nature portfolio

Peer Review File

Quaternary landscape dynamics boosted species dispersal across Southeast Asia

Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality.

14th May 21

Dear Dr Salles,

Your manuscript titled "Quaternary landscape dynamics boosted species dispersal across Southeast Asia" has now been seen by 3 reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to
• address these criticisms (that is, either to incorporate the suggestions or provide a compelling argument why the point made by the reviewer is not valid, or relevant to the editorial threshold as outlined below)
AND
• meet our editorial thresholds as outlined below,

then we would be happy to look at a substantially revised manuscript. However, please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

In the following, we list our main editorial thresholds:

Provide a robust integration of landscape evolution and connectivity models for the geomorphological evolution of Sundaland over the last 1 million years and ensure that your conclusions on the factors behind species diversification are compellingly supported by this modelling or softened accordingly

Clearly describe the species for which your modelling is applicable and fully discuss and take into account the limitations that this places on the conclusions you are able to draw

Ensure that your modelling approach, error propagation and data sources are fully explained and justified to the extent that your work is reproducible. For your information, we offer up to 5,000 words for the main text in addition to unlimited space in the Methods section

In addition, please supply point-by-point responses to all the reviewers' comments.

If the revision process takes significantly longer than three months, we will be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to accommodate necessary extensions nevertheless.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the referees' comments (which should be in a separate document to any cover letter) and any completed checklist:

[link redacted]

** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

Please do not hesitate to contact me if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

Joe Aslin

Associate Editor,
Communications Earth & Environment
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EDITORIAL POLICIES AND FORMAT

If you decide to resubmit your paper, please ensure that your manuscript complies with our editorial policies and complete and upload the checklist below as a Related Manuscript file type with the revised article:

Editorial Policy Policy requirements

For your information, you can find some guidance regarding format requirements summarized on the following checklist:(https://www.nature.com/documents/commsj-phys-style-formatting-checklist-article.pdf) and formatting guide (https://www.nature.com/documents/commsj-phys-style-formatting-guide-accept.pdf).

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

Overview

This paper modelled geomorphology evolution in Sundaland over the last 1 Myr using a physics model (Badlands) and inputs from rainfall, sea-level fluctuations and vertical tectonics. The main takeaway from this analysis is similar to that from a previous paper (Sarr et al 2019), in that the now submerged Sunda shelf was subaerial prior to 400 kya. The authors calibrated their landscape evolution model against results from seismic surveys and locations of halfbeak fishes.
Using changes in elevation, proximity to rivers and steepness of local slopes, the authors then parameterized landscape resistance maps that were claimed to be species agnostic and thus applicable to a wide variety of species. The resistance maps were then analyzed with Circuitscape to produce estimates of current density (equivalent to gene flow or movement). The authors then made conclusions about which parts of the shelf were important for maintaining gene flow.

This paper arrived at the same insight as Sarr et al 2019 in that Sunda shelf was subaerial before 400 kya, which is not surprising since the main estimate of subsidence rate came from this earlier paper. The geomorphology evolution model added additional insights in terms of detailed topography of the land and locations and captures of paleo-drainages.

The paper claimed that timings of intraspecific divergence from 1 meta-analysis (Husson et al 2019), when matched against its estimates of drainage reorganization and river capture, indicated that "distribution intraspecific divergence times is more likely driven by geomorphological changes rather than by sea- level oscillations". I find this claim to be not substantiated, since many other mechanisms (eg changes in vegetation, paleo-climatic changes, simple isolation by distance or lineage sorting, stochastic extinctions of populations, sea-level fluctuations) can also produce similar patterns. Importantly, this meta-analysis (and ED Fig 4) is the only external source of data used to validate the geomorphology evolution model. Looking at ED Fig. 4, it appears that any distribution of divergence times within of the last 500 kya can be construed as support of the model. Further, I find Husson et al 2019 to be a poor summary of phylogeographic studies carried out in SE Asia. It focused on vertebrates that live in closed-canopy forests (mainly birds and mammals, and even then only a subset of species were investigated) and largely ignored other taxa (eg plants, invertebrates). Thus, I believe that Husson et al 2019 does not provide a comprehensive look at the phylogeographic histories of SE Asian taxa.

