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Evidence of Sundaland's subsidence requires revisiting its biogeography

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ABSTRACT

It is widely accepted that sea level changes intermittently inundated the Sunda Shelf throughout the Pleistocene, separating Java, Sumatra, and Borneo from the Malay Peninsula and from each other. On this basis, the dynamics of the biodiversity hotspot of Sundaland is consistently regarded as solely contingent on glacial sea level oscillations, with interglacial high stands creating intermittent dispersal barriers between disjunct landmasses. However, recent findings on the geomorphology of the currently submerged Sunda shelf suggest that it subsided during the Pleistocene and that, over the Late Pliocene and Quaternary, it was never submerged prior to Marine Isotope Stage 11 (MIS 11, 400 ka). This would have enabled the dispersal of terrestrial organisms regardless of sea level variations until 400 ka and hampered movements thereafter, at least during interglacial periods. Existing phylogeographic data for terrestrial organisms conform to this scenario: available divergence time estimates reveal an 8 to 9-fold increase in the rate of vicariance between landmasses of Sundaland after 400 ka, corresponding to the onset of episodic flooding of the Sunda shelf. These results highlight how reconsidering the paleogeographic setting of Sundaland challenges understanding the mechanisms generating Southeast Asian biodiversity.

KEYWORDS

Sundaland, subsidence, sea level, vicariance, intra-specific divergence, terrestrial species

INTRODUCTION

A vast expanse of the Malay Archipelago is currently drowning beneath the Java sea and South China sea. This is, in essence, the significance of recent findings which indicate that Sundaland is subsiding at a rate of 0.2 to 0.3 mm/yr (Sarr et al., 2019). The massive continental shelf, at the crossroads of mainland Asia, the Malay peninsula, Borneo, Sumatra and Java, currently lies less than a hundred meters below sea level. With such subsidence rates, it follows that Sundaland was permanently subaerial prior to Marine Isotopic Stage 11 (MIS 11, at 400 ka; isotopic stages refer to alternating periods of warm and cool climate, odd-numbers refer to warm periods). Anticipated consequences are far reaching, for the hydrosphere and atmosphere (Sarr et al., 2019), and most importantly for the biosphere, in particular with respect to the dynamics of dispersal and divergence of terrestrial organisms across Southeast Asia.

Since the seminal work of A.R. Wallace (1869), Southeast Asia has served as a cornerstone for the field of biogeography. The islands of the Sunda shelf in particular host extraordinary biodiversity, with some 7-8% of all flowering plant and vertebrate species on Earth (Myers et al., 2000), that partly result from several dispersal waves from continental Asia and Oceania during the Plio-Pleistocene (Lohman et al., 2011). Interpreting the historical biogeography of the region relies on understanding the physical environment, specifically the interconnections between emerged lands of Indochina, Sundaland and Wallacea. Because the core of Sundaland is tectonically quiescent, as inferred from its lack of seismic activity, the current geographic framework used by biogeographers regards the Sunda shelf as exclusively reliant on eustatic sea level changes (e.g., Voris, 2000; Lohman et al., 2011; Leonard et al., 2015). According to this view, the platform would be fully exposed during glacial periods as it was during the Last Glacial Maximum, and mostly drowned during interglacials, as it is today (Molengraaff, 1921; Voris, 2000). The distribution of species across Sundaland would consequently be shaped by dispersal opportunities during glacial periods and vicariance during sea level highstands (van Den Bergh et al., 2001; Lohman et al., 2011).

SUNDALAND PALEO GEOGRAPHY REVISITED

This classic paleogeographic scenario appears to be mistaken, for the physiography of the currently flooded continental shelf reveals anything but stability: Sundaland was permanently subaerial prior to 400 ka (Sarr et al., 2019, Fig. 1). The demonstration is straightforward: if the shallow Sunda shelf remained stable throughout the Pleistocene, it would have been slowly yet extensively blanketed

by carbonates from coral reefs. It would now resemble the present-day Bahamas with an expansive carbonate platform instead of narrow fringing reefs. The argument is further supported by the stratigraphy of the uppermost cover of the Sunda shelf, which has many fewer sedimentary layers than the number of Plio-Pleistocene glacial cycles (only 2 in the shallowest parts of the shelf -Sarr et al. 2019- and up to 6 or 7 at greater depths -Alqahtani et al., 2015- which compares well with the number of interglacial stages and sub-stages since MIS11), and thus testifies to a limited number of successive flooding episodes. Last, the overwhelming presence of mangroves that festoon the islands of the Sunda shelf -while flights of uplifted coral reefs conversely dominate in Wallacea- come in support to subsidence: mangroves are more prone to develop along muddy subsiding environments than along sediment-starved uplifting coastlines. This episode of subsidence is driven by the sluggish, viscous forces of the Earth's mantle (Sarr et al., 2019), which dynamically sustained the emergence of the shallow Sundaland until the late Mid-Pleistocene, and drowned it only thereafter (Fig. 2a), thereby profoundly remodeling the paleogeography of Pleistocene Sundaland (Fig. 1).

REAPPRAISING THE PHYLOGEOGRAPHIC EVIDENCE

Attempts to unravel the biogeographic history of Sundaland have, thus far, been grounded on the premise that the Sunda shelf was only fully emergent during glacial lowstands. But Sundaland was continuously subaerial before 400 ka, and this requires a paradigm shift. As a starting point, we reappraised existing phylogeographic data in light of this new paleogeographic scenario. Our primary aim was to test whether divergence rates of lineages occupying different landmasses of Sundaland increased after the first inundation of the shelf.

