fig. 1). For example, the breadfruit (*Artocarpus*) clade is predicated to have colonized the Philippines earlier in its evolution (22 Mya versus 10 Mya as previously estimated; Fig. 1); for taros (*Alocasia*)**,** 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 *Cytandra* herbs, 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, whereas models assuming no extinction infer colonization of Sumatra only 6 Mya. Sulawesi is the location that shows more differences.

Mechanisms of speciation and species accumulation

Our revised models incorporating non-zero extinction reconstruct different patterns in the distribution of species diversity across IAA over time than zero-extinction models. For instance, the Philippines are estimated to have accumulated breadfruit species (*Artocarpus*) soon after colonization by the genus in the late Eocene (Fig. 2). Another interesting finding is that Borneo was richer in *Paphiopedilum* orchid species at 20 Mya than it is at the present. Because our models assume a constant rate of extirpation over time, the reduction in orchid species in Borneo is not associated with increased rate of extirpation. Instead, the decreasing orchid richness is caused by [global] processes that led to lineage extinction (Wilting et al., 2012). The low extinction scenario reconstructs Sulawesi to have low species richness through time (Fig 2), in contrast with the high extinction case where Sulawesi harbours high

diversity since the Eocene (Figures S25, S26). Sulawesi is the location that shows more striking differences in how diversity accumulated over time across the different scenarios of species extinction. Taken together, these new reconstructions of the biogeographic histories of the eight clades provide a substantially altered picture of much earlier accumulation of species diversity and richness across IAA and much less certainty on the inference that these taxa had spatially disparate origins (Fig. 2, Fig. S1-S24).

We find that the relative contribution of vicariance and in-situ speciation also depends on the assumed extinction rate, and that this contribution varies across taxonomic groups. The contribution of in-situ speciation increases with the assumed rate of lineage extinction. When lineage extinction is assumed to be low, vicariance is estimated to be higher than in-situ speciation, except in breadfruits and parachuting frogs where in-situ speciation is the main mechanism of speciation. By increasing extinction to a more realistic intermediate rate, our analysis shows that in situ speciation also dominates for *Pseuduvaria* treelets and taros (Fig. 3). For the models assuming high rates of extinction, in-situ speciation is the main mechanism behind diversification in all groups. 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).

Discussion

Our results suggest that the eight biological radiations in the Indonesian Archipelago we analysed 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 within the landmasses represented by all the modern islands far earlier than was previously thought, and that expansion across the region generally occurred soon after the rise of a taxonomic group. As we included groups with large differences in dispersal capacities and evolutionary age, our results suggest that the movement of species throughout the region was not strongly constrained and that a large part of IAA might have been connected by islands or island-like land bridges for an extended period over the past 45My. Importantly, it was necessary to account for species extinctions during lineage evolution to uncover these patterns. Under this scenario, vicariance processes are less likely to explain diversification, but instead, speciation events take place within the areas that now form the major islands of contemporary Southeast Asia.

By modelling extinction, we found that ancient dispersal of lineages across Indo-Australian Archipelago (IAA) took place much earlier than estimated by previous studies. Even though our conclusions are based on eight clades, they are congruent with recent geomorphological information (Husson et al. 2020) and fossil evidence. Fossil ostracods (Crustacea) have been found in the region of modern Java, and importantly, their subtidal lifestyle (based on eye tubercle morphology) suggests that land was available around 40- 38 MA (Yasuhara et al., 2017). The palynological record shows that mangroves were already inhabiting Sumatra during the Middle Eocene (~ 40-45 MA; Ellison et al., 1999; Renema et al., 2008). Because mangroves

occur at the interface between terrestrial and marine environments, this fossilized pollen also provides evidence of the presence of landmasses in the region at this time. These findings are incongruent with zero extinction biogeographic reconstructions that typically conclude more recent colonisation across the region, and they suggest that elevated rates of background extinction are required for accurate biogeographical reconstruction of the region. This conclusion is supported by climatic factors suggesting that lineage extinction is likely to be high in this region (Louys et al., 2007).

Our models consistently selected Borneo and continental Asia (plus New Guinea and Sumatra for three groups, the Philippines for two and Sulawesi once) as the geographic origin of the eight clades. 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 IAA (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 reconstructed common ancestor of *Cardiodactylus* crickets, which was previously thought to be of Sahul origin, is now shown to be present in Sundaland. When intermediate and high rates of extinction were assumed, our models suggest that continental Asia and Borneo have been occupied by all eight clades throughout their history.

Our results suggest that the estimate of the relative contributions of in-situ and vicariant speciation change when varying the assumed extinction rate. Models featuring high extinction rates estimate that, on average, in-situ speciation is higher than vicariant speciation. There are two potential 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. If extinction rates are high, many lineages are likely to disappear soon after they arise and inevitably before they have time to expand their geographic range. Accordingly, rates of vicariance are estimated to be relatively low in models that incorporate lineage extinction because these scenarios diminish the likelihood widespread lineages arise and decrease the opportunities for vicariant speciation. On the other hand, during an in-situ speciation event, the tally of local diversity increases by one species, which would then lower the probability that high extinction eliminates all species. For example, consider a scenario where lineage X occurring at areas A and B [in-situ] speciates to produce lineage Y in area A, while the parent lineage X remains present across both A and B. Even if extinction removes lineage X entirely, area A remains occupied by lineage Y. Therefore, models with high rates of species extinction will be associated with high rates of in-situ speciation as this results in areas that are unlikely to become devoid of all species. If extinction is ignored, this process would appear to represent a range contraction of lineage X, which according to our estimates, takes place at a low rate.

Our modelling approach simplifies the macroevolutionary dynamics taking place in the region. On the one hand, we assumed that diversification rates are uniform over time when in reality there are global, climate-related events that might have increased or decreased the rates of diversification. For instance, changes in atmospheric carbon dioxide concentration during Miocene has affected the radiation of many taxa at a global scale (Aduse-Poku et al., 2022; Spriggs et al., 2014; Zachos

et al., 2008). On the other hand, we assumed that diversification rates are uniform in space when, in fact, a combination of biotic and abiotic processes could have resulted in higher speciation rates in some locations than others. Similarly, lineages might experience increased probabilities of extinction in one area over another, although it would be truly challenging to detect such a signal from data as molecular phylogenetic trees are seldom informative on clade-wide extinction rates (Nee, Holmes, et al., 1994; Rabosky, 2010), and even less suitable for detecting differences in extinction rates between lineages. Although we recognise the potential importance of these patterns, they are not currently represented in our models, which aim to reconstruct the biogeographic history of the region when assuming different extinction rates, but do not estimate extinction rates from phylogenetic trees

Integrating extinction dynamics into ancestral reconstructions is crucial for reconciling evolutionary processes shaping the modern patterns of species diversity with geological and palaeontological evidence. A similar re-evaluation of lineage evolution incorporating non-zero rates of extinction was required to reconcile the contemporary biogeography of hummingbirds with the fossil record and demonstrated that the common ancestor of hummingbird species lived in North America (Herrera-Alsina et al., 2022) rather than South America (McGuire et al., 2014; McGuire et al., 2007). Our results encourage the use of interdisciplinary and complementary approaches to address questions that cannot, otherwise, be addressed comprehensively.

Methods

We collated published papers that reconstructed the biogeographic history of clades in Indo-Australian Archipelago (IAA) and selected those whose geographic range had limited departure from the following geographic localities: Borneo, Sulawesi, Sumatra, Java, Philippines, New Guinea and continental SE Asia. The taxonomic scope of these studies included plants, and both invertebrate and vertebrate animals: 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 herbs (*Cyrtandra*; Atkins et al., 2020). All those studies applied either DEC (Dispersal-Extinction-Cladogenesis; Ree & Smith, 2008) or DIVA(Dispersal-Vicariance Analysis Matzke, 2014; Ronquist, 1997) models for biogeographic reconstruction. The authors kindly provided phylogenetic trees and geographic information used for their analyses.

We used the modelling framework LEMAD (Lineage Extinction Model of Ancestral Distribution) to revisit the geographic distribution of the ancestors in these groups. Unlike previous methods, LEMAD explicitly models the distribution of extinct lineages in geographic reconstruction (Herrera-Alsina et al., 2022). DEC and similar approaches use the set of extant species to reconstruct past changes in geographic distributions, while LEMAD includes extant species but also models extinct species (see below) to reconstruct the biogeographic history. The amount of historical extinction in IAA is unknown but is likely to be high (Louys et al., 2007) and models other than LEMAD neglect this key process. Notice that DEC and other approaches

consider *local* extinction (also known as extirpation) which is the change from presence to absence of a lineage at a given location: a species/lineage could still exist in other locations and remain extant to the present. Radically different biogeographical reconstructions of regional biotas can be inferred when extinct lineages and their distributions are modelled explicitly (Herrera-Alsina et al., 2022). The inference of lineage extinction (hereafter extinction) rates from molecular phylogenetic trees is challenging and might lead to the estimation of biased rates because of taxonomic sampling issues (Nee et al. 1994) and heterogeneity of rates across lineages (Rabosky 2010). LEMAD does not attempt to estimate extinction rates, instead, it is used to explore the reconstructed ancestral distributions when assuming different extinction rate values in order to address this important source of uncertainty.