The paper created species-agnostic landscape resistance maps using changes in elevation, proximity to rivers and steepness of local slope and interpreted the Circuitscape model as being generally applicable to taxa in SE Asia (eg. Ln183-184 "instead of relative sea-level fluctuations, we found that the fast pace of physiographic changes is more likely to drive diversification processes in the region"). The authors need to provide justifications as to why these landscape features are important to many species (ie it is species agnostic instead of targeting at some taxa). Many species would have very different habitat and dispersal requirements. For example, a bird species can have a large elevational range (ie not restricted to one elevation band), find rivers to be barriers rather than corridors, and are not affected by steepness of local slopes. Does this model apply to freshwater species as well? It seems like the LEC+slope+proximity to river model may be applicable for frogs and amphibians (eg Funk et al 2005 Mol Ecol 14:483) and not as general as the authors claim it to be. Generally, multispecies resistances models (Koen et al 2014) tend to only consider species that use the same vegetation/habitat type (eg. closed forests, edge habitats, open prairie). The support of rivers as corridors for many forest species is not ubiquitous, In fact, they tend to be regarded as barriers. Eg Gascon, C. et al. PNAS 97, 13672-13677 (2000) and Naka, L.N. & Brumfield, R.T. Science Advances 4, eaar8575 (2018)).

Main text

Ln1

1,2 insufficient citations

1- does not talk about Quaternary diversification. Main focus was on geographic histories, biogeography (distribution patterns), adaptation to predicted climate change and conservation. Other appropriate papers like the following should be consulted. Sheldon and Leonard, Moyle

Sheldon, F., Lim, H.C., & Moyle, R. Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. Journal of Ornithology 156 (Supplemental 1), 91-113 (2015).

Leonard, J.A. et al. Phylogeography of vertebrates on the Sunda Shelf: a multi-species comparison. J Biogeogr 42, 871-879 (2015).

Moyle, R.G. et al. Phylogeny and biogeography of the core Babblers (Aves: Timaliidae). Syst Biol 61, 631-651 (2012).

Ln32

In addition to sea-level fluctuations, researchers have considered other factors to be important in driving diversification, such as changes in paleo-climate conditions, dispersals from other regions, formation of forest refugia due to expansion of open habitats, and adaptive divergence. This is a general statement that seems to suggest that sea-level increases were equally important for promoting speciation in a wide variety of taxa that occupy diverse habitats such as mountains, open/edge habitats and mangrove.

Ln 35

Find modern citations that relate the history of sea-level fluctuations to the phenomenon of species pump. Do researchers really propose sea-level fluctuations as a species pump or sometimes consider it to be a homogenizing force that retards diversification or divergence? eg Zroweicki 2014 on Anopheles,

Additionally, many studies find that species formation often predate the Quaternary, contrary to what was claimed in Ln1.

e g Hinckley 2020 on Tree Squirrels, Quek 2007 on mutualistic ants.

This paper incompletely surveyed the literature on species diversification in SE Asia and did not provide a nuanced look at the various hypotheses that have been put forth to explain temporal and spatial patterns of diversification.

Ln39

Elaborate these additional factors. Ref 6-10

9 – soil

10 – paleo-drainage connectivity

It is unclear what additional factors were proposed by the other cited references.

Ln43

“Limited work on roles of geomorphology”. The two cited references (10, 12) on diversification are on freshwater fishes. It seems to suggest that geomorphology modeling of this paper is only applicable to freshwater taxa that were affected by drainage changes.

Ln48

It is hard to tell what for which taxa this model of dispersal corridors is applicable. Please note

comments under Overview. It appears that landscape resistance based primarily on physiography is only applicable to a certain group of species and the authors need to qualify the generality of the connectivity model (or validate it across a wide variety of taxa). In other studies, multispecies resistance maps were made for species that share the same habitat requirements, eg. native forest- and wetland-dwelling species. Koen 2014 Methods in Ecol and Evol 5:626

Ln84
Most researchers have a nuanced view of whether sea-level changes are a species pump. Many studies found deeply diverged E-W lineages, indicating that there were rainforest refugia / areas of endemism despite repeated land bridge connections. Eg Sabah often shows deeply divergent lineages despite its permanent connection to the rest of Borneo. This pattern was found in many taxa from birds to Macaranga plants (Banfer et al 2016 Mol Ecol 15:4409). Thus, it is overly simplistic to implicate that scientists consider sea-level fluctuations as the primary mechanisms of generating species in SE Asia, and they only drive diversification, not homogenization or dispersals.

Ln86
Using the two papers (2 and 4) as evidence to support late Pleistocene increase in diversification rate is flawed.