Data collection

We searched the literature for divergence time estimates in pairs of lineages that are vicariant across the different landmasses of Sundaland: the Malay Peninsula, Sumatra, Borneo, and Java. The time of genetic divergence may be documented across pairs of islands or multiple islands; we retained these time estimates collectively. We first restricted our search to terrestrial organisms from evergreen forests since these organisms would be impacted by barriers to migration created by the transient marine physiography during periods of sea level highstands and/or by the changing edaphic and vegetation conditions during lowstands (Slik et al., 2011). The dispersal of open habitat organisms would conversely be less disrupted by the transient vegetation cover, if any at all, which make these organisms irrelevant to our purpose. Second, we excluded species-level phylogenetic studies, that would be appropriate for deeper geological times, and focused on intraspecific divergences. Third, we only considered divergence times derived from molecular data, using either estimates of mutation rates or secondary calibration stemming from a broader phylogenetic study.

Our search yielded 36 unambiguous vicariant sister-lineage pairs (Table 1, 22 of which had already been analyzed by Leonard et al. 2015), consisting of 21 mammals, 13 birds, one lizard and one plant pair. This stark selection has three drawbacks: i) the dataset is limited in size; ii) it is limited to vertebrates (and especially large ones), which reflects the most common sampling practices, at least at the intraspecific level; iii) given the over-representation of vertebrates in our dataset and our focus on intraspecific studies, the vast majority of compiled divergence events relies on mtDNA. The frequency distribution of divergence times (median estimates) is shown Figure 2b.

Estimation of divergence rates through time

While marine transgressions are expected to lead to vicariance among different landmasses for widespread terrestrial species, genetic divergence could also occur across the newly emerging channels. In the rest of this article, we refer to “divergence” for simplicity, keeping in mind that this measure conflates vicariance- and dispersal- induced lineage divergence. In order to test for an increase in divergence rate after the first inundation of Sundaland, we used the probabilistic model developed by Bacon et al. (2015) to study the biological consequences of the closure of the Central American Seaway (CAS) and subsequent separation of the Caribbean from the Pacific Ocean by the Isthmus of Panama. In this model, each divergence event between pairs of lineages is treated independently (i.e. regardless of the phylogeny connecting all of these lineages) and the timing of these events follows a Poisson law with a given rate that can vary through time. Four different biogeographic scenarios were compared: (i) a constant divergence rate through time, (ii) a linear increase or decrease in divergence rate over time, (iii) a shift in divergence rate at the Pleistocene boundary (as would be expected if glacial sea level oscillations were driving vicariance across Sundaland), and (iv) a shift in the divergence rate at 400 ka, coeval to the first inundation of Sundaland.

We first compared these four models using point estimates of the divergence times between pairs of lineages, using the Akaike Information Criterion corrected for small sample sizes (Akaike, 1973, hereafter AICc). We accounted for the uncertainty usually associated with divergence time estimates by resampling within the confidence interval associated with the age of each divergence event, whenever such an estimate was made available (15 out of 36 divergence time estimates, see Table 1). For each resampling step divergence times were thus sampled for each lineage pair, and this procedure was repeated 1,000 times to generate a distribution of AICc differences between models and of parameter estimates.

While we were primarily interested in the response of the whole biota to the transient paleogeography of Sundaland, we also considered the possibility that differences in dispersal ability might exist between different organisms. We thus fitted the four different divergence models to non-volant mammals and birds separately. Finally, we also tested whether the technique used to infer

divergence times in the original studies could influence our analyses, by using a subset of divergence times estimated only based on mutation rates.

Results

Intraspecific divergence times ranged from 75 ka to 5.7 Ma, with a median value of 830 ka. Among the four models of lineage divergence that we compared, the last model (shift in divergence rate at 400 ka) fit the data best by far (AICc 8:5 with all other models). When considering uncertainties in divergence times, we obtained similar results: the model with a divergence rate shift at 400 ka has a AICc 7:5 with all other models in a majority of the 1,000 divergence time resamples. Further, model selection was robust to the specific biology of the organisms, or to the analytical procedure used to calibrate divergences: relative model fit remained unchanged when considering only subsets of the complete database (Fig. 3a), i.e., bird and mammal lineages separately, or divergence times calibrated using mutation rate estimates only (of course, uncertainty increases with the size of the subsets).

Divergence rate estimates from the best fitting model revealed an 8 to 9 fold increase in the divergence rate of evergreen forest organisms after the first inundation of Sundaland (Fig. 3b, 95% CI across the 1,000 replicates: 5.77-12.86). This increase was similar when considering birds (95% CI: 5.47-14.61) or mammals (3.00-5.37) only, or when using divergence times estimated using mutation rates only (8.31-17.89).

DISCUSSION

This analysis supports a revised paleogeographic scenario for Sundaland that profoundly affected the biogeography of terrestrial organisms in the region. Before 400 ka, the subaerial Sunda shelf remained an open dispersal route for evergreen forest species, leading to relatively few divergence events. In the aftermath of the first marine incursion during MIS 11, the Sunda shelf seemingly acted as a barrier to dispersal, triggering the observed sharp increase in the rate of lineage divergence.

A new light shed on Pleistocene phylogeography in Sundaland

Existing phylogeographic data indicate that, in spite of their intermittent nature, Late Pleistocene transgressions of the Sunda shelf initiated intraspecific lineage divergence across the Sunda shelf after 400 ka. A plausible scenario for lineage divergence across Sundaland after 400 ka alternates glacial periods, during which terrestrial organisms would have been able to disperse across the Sunda shelf, and interglacials, when major landmasses were isolated by inland seaways. In this case, sea level oscillations that prevailed between 400 ka and present-day would have acted as a

“species pump” to increase the terrestrial biodiversity of Sundaland (Heaney, 1985; Brown et al., 2013), as the size of terrestrial habitats waxed and waned. Divergence would have been fostered during each of the 4 or 5 marine transgressions that flooded the Sunda shelf (Fig. 2a). Interestingly, we found no major differences between species of birds and mammals. This result may seem counterintuitive, and because water channels might not seriously hinder the dispersal of flying organisms like birds as it would for ground-dwelling organisms like mammals, it apparently challenges this scenario. However, all birds included in our analysis are relatively small evergreen forest passerines (Table 1), for which both experimental and genetic evidence suggests that they seldom cross large rivers, a phenomenon that is particularly well documented in the Amazon basin (Naka and Brumfield, 2018).