LEMAD generalizes the likelihood described in GeoSSE (Goldberg et al., 2011) for any number of areas and is flexible to include different scenarios of geographic speciation that facilitate the estimation of ancestral distribution. Like GeoSSE, the change in geographic distribution of species is a result of species colonizing locations (dispersal) and becoming extirpated from locations (i.e., the disappearance from a local area, also known as range contraction or local extinction). Unlike GeoSSE, LEMAD assumes that rates of speciation and extinction are uniform across regions. Extinction is modelled as an instantaneous process across the entire range of a lineage, which allows us to account for those events where populations experience a sudden decline in size and are unlinked to geographic range contractions (Goldberg et al., 2011). In LEMAD, both the phylogenetic tree and geographic information are jointly used to carry out the calculation. A system of equations is defined to represent 1) the probabilities of a given branch (i.e., an existing branch) being present at the different geographic location, and 2) the probabilities of a branch that, having existed at a different geographic location, went extinct. For instance, consider that lineage Z can have any of three distributions (area A, area B or being present in both A and B), LEMAD defines 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 before going extinct. The same computation is carried out for area B and the area represented by both A and B. The assumed extinction rate is defined by the user. The equations also include a term that accounts for changes in geographic distributions i.e., lineages colonizing or disappearing from locations. These equations are numerically integrated along all the tree branches from the tree tips (using the geographic information of extant lineages) to the root. Once the likelihood is optimized, these probabilities are retrieved at each node along with the rate estimates for dispersal/extirpation, in-situ and vicariant speciation (geographically mediated divergence resulting in allopatry, i.e., complementary ranges).

Vicariant and in-situ speciation can be modelled in two different ways. On the one hand, the DEC model (Ree & Smith, 2008) assumes that during vicariance, one of the daughter lineages will be present in only one region (e.g., the four species ABC and D are partitioned geographically into A-BCD or B-ACD; narrow vicariance); for in-situ speciation, the DEC model 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, the DIVA model (Ronquist, 1997) assumes that widespread species can split their ranges with no restriction in the number of areas inhabited by daughter lineages, as long as they form complementary distributions

(e.g., a species present in regions A, B, C and D can split into AB-CD or A-BCD; widespread vicariance). In DIVA, the in-situ subset mode is not assumed. In the 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. In the LEMAD analysis and in contrast to some of the original IAA studies, our models did not include a time-stratified component or jump dispersal.

For each dataset, we ran four models that differed in the assumed rates of extinction. The decision on what extinction rate to assume is not straightforward. In the field of macroevolution, estimates for extinction rates calculated from phylogenetic trees are generally small, often close to zero, which contradicts the fossil record (Nee, May, et al., 1994). We fitted a standard birth-death model (BD) to each phylogenetic tree and confirmed that the extinction rate was estimated to be close to zero. With highly incomplete fossil record and with no external evidence that could suggest a reliable rate of extinction for the revised datasets, we took an alternative approach. Instead of using those clearly underestimated extinction rates from a BD model, we assumed that extinction could have been almost as frequent as speciation, as shown in datasets with the most complete fossil records (Barnosky et al., 2011; Budd & Mann, 2018). We therefore used the speciation rate estimate under a BD for each dataset and termed this rate BD_mu. This was the assumed extinction rate for the first model. In the second model, we assumed a much higher rate of extinction (10 x BD_mu; De Vos et al., 2015). The third model assumed low extinction (BD_mu/10). It is reasonable to assume that the extinction rate adopted for the second and third models bracket the actual range of values for each lineage, while that adopted in the first model is a tentative estimate of its long-term mean. Finally, we fit models assuming zero extinction. Note that during LEMAD likelihood optimization, speciation and range evolution rates are adjusted according to the assumed extinction rate (i.e., speciation rate is in all cases higher than extinction). We allowed the rates of in-situ and vicariant speciation and range evolution (i.e., colonization, and local extinction -hereafter extirpation-) to be free parameters in the model. We found that $LEMAD_{DEC}$ models had better likelihood than $LEMAD_{DIVA}$, so we report the results of the former. All analyses were carried out using one phylogenetic tree per clade that was provided by the authors of the original papers.

Figure Captions

Figure 1. Geographic origins of eight clades in the Indo-Australian Archipelago. For each dataset, we reconstruct the geographic distribution of the clade's common ancestor while assuming intermediate and zero rates of lineage extinction.

Figure 2. Reconstructed species richness over time across the Indo-Australian Archipelago under intermediate rates of extinction scenario for eight taxonomic groups. 1: Crabs, 2: Parachuting frogs, 3: *Pseuduvaria* treelets, 4: Orchids, 5: Breadfruit, 6: Taros, 7: *Cyrtandra* herbs, 8: Crickets. Colour code shows the relative number of species inhabiting each location at each time point. Notice that widespread ancestors contribute to the species richness of several locations. Time scale on the left is in million years. Similar figures but assuming low and high rates of extinction can be found in Supplementary Material.

Figure 3. 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.

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Figure 1

Group	Geographic origin when extinction modelled	Geographic origin when extinction = 0.
Breadfruit		
Orchids		
Pseuduvaria treelets		
Taros		
Crabs		
Crickets		
Parachuting frogs		
Cyrtandra herbs		

Figure 2

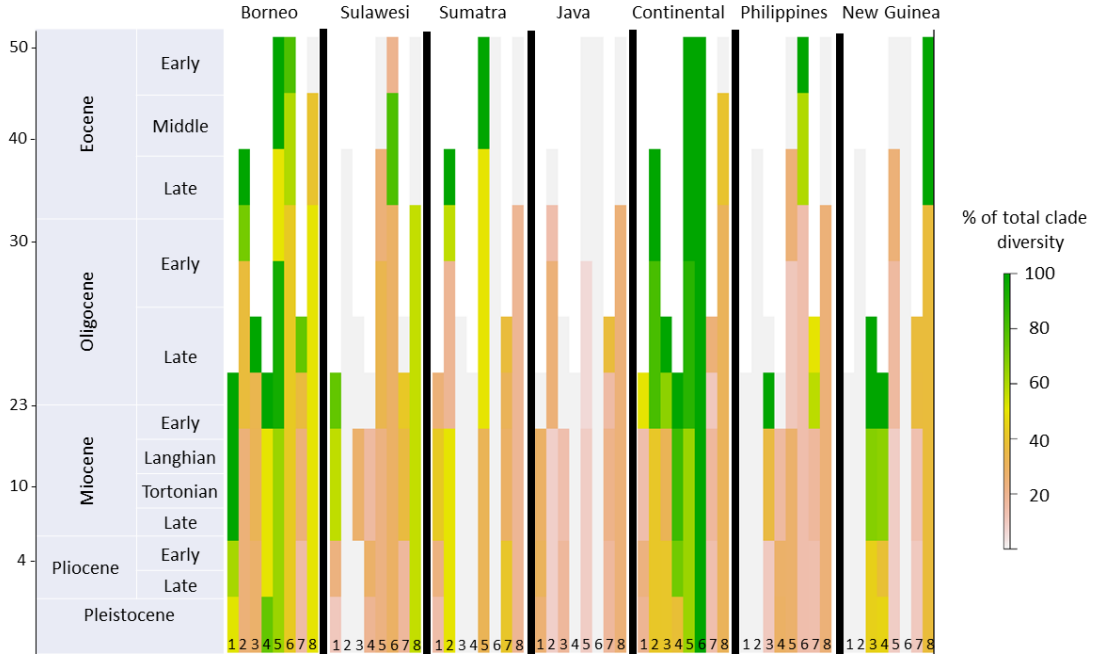
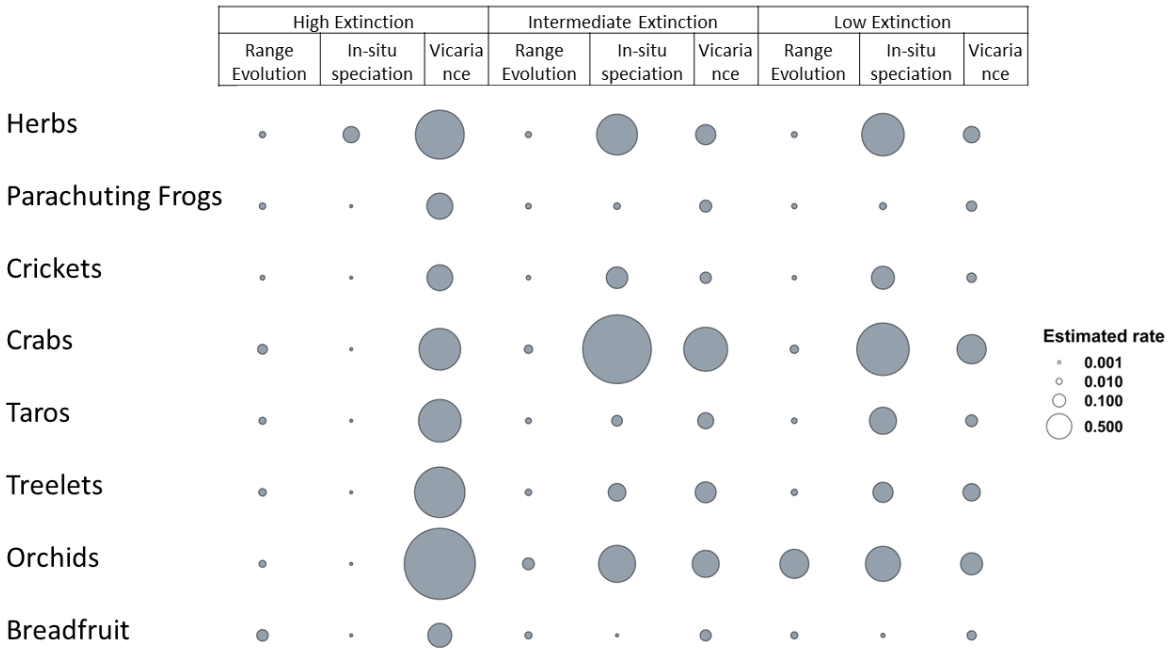