Mason et al found “early diversification between east and west Bornean lineages in colugos, lesser mouse deer and Sunda pangolins, but not in great mouse deer”. As one can tell from their Fig. 3, most splits across E and W Sundaland (ie between Borneo and Malaysia/Sumatra) predated late Pleistocene. There is no evidence that there is an increase in diversification during late Pleistocene.

Lohman et al stated this “Present distribution patterns of species have been shaped largely by pre-Pleistocene dispersal and vicariance events, whereas more recent changes in the connectivity of islands within the Archipelago have influenced the partitioning of intraspecific variation”. The formation of intraspecific variation and population structure is not the same as diversification.

Sholihah et al. found that a large proportion of speciation events occurred during the Pleistocene but this is based on molecular OTUs, not actual “taxonomic” species. Other studies have found such species delimitation techniques tend to overestimate the number of species (ie overspilt species), Sukumaran and Knowles 2017 PNAS 201607921 (2017).

Ln 86
I am not sure how Husson et al (6) is considered to be the existing phylogeographic dataset. This meta-analysis looked mainly at vertebrates (only 1 plant species, Shorea) and most taxa are birds or mammals. Husson et al also seemed to cherry pick data, selecting only a subset of species to use in their meta-analysis. For example, Leonard et al (2015) looked at 18 species of birds and their divergence times within Sundaland, but Husson et al (2015) only cited five. Also, this paper is predisposed to find recent divergence times (ie supporting Late Pleistocene increase in diversification rate) because it focused only on divergence times within recognized species. If sister species or congenerics were studied, it might find similar diversification rates during and before Pleistocene.

Ln89
I don’t think paleo-drainage systems have been invoked to explain spatial distribution of SE Asia

biota much. Voris 2000 only gave a series of bathymetric maps (no biogeographic studies). Molengraaf looked at coral reefs and freshwater fishes, and Sholihah looked at freshwater fishes. Thus, it seems to be relevant to only to freshwater aquatic species.

Ln103
Does catchment characteristics mean catchment areas? Most the correlation coefficients have intermediate negative values, but no p-values. It makes tautological sense that increased sea-level meant smaller basins, but how do the correlation coefficients tell us that changes in basin boundaries and basin capture events were correctly modeled as well. In other words, what else do these correlation coefficients tell us other than that basins became smaller when sea-level rose.

Ln121
Woodruff 2010 talked about future climate change caused by increased CO2 emission (pg 929) and did not focus on paleoclimatic variation and is thus not a suitable citation.
Check Lim et al (2011) Evolution 65, 321-334, Lim et al (2015) Current Zoology 61, 922-934 and other papers as examples of papers that used environmental niche modeling and paleoclimatic models.

Ln 125-131
"…our simulations demonstrate that [physiographic changes of river basins] are likely critical to some species.". The main support for this appears to have come from ED Fig 4. This figures show a series of marine transgressions, and connection or disconnection of basins. Superimposed are some estimates of intraspecies divergence times. It is not clear how having divergences and physiographic changes both occurring within the last 500kya means that physiographic changes of river basins are critical to some species. In my opinion, these data from Husson et al do not constitute strong evidence for intraspecific divergences times being driven by geomorphological changes rather than by sea-level oscillations or other processes.

Ln137
The authors are not explicit about what types of species the LEC+river closeness+local slope model is suitable for. In other words, it is hard to envision what species or species groups this model is useful for. Many species would have very different habitat and dispersal requirements (eg volant vs non-volant animals). For example, a bird species can have a large elevational range (ie not restricted to one elevation band), find rivers to be barriers rather than corridors and are not affected by steepness of local slopes. Is this model applicable to aquatic or terrestrial species? It seems like this model may be applicable for frogs and amphibians (eg Funk et al 2005 Mol Ecol 14:483) and not as general as the authors claim it to be.
Many multispecies resistances models (Koen et al 2014) rely on species requiring the same vegetation/habitat type (eg. closed forests, edge habitats, open prairie).

Ln163 and Ln183
"…we found that the fast pace of physiographic changes is more likely to drive diversification processes in the region."

This paper needs to find currently available phylogeographic data or generate data to backup up its hypotheses regarding movement corridors (eg. Fig 3). For example, it is true that for a large suite of species, the Malay Peninsula and Sumatra is a place where genetic differentiation is low. And are populations in southern, eastern and northern Borneo (gray areas in Fig 3) highly differentiated from each other.

Methods
Ln292
The PaleoClim database presumably simulated paleo-climatic conditions while treating Sundaland as not having experienced subsidence (the previous paradigm). A permanently subaerial Sunda shelf should reduce maritime impact in the region. How will this affect estimates of rainfall?