As an alternative to this clearcut “species pump” hypothesis, some authors invoke the disrupting effect of changing climatic and edaphic conditions on the vegetation cover of the episodically flooded Sunda shelf. More specifically, the emerged Sunda shelf during glacial periods might not have been covered by evergreen forests but rather by seasonal forests, herbaceous swamps, peatlands or even dry savanna, possibly because of the loss of fertility caused by the episodes of marine submersion (e.g. Bird et al., 2005; Cannon et al., 2009; Slik et al., 2011; Raes et al., 2014; Morley, 2018). Under such conditions, the Sunda shelf would have acted as a permanent barrier for evergreen forest organisms over the last 400 ky. Unfortunately, uncertainties in divergence time estimates often encompass glacial-interglacial cycles (Carstens and Knowles, 2007), which precludes discriminating between the two scenarios. Whether dispersal of evergreen forest organisms after 400 ka was only impeded by epicontinental seaways during interglacials or whether drylands corridors also limited dispersal during glacial periods thus remains an open question.

Conversely, prior to 400 ka, dispersal across the subaerial Sundaland would have been continuously possible for terrestrial species, which explains the low rates of divergence between 6 Ma and 400 ka (Fig. 2b). Incidentally, early humans transited among them from mainland Asia across the Sunda shelf during Early and Middle Pleistocene, purportedly during glacial low sea level stands (Bettis et al., 2009). We contend that instead, because Sundaland was permanently subaerial during the early and mid-Pleistocene, *Homo erectus*, together with other terrestrial organisms, could have travelled dry-shod at any time across the entire shelf, regardless of sea level oscillations.

Methodological limitations

While our aim was to draw attention on the consequences of the revised paleogeography for understanding the phylogeography of terrestrial organisms in Sundaland, we acknowledge that our dataset suffers from some limitations. The first limitation is the sample size and the restriction to vertebrates, and in particular birds and mammals. Studies of plants and arthropods do exist in the

region (e.g., Braby et al., 2015; Tanzler et al., 2016; Williams et al., 2017), but unfortunately estimates of divergence times between intraspecific lineages that are vicariant across landmasses of Sundaland are, to our knowledge, virtually nonexistent. The second limitation comes from the almost exclusive reliance on mtDNA data to infer and date phylogenetic relationships between lineages. Regrettably, few studies using nDNA exist in the region, and are limited to one or a few loci (Manawatthana et al., 2017). Next-generation sequencing of nDNA (Harrison and Kidner, 2011) will undoubtedly soon alleviate this issue.

The statistical method that we used to measure divergence rates also has its drawbacks. The main critique points to the reliance on estimates of divergence times from gene trees, which leads to overestimated divergences between lineages (Marko et al., 2015). This criticism has been levied against the study that introduced this technique of using organismal divergence times to substantiate geologic changes in the Central American Seaway (CAS, Bacon et al., 2015). However, it does not apply to our analysis since we actually demonstrate that divergence times across Sundaland are disproportionately concentrated in a recent period, the last 400 ky. Of course, directly measuring divergence times from complete phylogenies would provide more accurate estimates of divergence rates through time, but this kind of data is usually lacking, especially for recent timescales, as in the current study.

CONCLUSIONS

The sharp correspondence between geological and biological evolution underscores the effects of geological changes on the evolutionary history of different lineages. Albeit they have only been operating over the last 400 ka, because Sundaland lies at a strategic geographic position, and because they seem to be very dynamic, these structuring mechanisms have largely contributed to shape the distribution of species at present-day in the entire region. These results, based on joint observations of phylogeography and geology, prompt reconsideration of the patterns of diversification in Sundaland.

More generally, the parallel to the case of the Central American Seaway is relevant beyond the methodological aspects: while Bacon et al. (2015) took advantage of the patterns of diversification to establish the timing of a geological event, this history of Sundaland exemplifies how the geological record conversely informs on the diversification patterns. But in Sundaland also, the timing of divergence can narrow uncertainties in the timing of paleogeographic changes (e.g., Picard et al., 2008). While geomorphological data bracket subsidence rates of the Sunda shelf between 0.2 and 0.3 mm/yr, phylogeographic data arguably curtail the range to its lower end (Fig. 2a). Likewise, the similarities between these Sundaland and CAS have also been invoked when considering the impact of the geological evolution on the oceanic circulation pattern (e.g. Coates and Stallard, 2013), or on

the Miocene to present-day climate system (Brierley and Fedorov, 2016). Both regions highlight the tight relationships between climate, biogeography, and geology, as anticipated by A. von Humboldt.

Figure 1: Interglacial paleogeography of the Sunda shelf during Pleistocene. a) Prior to 400 ka (Marine Isotope Stage 11), Sundaland was permanently subaerial, regardless of sea level oscillations (indicative reconstruction), and drained by a fluvial network (Molengraaff, 1921). b) After 400 ka, the Sunda shelf was inundated during interglacial sea level highstands (as since the Holocene deglaciation). Blue curves delineate the -50 m and -120 m isocontours at present-day. Black arrows indicate potential dispersal routes for terrestrial organisms, that were active prior to 400 ka (solid) and broken thereafter (dashed).

Figure 2: a) Relative sea level in the Sunda shelf. Orange domain depicts the elevation of the core of the Sunda shelf, that currently stands between 50 m and 120 m below current sea level (blue line) and subsides at a rate of 2.5 mm/yr (uncertainty in gray, from 2 to 3 mm/yr, Sarr et al., 2019). Elevation accounts for both absolute sea level change (Bintanja and van de Wal, 2008) and subsidence. Inset: enlarged view of the most recent 800 ky, highlighting the first inundation of the shelf during Marine Isotope Stage 11 (MIS 11, 400 ka). White curve shows relative sea level (i.e., in the absence of subsidence). b) Divergence time (blue lines) for 36 vicariant terrestrial organisms. The histogram shows the distribution of intraspecific divergence times. Dashed line indicates the timing of first marine transgression over the shelf.