Borneo
Sulawesi
Sumatra
Java
Continental
Philippines
New Guinea
50
40
30
23
10
4
Eocene
Oligocene
Miocene
Pliocene
Pleistocene
Early
Middle
Late
Early
Late
Early
Langhian
Tortonian
Late
Early
Late
1 2 3 4 5 6 7 8
% of total clade diversity
100
80
60
40
20

Figure 3


High Extinction
Intermediate Extinction
Low Extinction
Range Evolution
In-situ speciation
Vicariance
Herbs
Parachuting Frogs
Crickets
Crabs
Taros
Treelets
Orchids
Breadfruit
Estimated rate
0.001
0.010
0.100
0.500

Supplementary Material

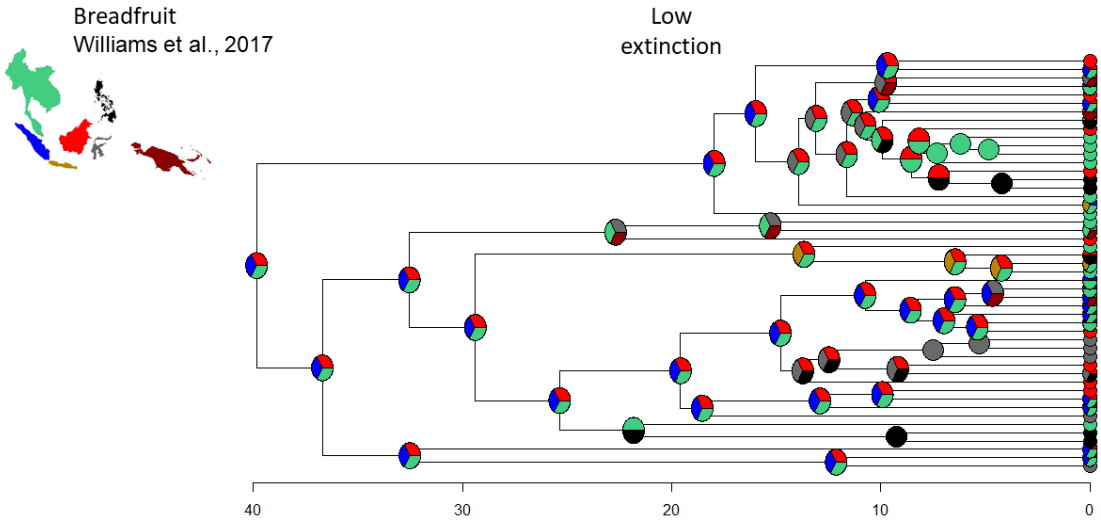


Figure S1. Ancestral distribution of breadfruit species (*Artocarpus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

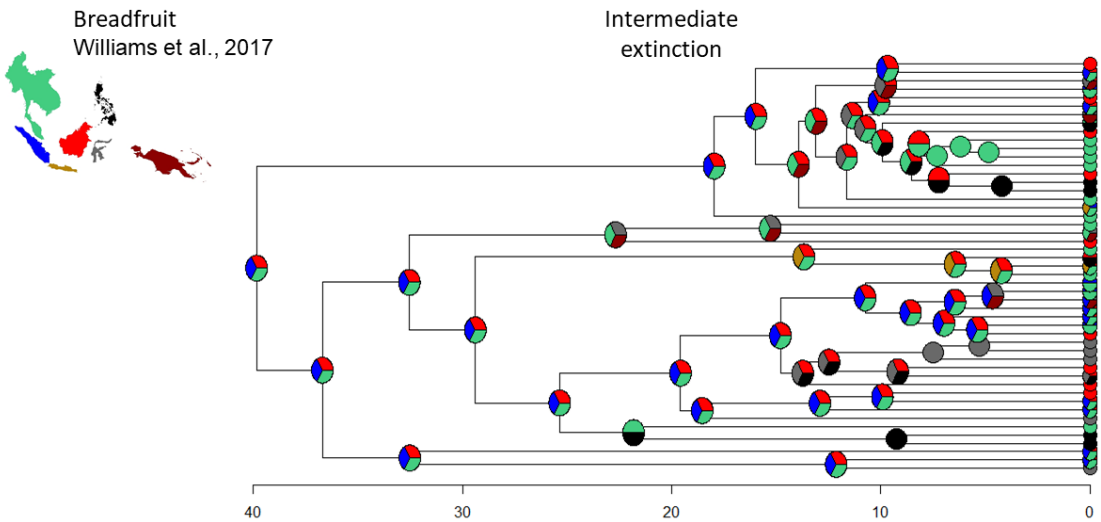


Figure S2. Ancestral distribution of breadfruit species (*Artocarpus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that

extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

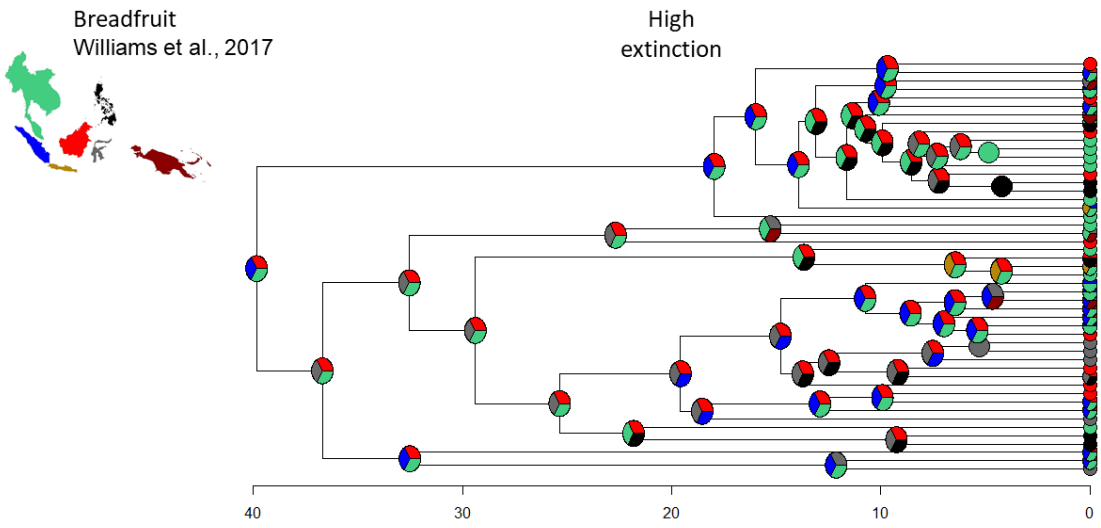


Figure S3. Ancestral distribution of breadfruit species (*Artocarpus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

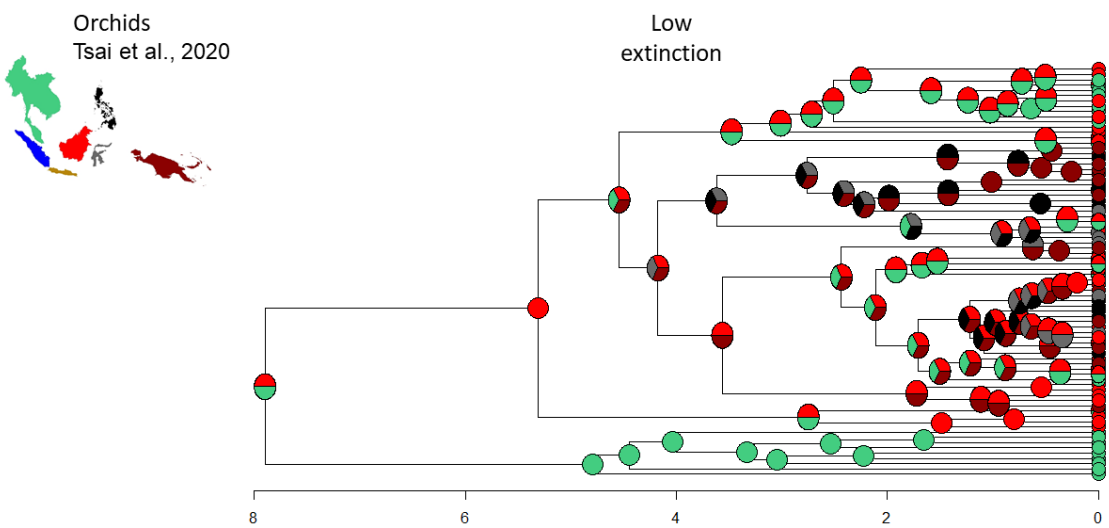


Figure S4. Ancestral distribution of orchid species (*Paphiopedilum*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