Ln330
Reference 13 is Voris 2000. It shows a series of bathymetric maps but does not study freshwater taxa directly.

Ln389
peak instead of pick

Reviewer #2 (Remarks to the Author):

I enjoyed reading this paper. It's nice to see growing acknowledgment that historical contingency is integral to understanding modern and historic species distributions and I think this paper adds to that body of work. I think the authors do a decent job of synthesizing various factors which influence species distribution over time and showing how these can be related to our empirical understanding of a region.

My "Full Comments" are arranged chronologically as they occurred to me while I read the paper. My primary concern, reflected there and in "Major Comments" is that certain material that could help orientate a reader to the authors' aims seems buried deeply now. Surfacing that would be useful.

My other major concern is that the work seems far less reproducible than it could in principle be. With a complicated modeling endeavour like this it's easy for issues to slip into the computational pipeline. Having that pipeline documented and easily re-run would greatly increase my confidence in the results.

Assuming the authors already have a reproducible workflow available, I think my concerns can be addressed with only Minor Revision; however, I would have a hard time recommending the paper for publication without a reproducible workflow archived in an appropriate place.

Major Comments
==========

1. Reproducibility. The authors state that "Two main scientific software are used in this study; Badlands and Circuitscape. In addition, a series of Python libraries are required and provided in a Docker container (geodels/gospl:bio)." This is nice, but I am interested in the software actually used to produce the results in the paper, not the collection of libraries composed to generate that software. A docker container with a script that generates the output figures shown in the paper would be ideal.

2. What species are the authors talking about? It takes until Line 411 to get this basic modeling detail. For a long time I was very confused.

3. What are the different scenarios and what are they testing? In the paper proper the authors refer obliquely to a variety of scenarios, but without much if any detail about what they are and why they are chosen. The supplemental doesn't provide much additional enlightenment. I see different sea level models and tectonic forcings, but how are these coupled to produce a realization? Is it a full-factorial design or something more judicious? What scenario are the results based on (or set of scenarios for judging sensitivity)?

Full Comments
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L79: Perhaps this is just the Nature style, but the sudden introduction of scenarios here catches me off-guard. Additionally, I don't see a clear list of scenarios anywhere in the paper or supplement. See Barnes and Clark (2017, "Sixty-Five Million Years of Change in Temperature and Topography Explain Evolutionary History in Eastern North American Plethodontid Salamanders") p 3-5 for a good example of explaining scenarios.

Extended Data Figure 1: Figure b here looks as though uplift data does not necessarily follow topographic boundaries. As a result, I think, the fitted surface's lower right blue line cuts directly through a swath of topography that appears, to me, as though it might reasonably be thought of as uplifting. Have you experimented with adding or dropping points to shape this poorly-constrained surface to see how this affects your results?

Figure 2: how are these basin boundaries generated? Is it appropriate that their outboundaries remain unchanged over 500ka?

L107-119: Is the evidence for these capture events derived solely from simulation, or is there empirical data to support it as well?

L117-119: Again, I have a poor sense of which simulations and scenarios have been run, and why.

L123: "drainage basin connectivity [...] pysiographic changes of river basins unaccounted for". These statements seem to contradict each other. Is the implication that drainage basin connectivity is static in the other models you're referring to? Stokes and Perron (2020, "Modeling the Evolution of Aquatic Organisms in Dynamic River Basins") might be a useful counterexample here.

L561: "With these forcing conditions" Which forcing conditions? "For the other forcing conditions" Which ones? It's hard to follow what's going on in this figure with respect to the argument you're making.

Extended Data Figure 5: It looks as though the river model you're using has a static river network

which is cropped by the coastline at any given point. That is, the rivers' streambed locations remain unchanged over the 75,000 years between the two images. Could you confirm that this is correct? Could you comment on whether it is appropriate?

L146: "evaluatetemporal" needs a space

Figure 3: I find it the mottled landscape towards the center right of these images interesting. I presume this is from an area with varied topography, but I don't understand why the whole region wouldn't be black: living on a ridge can be as much an impediment to travel as living in a valley... for some species. Perhaps the mottled nature is true for some species and I'm just thinking of the wrong ones. This raises a general point with the paper, "species" seems to be used in a generic way but the connectivity and other landscapes look vastly different depending on what species you are. For instance, in L126, you refer specifically to "lowland freshwater biotas", but Figure 3 shows corridors for migration that seem only loosely constrained by any freshwater river networks (which, after all, seem to be static in your model). Is it possible to draw conclusions for a broad ensemble of species all at once? It seems to me that multiple model runs might be needed depending on the assumed characeristics of the species in question.