Figure 3: a) Comparison of alternative models of divergence rate. Boxplots show the distribution of AICc values obtained across the 1,000 resamples of divergence time estimates for three models of divergence, in comparison to the constant rate model. AICc comparisons are shown for the full dataset (left), as well as three subsets (birds, mammals, dating using mutation rates). b) Divergence rate shift after 400 ka. Violin plots show the distribution of the ratio of the divergence rate after 400 ka to the divergence rate before, obtained across the 1,000 resamples of divergence time estimates. Boxplots within each violin plot show the median of each distribution, as well as the 25% and 75% quantiles.

Table 1: Intraspecific divergence times. For each divergence event studied here, the table gives the species name, taxon and group, the landmasses between which vicariance occurred, the study from which divergence times were extracted, the study from which the original genetic data was obtained, the type of genetic data and the kind of method used to date divergence. A list of the data sources is found in Appendix 1, Supporting Information.

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Biosketches

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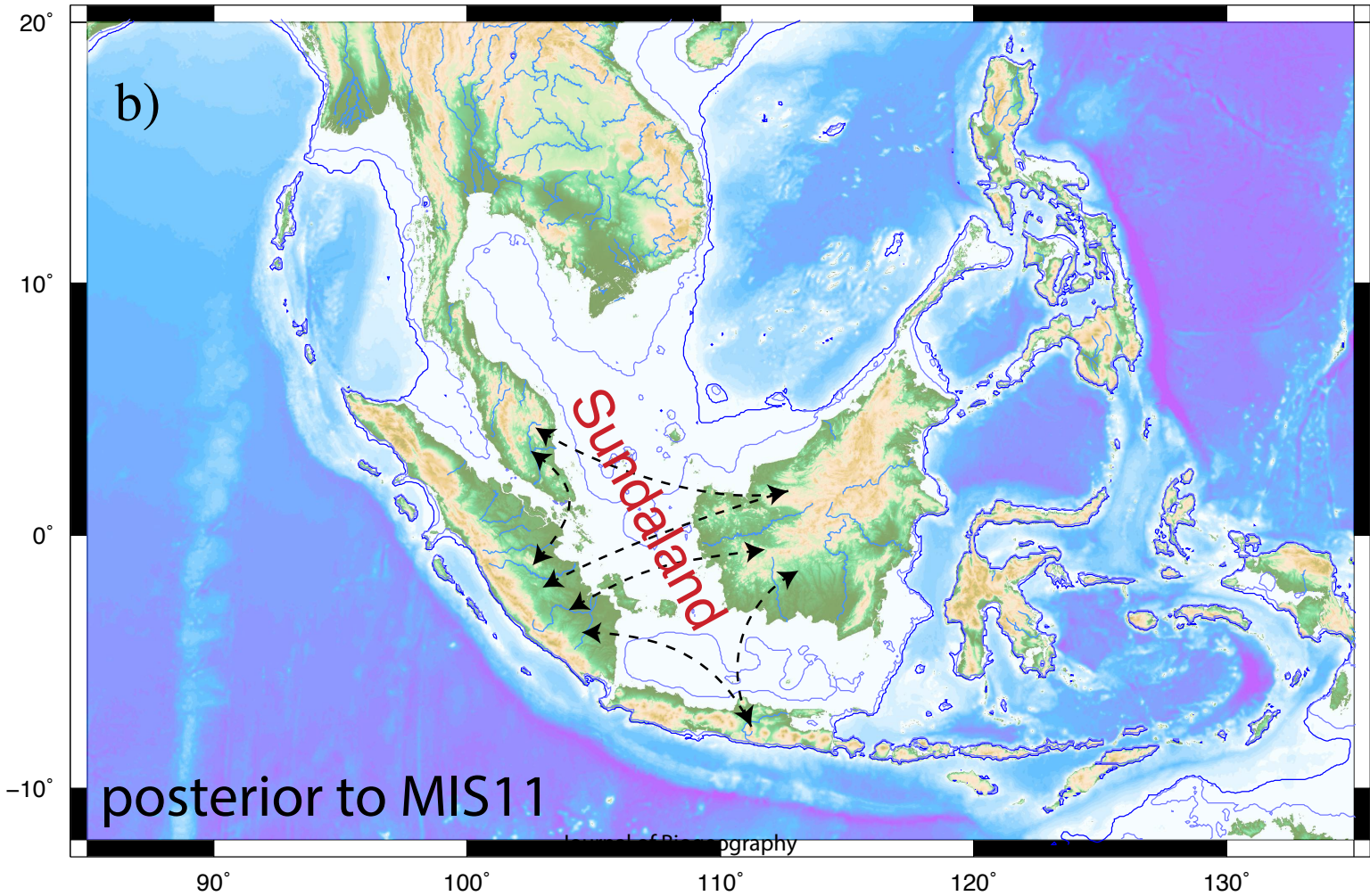
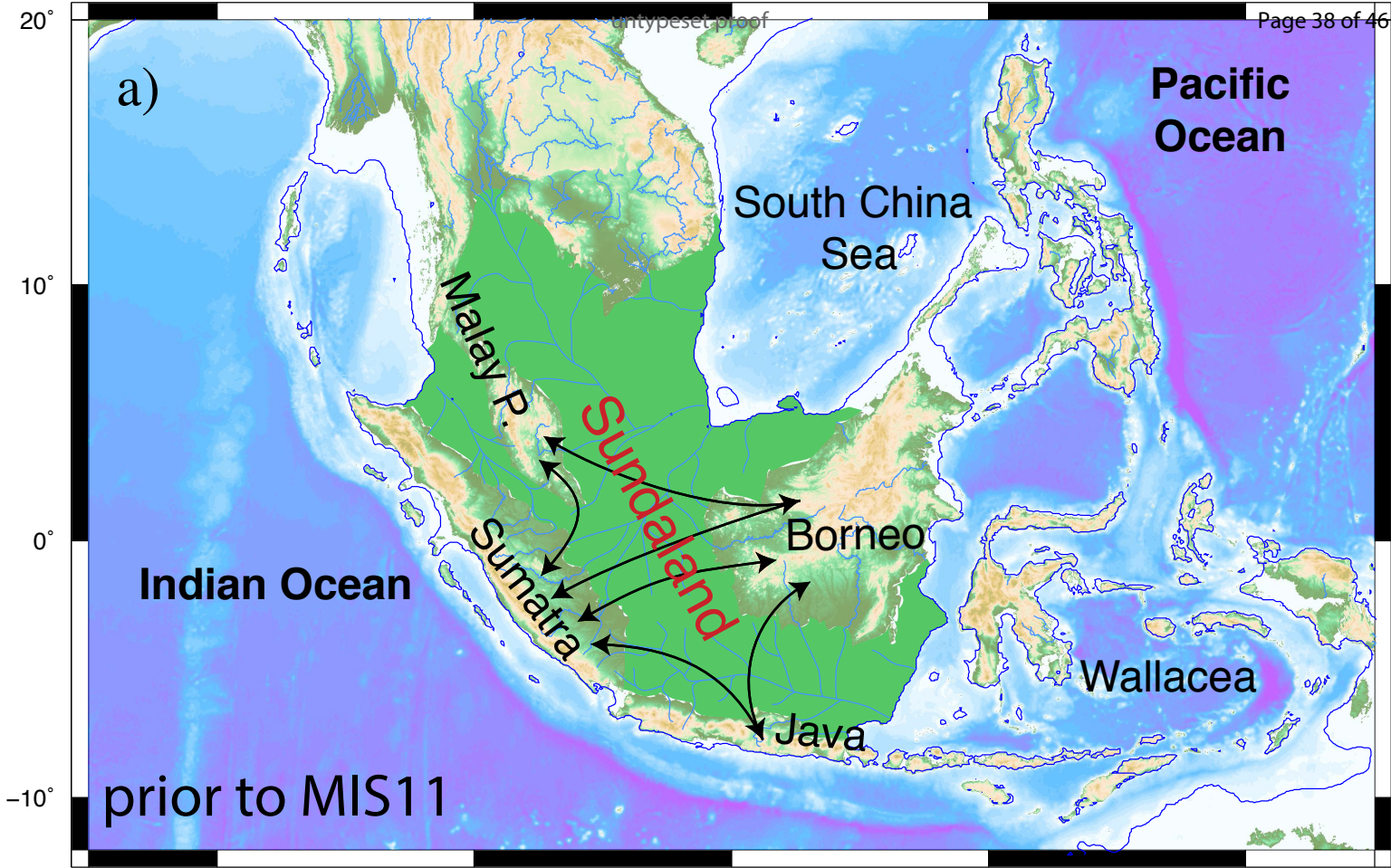
Sri Yudawati Cahyarini is a researcher at LIPI (Bandung, Indonesia). Her research focuses on extracting the history of Quaternary climate changes in SE Asia from the geological archive.