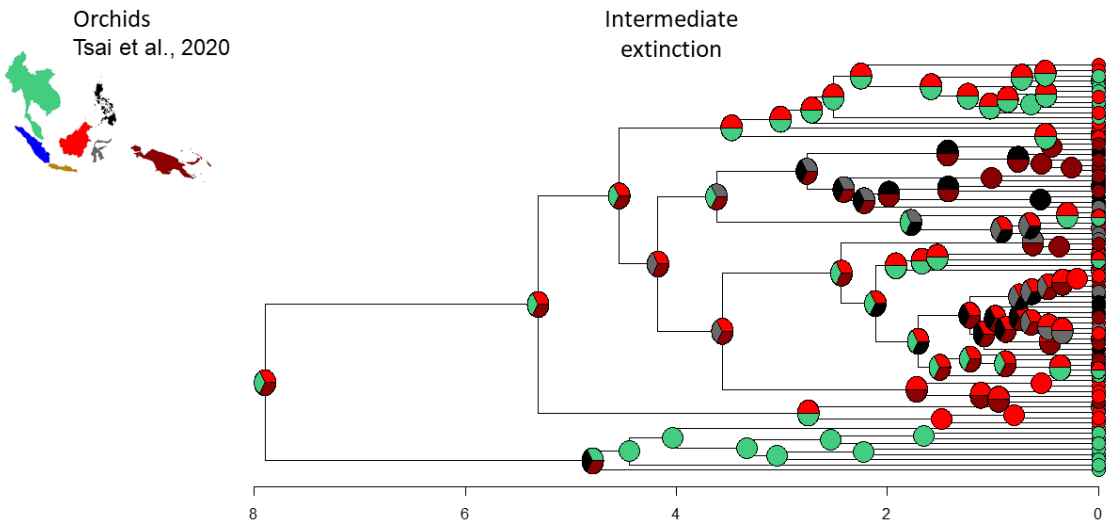


Figure S5. Ancestral distribution of orchid species (*Paphiopedilum*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

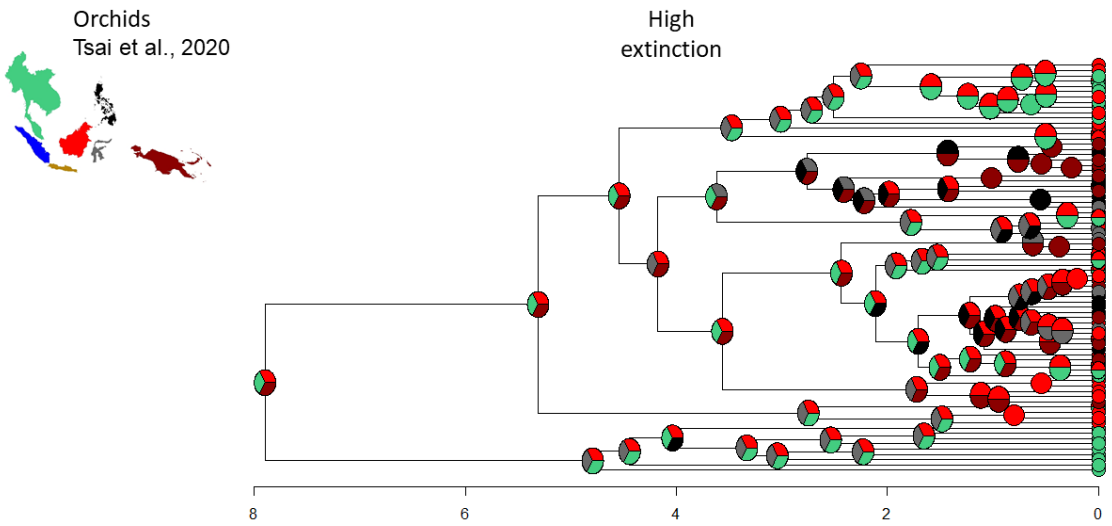


Figure S6. Ancestral distribution of orchid species (*Paphiopedilum*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

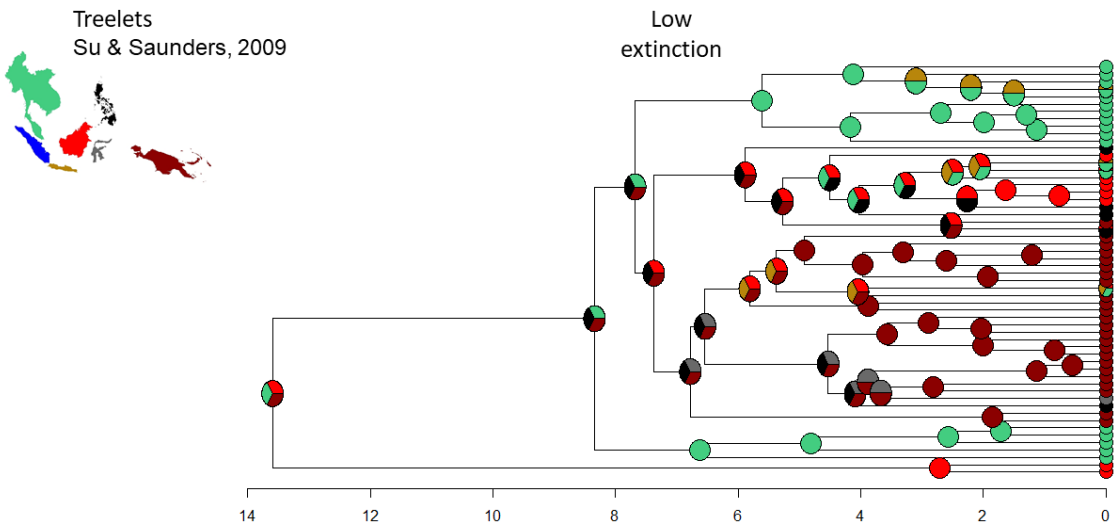


Figure S7. Ancestral distribution of treelet species (*Pseuduvaria*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

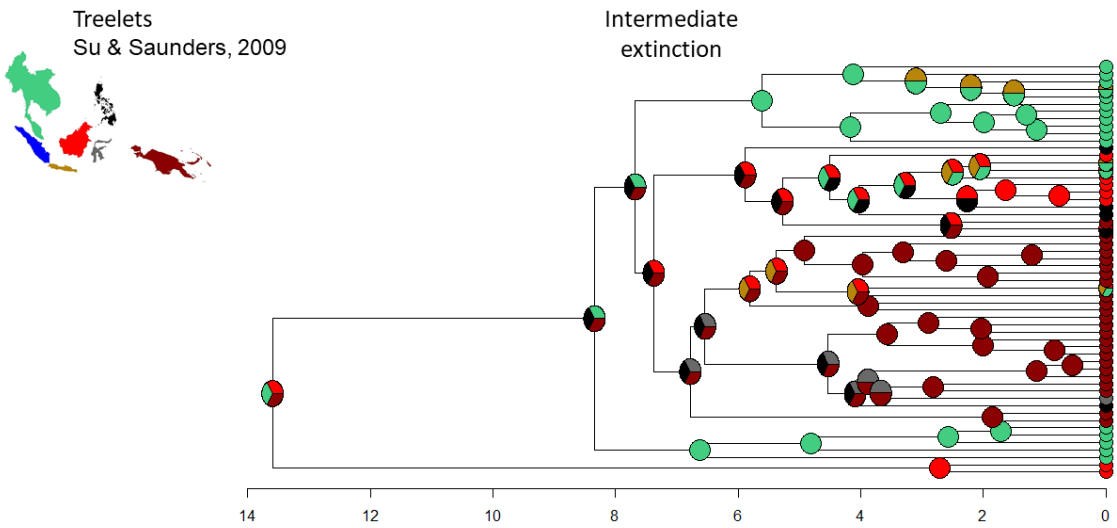


Figure S8. Ancestral distribution of treelet species (*Pseuduvaria*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

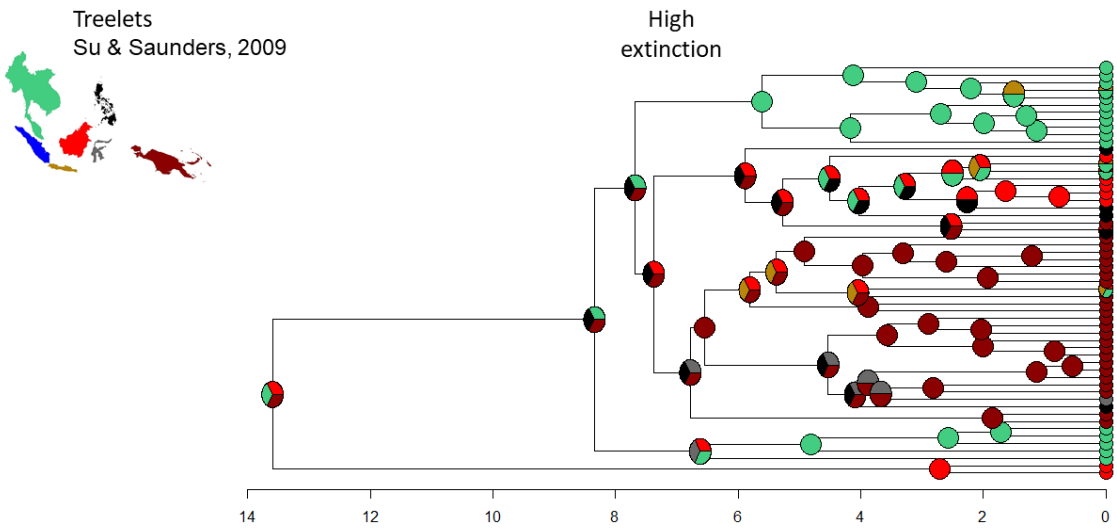


Figure S9. Ancestral distribution of treelet species (*Pseuduvaria*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