Extended Data Figure 6: What's that big spike at 235m in Panel A?

L591: "for the model with laterally variable tectonic and sea-level fluctuations" - I'm still having difficulty understanding what all these models are and how/why they're used.

L185: "from landscape evolution simulations" - I'm concerned at this point that the static river network layout discussed above seems to indicate that the landscape itself is unchanged. Given that, I'm unsure what you mean by landscape evolution simulation.

Bibliography: Thank you for including doi numbers here.

L280: How did you determine the initial landscape surface to run the models on? Barnhart et al (2020, "Projections of Landscape Evolution on a 10,000 Year Timescale With Assessment and Partitioning of Uncertainty Sources") are able to nicely account for initial conditions based on glacial smoothing during the LGM, but Sundaland doesn't seem a likely candidate for that process.

L283: I see you're using the Braun and Willet method. A couple of notes on this.

Campforts et al (2017, "Accurate simulation of transient landscape evolution by eliminating numerical diffusion: the TTLEM 1.0 model") criticize the Braun and Willet method for having too much numerical diffusion, leading to the fast degradation of knickpoints. If your landscape features sharp changes in elevation, this may be important.

Barnes (2019, "Accelerating a fluvial incision and landscape evolution model with parallelism") demonstrates that the stack-based method used by Braun and Willet is inefficient in parallel sets and provides a fast alternative. This would be useful if you were propagating uncertainty in your model, though it doesn't seem you are.

Anand et al (2020, "Linear layout of multiple flow-direction networks for landscape-evolution simulations") discuss ways of extending Braun and Willet's approach to multiple flow methods.

L293-315: There's a "wall of text" effect going on here. Is it possible to succinctly summarize somewhere the different scenarios that were run?

L317: Can submerged sediments be swept away by the ocean?

L329: I appreciate this explanation of how the paleosurface is generated. Teasing at this earlier or providing a high-level overview of the model/calibration approach to orientate the reader might be helpful.

L329: I'm curious for details of how this iterative landscape modification approach works.

L369: Note that the path costs are symmetric so it may be possible to leverage memoization to accelerate this algorithm. Since you're considering all-pairs, Floyd–Warshall would be another approach to consider.

L387: Barnes and Clark (2017, "Sixty-Five Million Years of Change in Temperature and Topography Explain Evolutionary History in Eastern North American Plethodontid Salamanders") see a similar result owing, essentially, to climate change alone. It's unclear to me whether climate is incorporated into the model you're discussing at this point, but it seems like a more likely explanation for a mid-elevation clustering than sea-level change alone since the latter would affect species living in the lowlands, but only have a direct impact on those at higher elevations whereas climate affects species across the entire elevation gradient and occurs in sync with sea level changes.

L411: "to represent [...] of non-volant terrestrial species" I feel (as evidenced by the above comments) like this statement is really buried deeply in the paper and should be expressed earlier to orientate readers. It's especially confusing given earlier statements about freshwater biota in the paper proper.

Reviewer #3 (Remarks to the Author):

Review for “Quaternary landscape dynamics boosted species dispersal across Southeast Asia” by Salles et al.

Note that my expertise lies primarily in (palaeo)climatology and climate-landscape dynamics. My ability to comment on the species dispersal aspects of the work is limited by my more basic understanding of these topics. I therefore strongly recommend other reviews to complement mine in expertise.

The authors re-examine the Quaternary species burst with the aid of landscape evolution and connectivity models. They highlight the problem mainly from a physical geographer’s view point. Their model results suggest a fragmentation into multiple habitats through changes in the drainage systems.

The study represents a significant amount of work that may be of interest to multiple scientific communities. The overall approach (coupling of multiple, very different models) represents the most notable novelty of this study. The manuscript is generally well written, but leaves many questions

pertaining to the actual experiments that were conducted. This may be be due to a combination of the short manuscript format, the large amount (and many dimensions) of the work and the general structure of the manuscript. The short format of the manuscript may act as a disadvantage in communicating important aspects of the work in sufficient detail and thus compromise the benefit to different scientific communities somewhat.
The conclusions seem supported by the work presented here, but it is difficult to comment on how much this is the case, since important information regarding the experiment setup and propagation of errors cannot be found in adequate detail in the manuscript. Despite my experience in palaeoclimate models and their use as constraints for landscape evolution models (LEMs) and other models, I would not be able to reproduce the study from the descriptions provided here.
Furthermore, if my interpretations of the palaeoclimate constraints are correct, the coupling to palaeoclimate may be oversimplified and overstated. I regard this as the main shortcoming of the manuscript. More specific comments are provided below:

1. Tectonic, climatic and other constraints are fed into the landscape evolution model, which then drives the connectivity model and then provides the basis for clustering. Given the many processing steps (even beyond this modelling chain), a visualisation and/or very clear communication of the processing chain would be very beneficial. These are of particular importance when multiple methods are applied to address a specific problem.