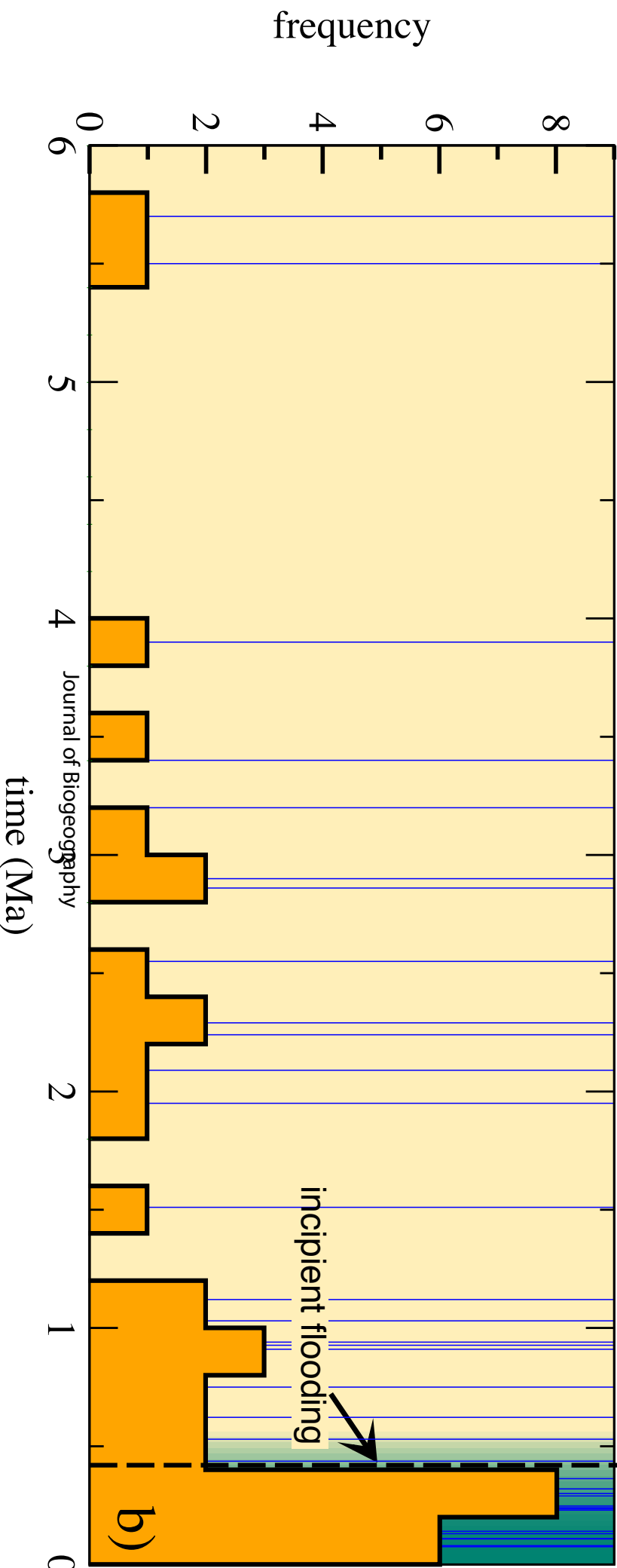
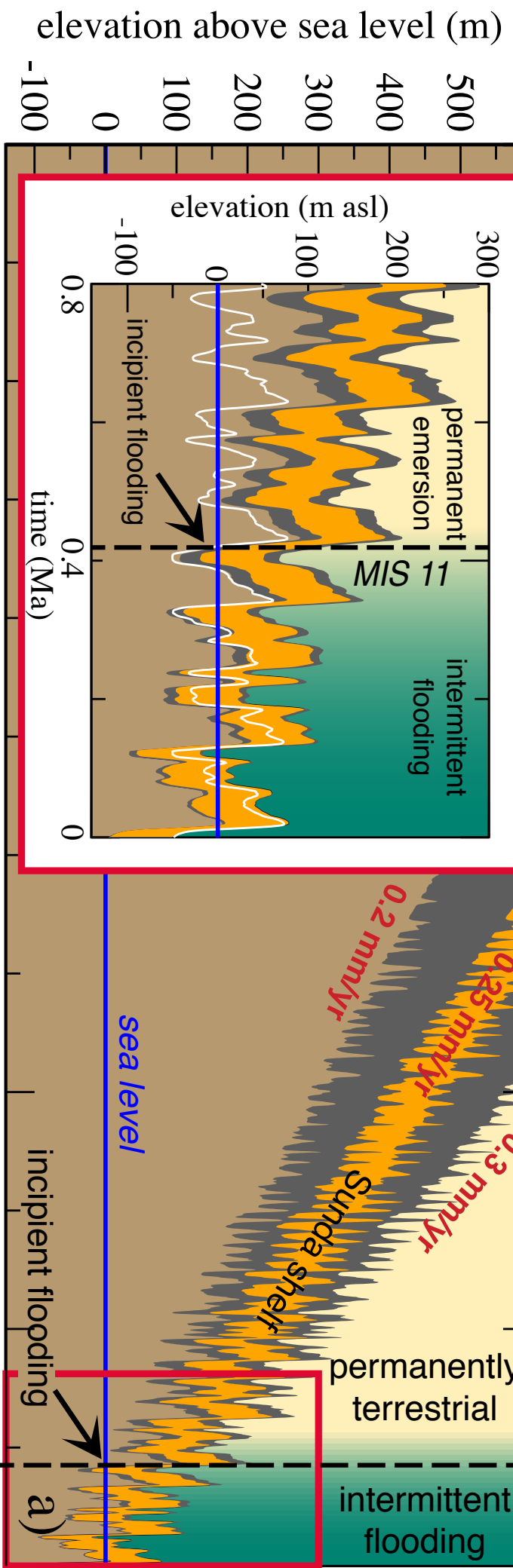
Acknowledgements