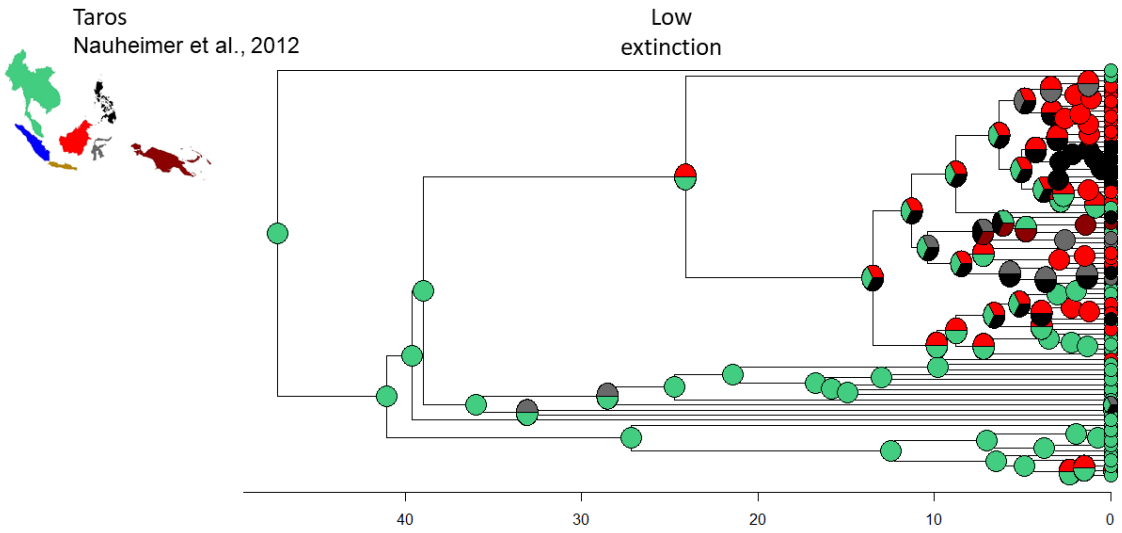


Figure S10. Ancestral distribution of taro species (*Alocasia*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

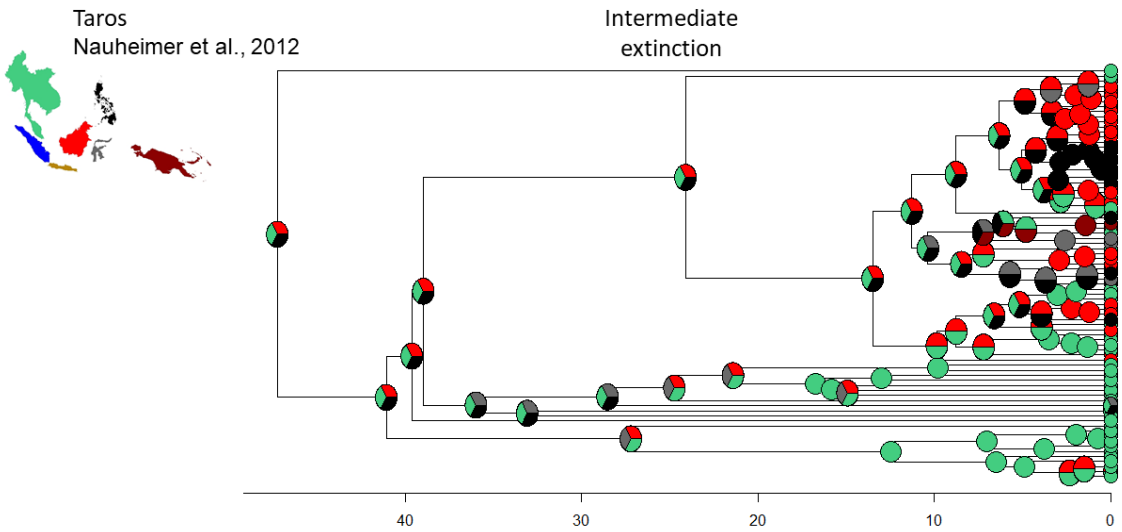


Figure S11. Ancestral distribution of taro species (*Alocasia*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

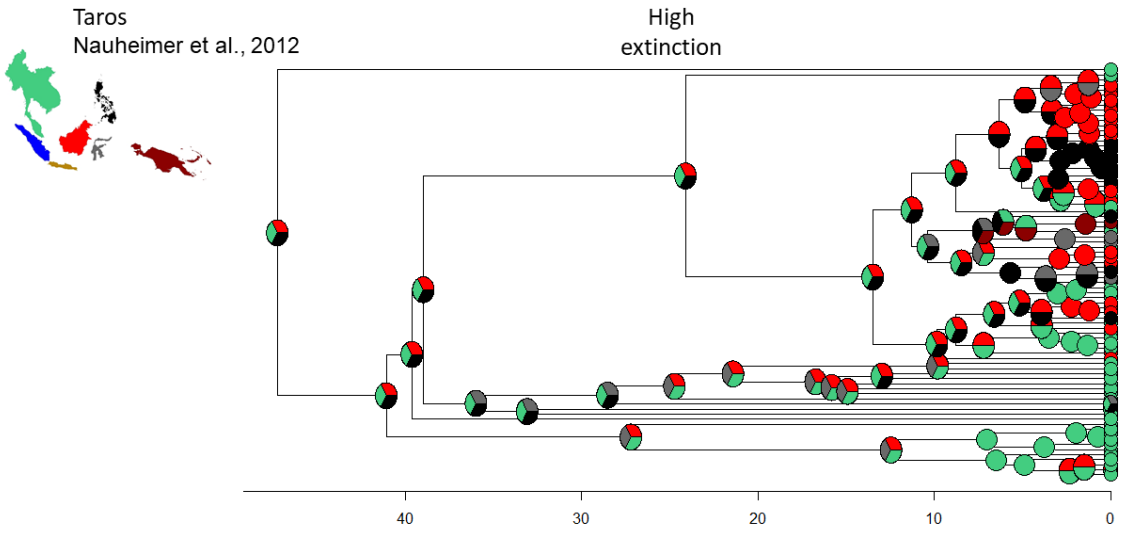


Figure S12. Ancestral distribution of taro species (*Alocasia*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

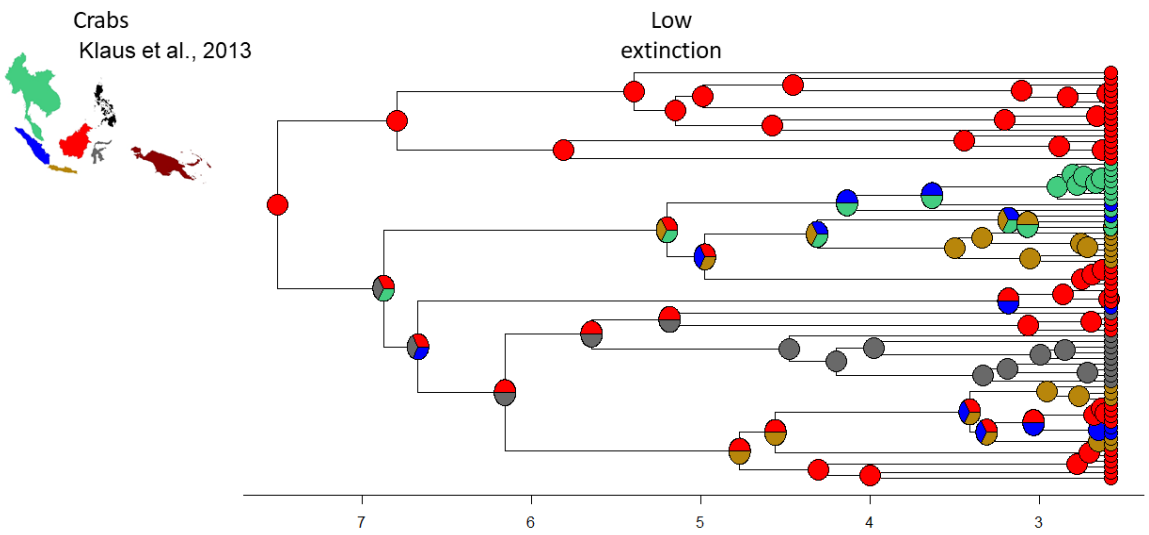


Figure S13. Ancestral distribution of crab species (*Parathelphusa*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the

distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

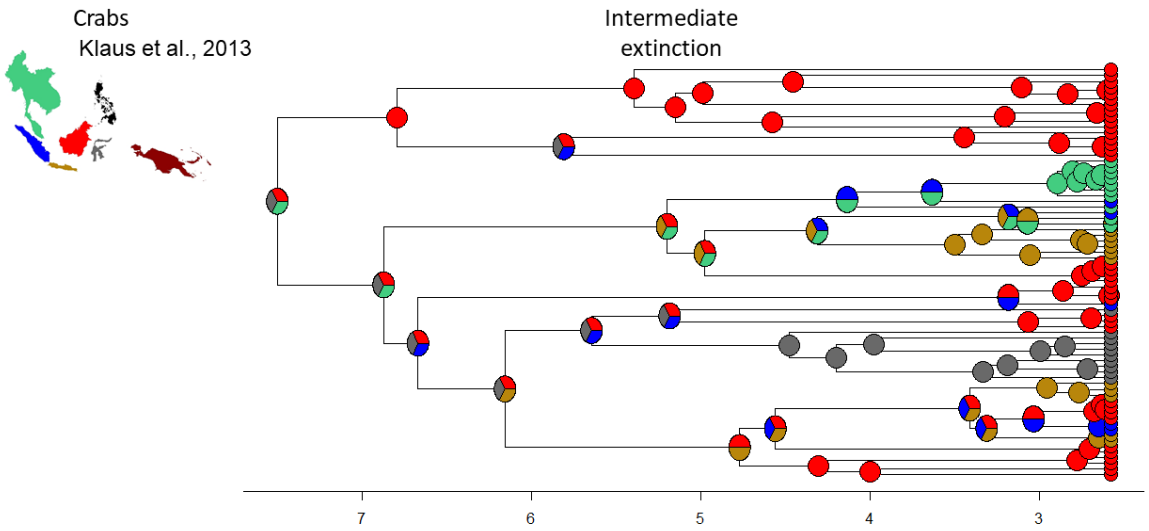


Figure S14. Ancestral distribution of crab species (*Parathelphusa*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

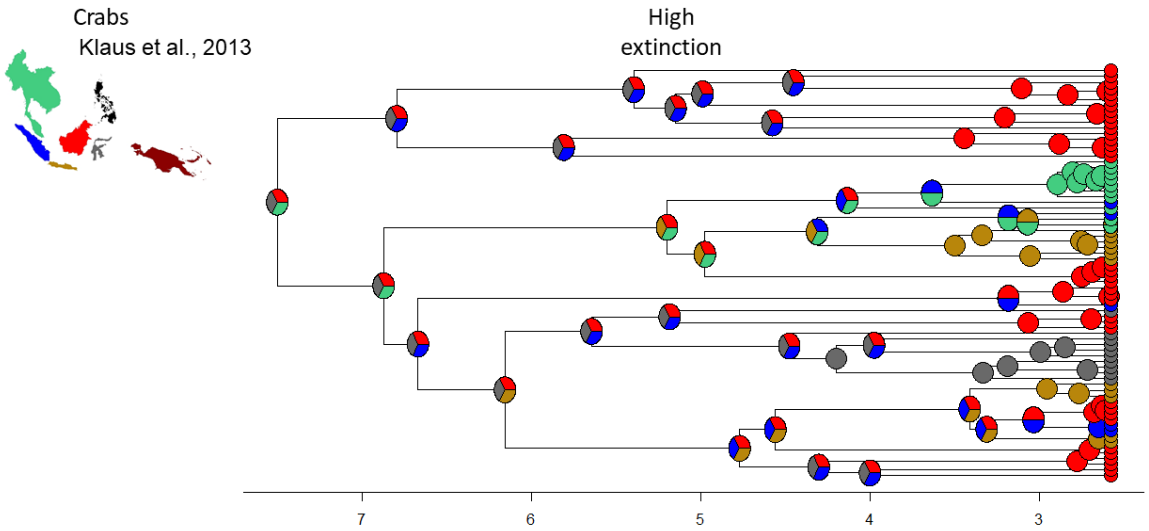


Figure S15. Ancestral distribution of crab species (*Parathelphusa*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death

model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

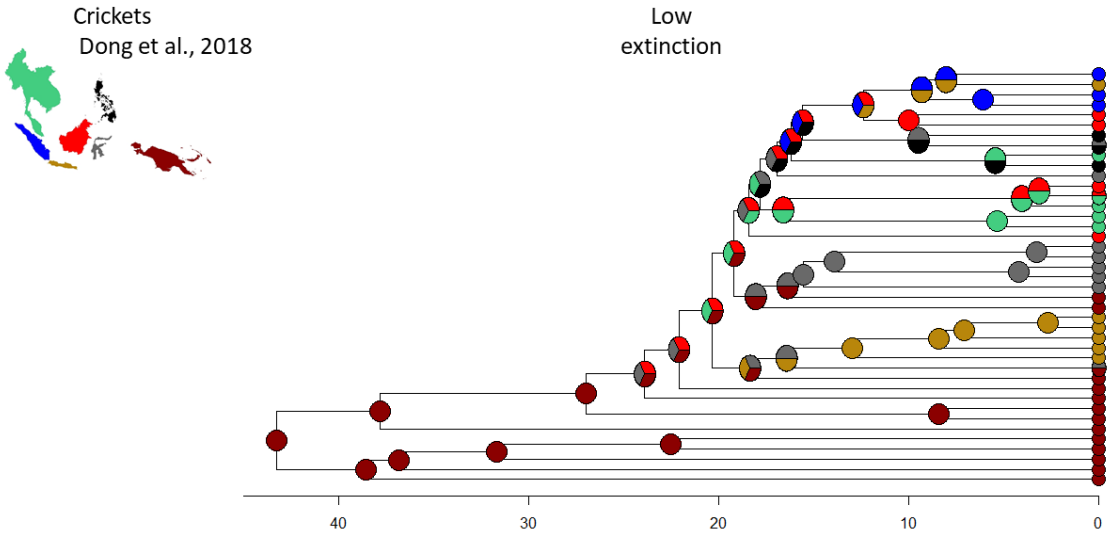


Figure S16. Ancestral distribution of cricket species (*Cardiodactylus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

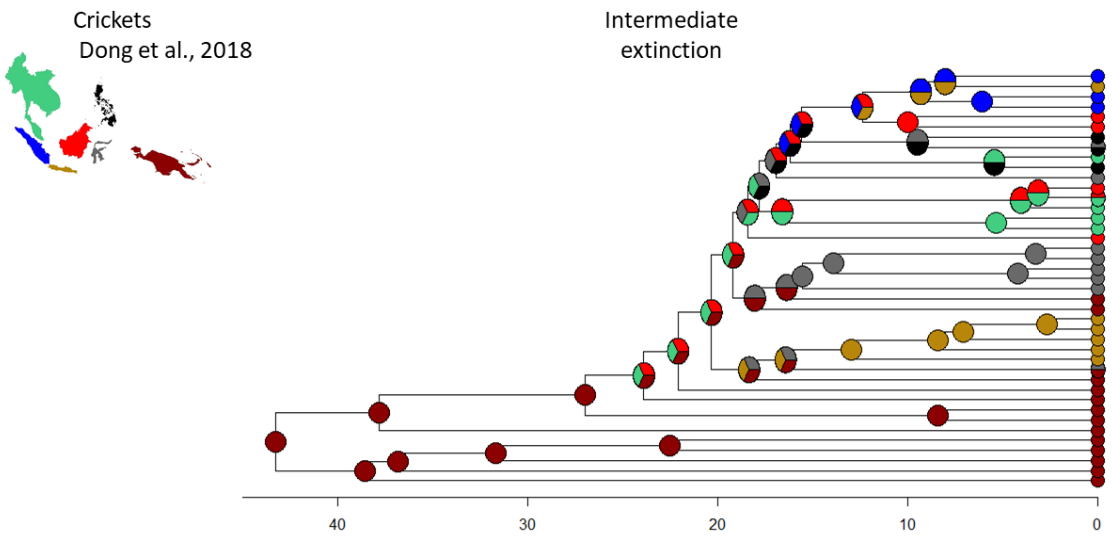


Figure S17. Ancestral distribution of cricket species (*Cardiodactylus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

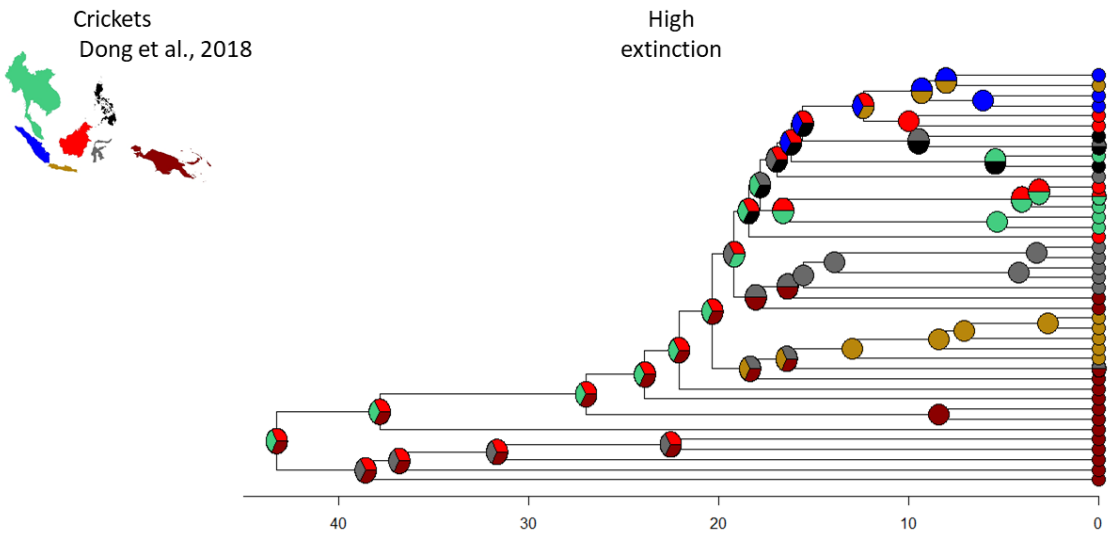


Figure S18. Ancestral distribution of cricket species (*Cardiodactylus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