2. The reason for the choice of time slices in the presented figures is unclear:
Figure 1: Is there a reason for this particular/uneven temporal spacing in the presentation of results in Figure 1? These time slices are not mentioned as any particularly meaningful ones for the problem. Is the choice made due to technical constraints or scientific merit? What happens between the time slices? Are these 3 particularly representative of the modelled changes?
Figure 2: Same as Figure 1.

3. Comment on parameterisations and assumptions in “Methods – surface processes model and forcing mechanisms”:
Multiple decisions and assumptions are made here, such as assumptions about soil properties. The reason for those is oftentimes unclear and it is equally unclear how sensitive results may be to different parameterisation, such as not treating regolith and bedrock the same. Furthermore, it is unclear if the experiments comprise transient or time slice specific simulations. The modelling intervals are not presented clearly either. These items need to be communicated very clearly to allow reproduction, and is especially important since the manuscript is relevant to a diverse audience of scientists that may be used to very different type of modelling.

4. Comment on palaeoclimate constraints in “Methods – surface processes model and forcing mechanisms”:
If I understand the manuscript correctly, the authors simulate from the Calabrian (1Ma) onward. Given that the palaeoclimate model results from Brown et al. (2016) are used, the authors should consequently be restricted to the time periods published. Only one of the 3 simulations published in the cited literature, namely MIS19, falls into the time span investigated here (i.e. the last 1 million years). The mid-Pliocene and Late Pliocene are irrelevant. However, the authors mention that they have used 9 simulations. The same project (PaleoClim) includes palaeoclimate simulations from Fordham et al. (2017), Otto-Biesner et al. (2006) and others, but the authors of this study do not cite them. Neither do they mention the time periods they used as constraints for modelling. The PaleoClim simulations that match the investigated time period in this study add up to 8 (not 9). This

needs to be addressed and appropriate credit needs to be given to these other studies if they were used. This is essential to uphold high standards in publishing and referencing, as well as to allow others to reproduce this study.
The second concern I have regarding the palaeoclimate simulations is the temporal spacing. If indeed the 8 simulations are used, i.e. 1 by Brown et al. (2017), 1 by Otto-Bliesner et al. (2006) and 6 by Fordham et al. (2017), 6/8 simulations fall into the time period after the LGM (21ka) and 4/8 between 1Ma and 13ka. The presentation of results focuses primarily on results prior to the LGM (and up to 13ka including the highlighting of migrational corridors). There is no information on how the authors attempted to integrate the different contraints for LEM modelling. Were palaeoclimates interpolated over time? If so, how was this done when only 2 simulations prior to 21ka exist and no further palaeoclimate information was considered?
Beyond these points, I am unable to comment on the merits of this aspect of the work, because it is not described in sufficient detail.

5. In more complex approaches like employed for this study, uncertainties accumulate over the different processing steps, time and models. These ought to be adequately acknowledged. Palaeoclimate simulations, esp. those conducted with GCMs (the Hadley Centre GCM for Brown et al.) come with significant uncertainties due to (a) uncertainties in palaeoevironmental boundary conditions, (b) GCM specific parameterisations that may even be propagated when nesting RCMs into GCMs for downscaling. There is no adequate discussion of what these uncertainties are for the study region and how these would propagate through this study's experiments and compromise the study's results. I cannot comment much about the tectonic (and other) constraints, but the same may apply there. Such discussions (and sensitivity experiments where possible) are important.

6. The topic of species dispersal (outside human dispersal) lies outside my area of expertise, but I imagine the following questions may be asked by a diverse audience nevertheless:
What are the implications of the biological cennectivity model being species agnostic? How relevant are species specific traits and how much of it is lost in the analysis. Furthermore, how are non-external pressures for species dispersal considered? Are such mechanisms relevant for this particular study?

7. Presentation: The figures are of high quality. However, font size is too small in most cases. For example, in Fig. 2 b, some font sizes seems half of that in the figure caption (or less). This makes the figures really hard to read in places. I recommend adjustments wherever it is possible.