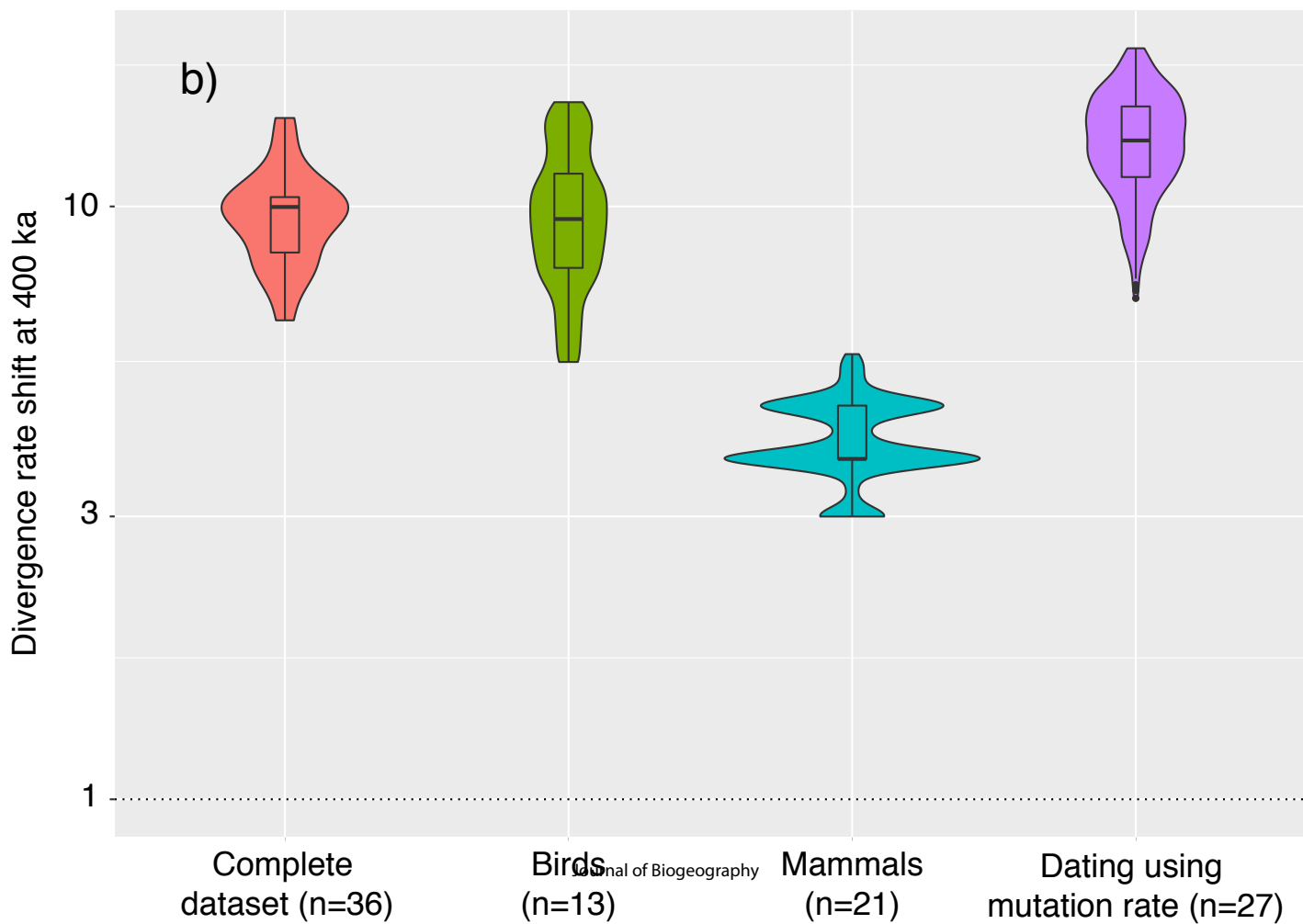
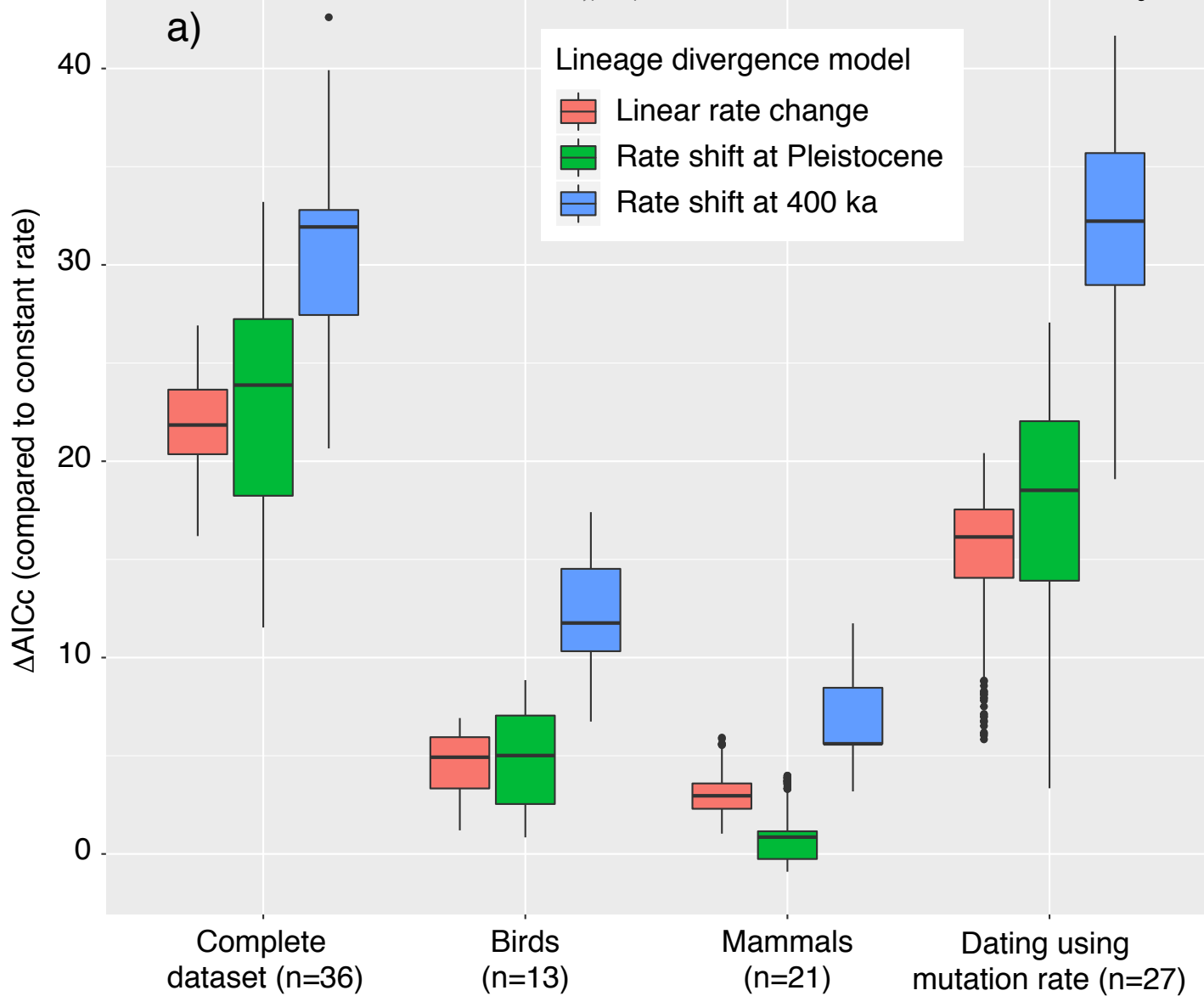
This research benefited from the support of the National Geographic Society (Grant #NGS-50778R-18, The journey of *Homo erectus* across Sundaland). This paper benefited from the fruitful reviews by David Lohman and two anonymous reviewers. All analyses were run in R 16 (R Core Team, 2019). The code used for fitting the different versions of the Poisson divergence model is made available at <https://github.com/fcboucher/Poisson-rates-whole-biotas>.