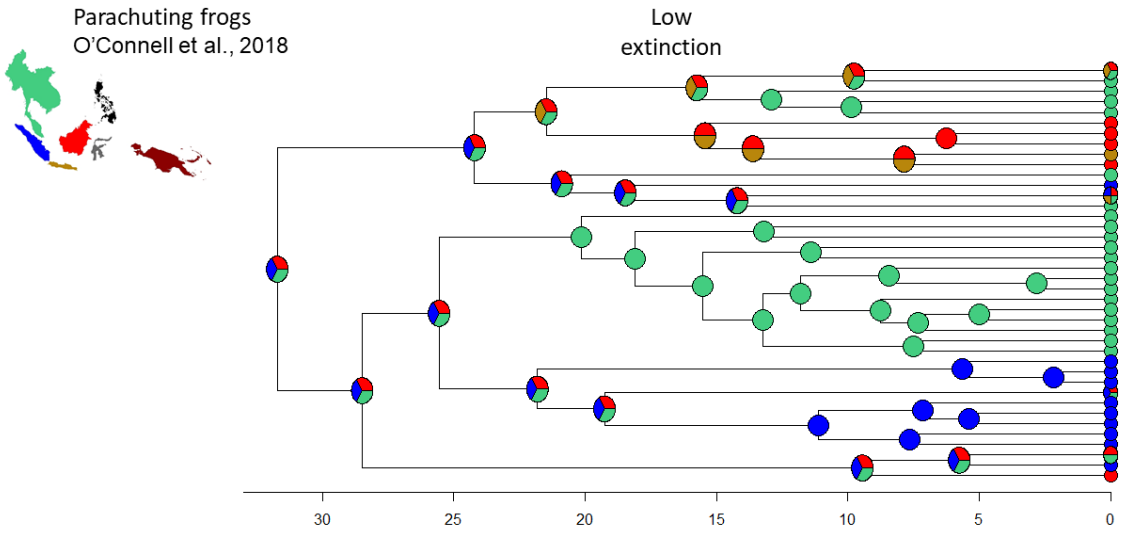


Figure S19. Ancestral distribution of parachuting frog species (*Rhacophorus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

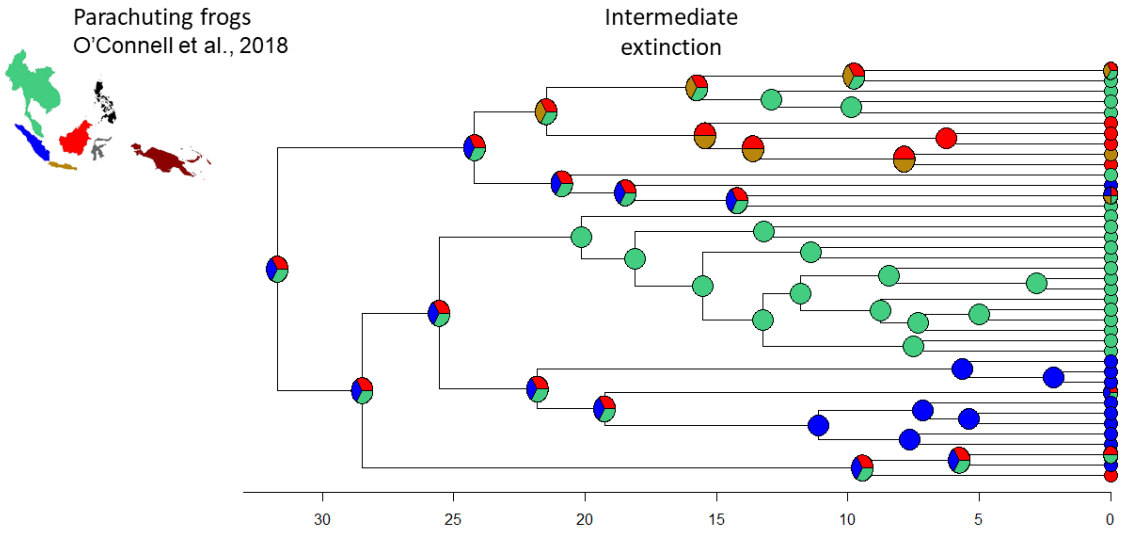


Figure S20. Ancestral distribution of parachuting frog species (*Rhacophorus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that

the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

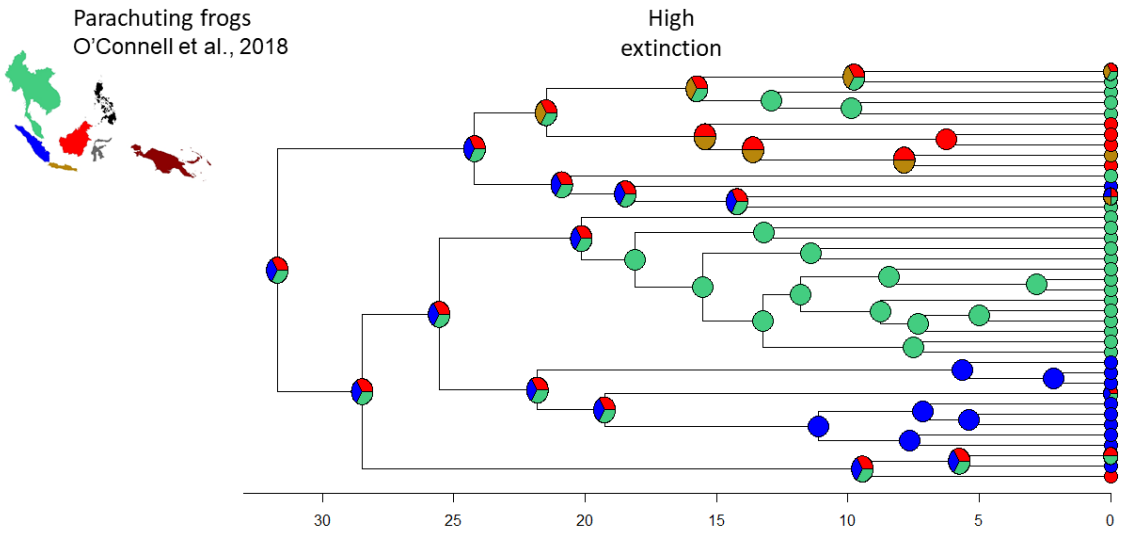


Figure S21. Ancestral distribution of parachuting frog species (*Rhacophorus*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

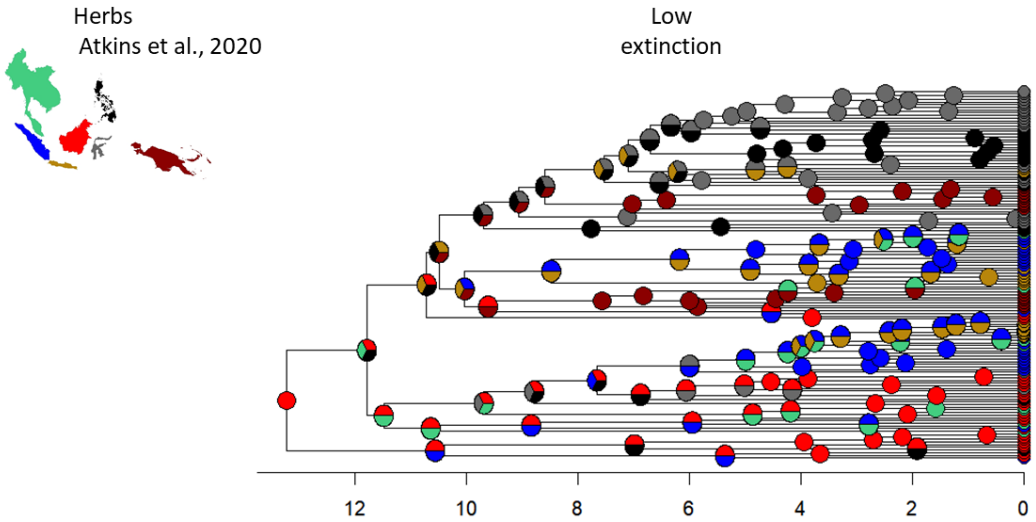


Figure S22. Ancestral distribution of tree species (*Cyrtandra*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is one-tenth of speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