Rebuttal letter

First and foremost, we would like to thank the reviewers for their comments and feedbacks on the manuscript.

Point-by-point responses to reviewer 1

General comments

GC1: This paper arrived at the same insight as Sarr et al 2019 in that Sunda shelf was subaerial before 400 kya, which is not surprising since the main estimate of subsidence rate came from this earlier paper.

Response: From the five proposed scenarios, only one of them uses the uniform subsidence rate (0.25 mm/yr) presented in Sarr et al. (2019). Another one assumes that Sundaland is tectonically quiescent (the *no tectonic* case) and that flooding of the shelf is only contingent on eustatic sea-level changes (Voris, 2001). The three other cases are forced with a new tectonic map designed based on georeferenced calibration points and tectonic polygons provided in the Extended Data Table 1 and presented in Extended Figure 1b. In addition, Sarr et al. (2019) estimated broad scale regional exposure of the shelf based on coral reef growth and seismic stratigraphy but did not focus on the landscape dynamic and geomorphological evolution of the region. Our study refines the flooding history of Sundaland over the last 500 kya for different tectonic and climatic forcing. As a result, it provides, for the first time, quantitative estimates of flooding episodes, landscape dynamics, catchments reorganisation and river captures across the Sunda Shelf. This is therefore largely independent from the approach of Sarr et al. (2019), which only serves as one calibration point among many other in the tectonically variable scenario. Incidentally, we cannot concur with this comment, for Sarr et al. (2019) assumed a uniform subsidence and indeed concluded that the shelf was flooded at 400 ka. Here, we find that pervasive, entire flooding of the shelf only occurred later during MIS5, ~125 ka.

GC2: Timings of intraspecific divergence from 1 meta-analysis (Husson et al 2020), when matched against its estimates of drainage reorganization and river capture, indicated that "distribution intraspecific divergence times is more likely driven by geomorphological changes rather than by sea-level oscillations". I find this claim to be not substantiated, since many other mechanisms (eg changes in vegetation, paleo-climatic changes, simple isolation by distance or lineage sorting, stochastic extinctions of populations, sea-level fluctuations) can also produce similar patterns.

Response: Following the reviewer's comment, we modified the above claim and rather than attributing solely the observed diversification patterns to any specific factor, this study draws the attention on the potential role of overlooked physiographic changes. We have modified the manuscript to convey this message more clearly in our revised manuscript (Ln 19-22, 67-70). We found that the fast pace of physiographic changes in the region predates measured divergence times and population splits defined in Fig. 2. From the analyse of connectivity across the exposed shelf we also show that geomorphological evolution facilitates habitat fragmentation and promotes preferential pathways over the past 500 kyr.

GC3: Importantly, this meta-analysis (and ED Fig 4) is the only external source of data used to validate the geomorphology evolution model. Looking at ED Fig. 4, it appears that any distribution of divergence times within of the last 500 kya can be construed as support of the model. Further, I find Husson et al 2020 to be a poor summary of phylogeographic studies carried out in SE Asia. It focused on vertebrates that live in closed-canopy forests (mainly birds and mammals, and even then only a subset of species were investigated) and largely ignored other taxa (eg plants, invertebrates). Thus, I believe that Husson et al 2020 does not provide a comprehensive look at the phylogeographic histories of SE Asian taxa.

Response: Regarding the first point, we emphasize that divergence occurred after MIS11 (400 ka), and not after 500 ka as suggested by the reviewer. The resolution is indeed not sufficient to go beyond this information, but we stress that the important point is that divergence events largely postdate the first transgression, during MIS11. The fact that "any distribution of divergence time within the last [400 kyr, not 500 ky]" does not go against our conclusion whatsoever.
Regarding the second aspect, we have revised the manuscript and restricted our analysis to lowland evergreen rainforests species as in Husson et al. (2020) (added paragraph from line 109 to 120). We have added a new paragraph in the section named "*Geomorphically derived cost surfaces for lowland evergreen rainforests species*" from line 111 to 121 where we explain why we applied our approach to these particular species.
As mentioned by the reviewer, the choice of species is limited in sample size and restricted to vertebrates even though a few studies of plants and arthropods exist in the region. However, Husson et al. (2020) have compiled 36 unambiguous vicariant sister-lineage pairs, consisting of 21 mammals, 13 birds, one lizard and one plant pair from which 21 have divergence times within our study timeframe (500 kyr). To this initial database, we have added estimated time of divergence and confidence interval for songbird species (Fig. 2c) from Cros et al. (2020) and age estimates of population splits within vertebrate species between Borneo, Sumatra, and the Malay Peninsula from Leonard et al. (2015).