Supplementary materials

Table S1







Evidence of Sundaland's subsidence requires revisiting its biogeography

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Appendix 1 - Data sources for Table 1 (Intraspecific divergence times)

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Source for div	Source for ger	Taxon	Group	Geographic sp	Time mean	Time min	
Leonard et al.	Patou et al.	2004	Paradoxurus f	Carnivores	Malay Penins	1.95 NA	
Luo et al.	2004	Luo et al.	2004	Panthera tigris	Carnivores	Sumatra vs Ma	0.108 0.059
Wilting et al.	2004	Wilting et al.	2004	Panthera pardus	Carnivores	Java vs Malay	0.622 0.393
Wilting et al.	2004	Wilting et al.	2004	Neofelis nebulosa	Carnivores	Sunda islands	2.86 1.71
Wilting et al.	2004	Wilting et al.	2004	Neofelis nebulosa	Carnivores	Sumatra vs Borneo	0.437 0.03
Patel et al.	2004	Patel et al.	2004	Prionailurus bengalensis	Carnivores	Sunda islands	0.927 0.568
Patel et al.	2004	Patel et al.	2004	Prionailurus bengalensis	Carnivores	Java vs (Borneo	0.235 0.135
Martins et al.	2004	Martins et al.	2004	Muntiacus muntjak	Cervids	Sunda islands	1.12 0.53
Karin et al.	2004	Karin et al.	2004	Eutropis rugifrons	Lizard	Borneo vs (Sulawesi	5.5 3.49
Leonard et al.	2004	Moyle et al.	2004	Enicurus leschenaultii	Passerines	Borneo vs (Sulawesi	0.247 NA
Leonard et al.	2004	Lohman et al.	2004	Copsychus saevus	Passerines	Borneo vs (Sulawesi	0.395 0.32
Leonard et al.	2004	Lim et al.	2004	Stachyris erythrogastra	Passerines	Borneo vs (Sulawesi	3.9 NA
Leonard et al.	2004	Lim et al.	2004	Stachyris polioptila	Passerines	Borneo vs (Sulawesi	1.03 NA
Leonard et al.	2004	Lim et al.	2004	Malacocincla leucostriata	Passerines	Borneo vs (Sulawesi	2.55 NA
Fuchs et al.	2004	Fuchs et al.	2004	Alphoixus brunneiceps	Passerines	Borneo vs Sumatra	3.2 2.2
Manawatthan	2004	Manawatthan	2004	Charlottia charlottae	Passerines	Borneo vs (Sulawesi	5.7 3.7
Steiner et al.	2004	Steiner et al.	2004	Dicerorhinus sumatrensis	Perissodactyle	Borneo vs (Sulawesi	0.3631 0.291
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon heugeni	Piciforms	Borneo vs (Sulawesi	0.53 NA
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon heugeni	Piciforms	Malay Penins	0.08 NA
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon chinensis	Piciforms	Borneo vs (Sulawesi	0.91 NA
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon chinensis	Piciforms	Malay Penins	0.11 NA
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon auriceps	Piciforms	Borneo vs (Sulawesi	0.23 NA
Leonard et al.	2004	den Tex & Lec	2004	Psilopogon auriceps	Piciforms	Malay Penins	0.075 NA
Nater et al.	2004	Nater et al.	2004	Pongo pygmaeus	Primates	Sumatra vs Borneo	2.09 1.27
Leonard et al.	2004	Gorog et al.	2004	Leopoldamys leucurus	Rodents	Borneo vs (Sulawesi	2.29 NA
Leonard et al.	2004	Gorog et al.	2004	Leopoldamys leucurus	Rodents	Malay Penins	2.24 NA
Leonard et al.	2004	Gorog et al.	2004	Maxomys whiteleyi	Rodents	Borneo vs (Sulawesi	0.75 NA
Leonard et al.	2004	Gorog et al.	2004	Maxomys whiteleyi	Rodents	Malay Penins	0.29 NA
Leonard et al.	2004	Gorog et al.	2004	Maxomys surinensis	Rodents	Borneo vs (Sulawesi	1.51 NA
Leonard et al.	2004	Gorog et al.	2004	Maxomys surinensis	Rodents	Malay Penins	0.94 NA
Leonard et al.	2004	Achmadi et al.	2004	Maxomys rajah	Rodents	Borneo vs (Sulawesi	0.24 NA
Leonard et al.	2004	Achmadi et al.	2004	Maxomys rajah	Rodents	Malay Penins	0.13 NA
Leonard et al.	2004	den Tex et al.	2004	Sundasciurus	Rodents	Borneo vs (Sulawesi	0.3 NA
den Tex et al.	2004	den Tex et al.	2004	Sundasciurus	Rodents	Borneo vs Ma	2.9 NA
Ohtani et al.	2004	Ohtani et al.	2004	Shorea leprosifolia	Plants	Borneo vs (Sulawesi	0.140671 0.04543

Time max	Type Interval	Phylogeny ma	Phylogeny inf	Calibration
NA	NA	mtDNA	Maximum-like	Mutation rate
	0.157 95% CI	mtDNA	Maximum-par	Mutation rate
	0.886 95% CI	mtDNA	Bayesian conc	Secondary calibration
	4.02 95% CI	mtDNA	Bayesian Anal	Secondary calibration
	0.845 95% CI	mtDNA	Bayesian Anal	Secondary calibration
	1.3 95% HPD	mtDNA	Bayesian conc	Mutation rate
	0.332 95% HPD	mtDNA	Bayesian conc	Mutation rate
	2.22 95% HPD	mtDNA	Bayesian conc	Secondary calibration
	8.36 95% HPD	mtDNA	Bayesian conc	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
	0.47 Two dates	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
	4.1 95% HPD	mtDNA	Bayesian conc	Mutation rate
	7.4 95% HPD	mtDNA + nDN	Multi-species	Mutation rate
	0.435 95% HPD	mtDNA	Bayesian conc	Secondary calibration
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
	3 95% HPD	mtDNA	Bayesian conc	Secondary calibration
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Maximum-like	Mutation rate
NA	NA	mtDNA	Bayesian conc	Secondary calibration
	0.417525 90% HPD	cpDNA	IM model (Ba)	Mutation rate