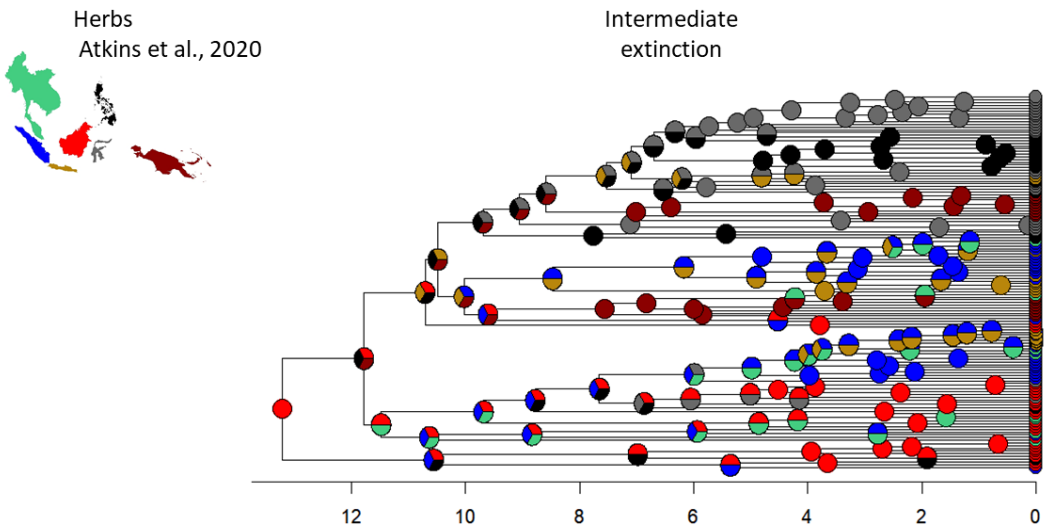


Figure S23. Ancestral distribution of tree species (*Cyrtandra*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate equals the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization

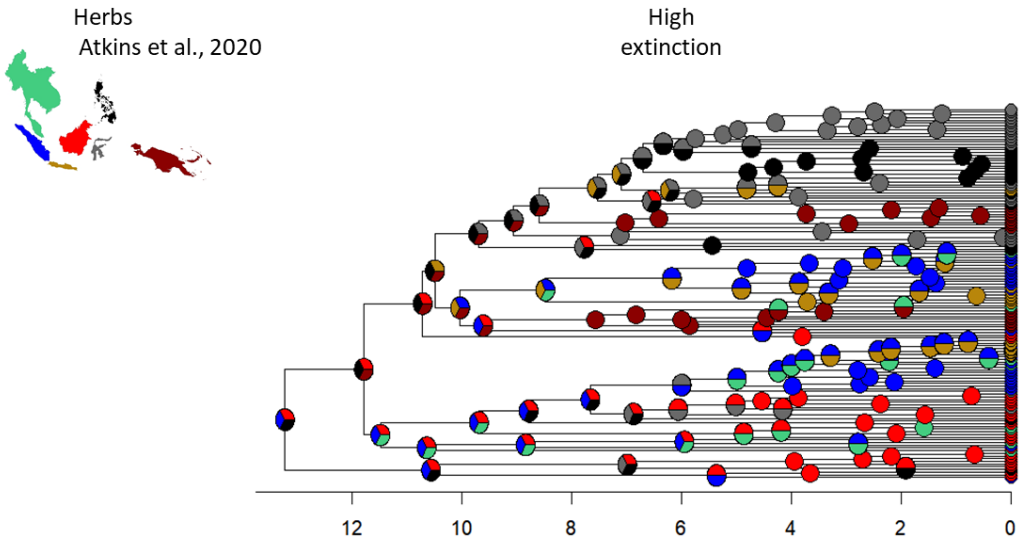


Figure S24. Ancestral distribution of tree species (*Cyrtandra*) reconstructed using LEMAD (Lineage Extinction Model of Ancestral Distribution) and assuming that extinction rate is ten times the speciation rate estimated from fitting a birth-death model to the phylogenetic tree. Nodes with more than one colour indicate that the distribution for that ancestor is estimated to include more than one area. Note that speciation rate will be adjusted accordingly during the likelihood optimization.

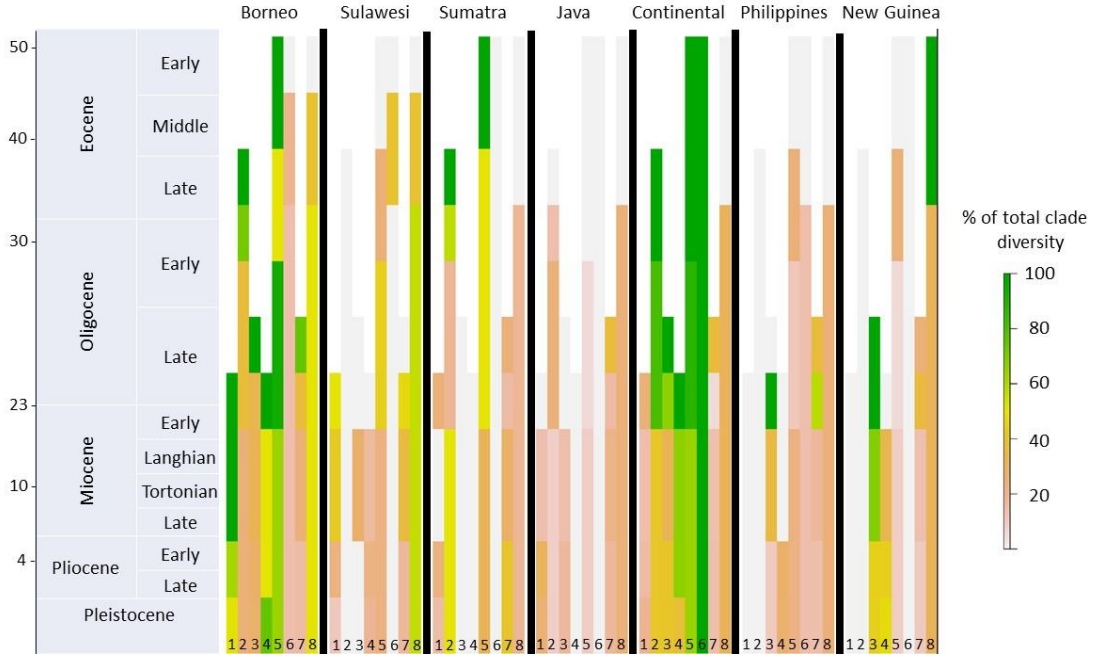


Figure S25. Reconstructed species richness over time across the Indo-Australian Archipelago under low rates of extinction scenario for eight taxonomic groups. 1: Crabs, 2: Parachuting frogs, 3: *Pseuduvaria* treelets, 4: Orchids, 5: Breadfruit, 6: Taros, 7: *Cyrtandra* herbs, 8: Crickets. Colour code shows the relative number of species inhabiting each location at each time point. Notice that widespread ancestors contribute to the species richness of several locations. Time scale on the left is in million years.

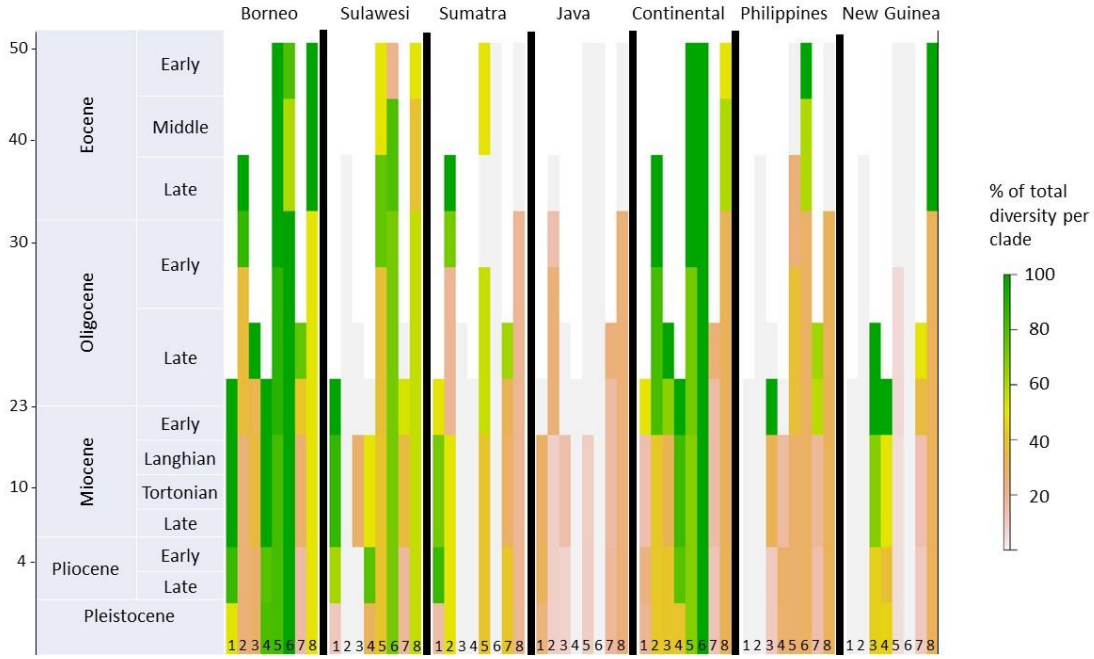


Figure S26. Reconstructed species richness over time across the Indo-Australian Archipelago under high rates of extinction scenario for eight taxonomic groups. 1: Crabs, 2: Parachuting frogs, 3: *Pseuduvaria* treelets, 4: Orchids, 5: Breadfruit, 6: Taros, 7: *Cyrtandra* herbs, 8: Crickets. Colour code shows the relative number of species inhabiting each location at each time point. Notice that widespread ancestors contribute to the species richness of several locations. Time scale on the left is in million years.