GC4: The paper created species-agnostic landscape resistance maps using changes in elevation, proximity to rivers and steepness of local slope and interpreted the Circuitscape model as being generally applicable to taxa in SE Asia (eg. Ln183-184 "instead of relative sea-level fluctuations, we found that the fast pace of physiographic changes is more likely to drive diversification processes in the region"). The authors need to provide justifications as to why these landscape features are important to many species (ie it is species agnostic instead of targeting at some taxa). Many species would have very different habitat and dispersal requirements. For example, a bird species can have a large elevational range (ie not restricted to one elevation band), find rivers to be barriers rather than corridors, and are not affected by steepness of local slopes. Does this model apply to freshwater species as well? It seems like the LEC+slope+proximity to river model may be applicable for frogs and amphibians (eg Funk et al 2005 Mol Ecol 14:483) and not as general as the authors claim it to be. Generally, multispecies resistances models (Koen et al 2014) tend to only consider species that use the same vegetation/habitat type (eg. closed forests, edge habitats, open prairie). The support of rivers as corridors for many forest species is not ubiquitous, In fact, they tend to be regarded as barriers. Eg Gascon, C. et al. PNAS 97, 13672-13677 (2000) and Naka, L.N. & Brumfield, R.T. Science Advances 4, eaar8575 (2018)).

Response: Our geomorphically derived cost surfaces have been designed to evaluate connectivity pathways for lowland evergreen rainforests species since these organisms would be impacted by barriers to migration created by flooding episodes during sea-level highstands, would be affected by steepness of local slopes and would also be dependent on changes associated to drainage basin reorganisation and river captures under the assumption of limited rainforest habitats. As mentioned by the reviewer, even for the chosen species group, rivers might be alternatively regarded as corridors or barriers to migration. To account for both cases, we defined different cost surfaces related to closeness to rivers when evaluating landscape connectivity across Sundaland. The analysis performed in the first version of the manuscript has been extended to account for both cases as shown in Figs. 5, 6 and ED Fig. 5.

Main text comments

C1: Ln1 insufficient citations

Following reviewer's comment, we have added key citations for the introduction paragraph.

C2: Ln 32 - general statement that seems to suggest that sea-level increases were equally important for promoting speciation in a wide variety of taxa that occupy diverse habitats such as mountains, open/edge habitats, and mangrove.

We have moderated our initial claim regarding the impact of eustatic sea-level fluctuations on species diversity and as suggested by the reviewer other factors are important to consider. We have added several citations (Ln 20-22) to different studies that either show a possible diversification which predates the Quaternary and highlight other contributors such as edaphic properties, habitats fragmentation or paleo-climate conditions.

C3: Ln 35 - Find citations that relate the history of sea-level fluctuations to the phenomenon of species pump.

The biogeography of Sundaland with respect to Quaternary sea-level changes has been well reviewed (Whitmore, 1981; Heaney, 1986; Whitmore, 1987; Voris, 2000; Woodruff and Turner, 2009; Cranbrook 2010; Lohman et al., 2011; Morley 2012; de Bruyn et al., 2014; Wurster and Bird, 2014). We have added more citations which relate to this in general, and to the species pump in particular, in this section (Ln 13-22).

C4: Do researchers really propose sea-level fluctuations as a species pump or sometimes consider it to be a homogenizing force that retards diversification or divergence?
Additionally, many studies find that species formation often predate the Quaternary, contrary to what was claimed in Ln1. This paper incompletely surveyed the literature on species diversification in SE Asia and did not provide a nuanced look at the various hypotheses that have been put forth to explain temporal and spatial patterns of diversification.

We agree with the reviewer's comment and have updated the introduction to nuance our initial claims therefore softening the potential role of sea-level on species diversification. As mentioned by the reviewer diversification happened before 400 ka and major events occurred prior to that, but on deeper times and not so coeval. As previously discussed in our answer to C1, additional citations have been included. In particular, the two proposed citations (Hinckey et al., 2020 and Quek et al., 2007) are cited in our introduction section.

C5: Ln39- Elaborate these additional factors. Ref 6-10 -- 9 – soil, 10 – paleo-drainage connectivity: It is unclear what additional factors were proposed by the other cited references.

We have highlighted in our introduction other contributors such as edaphic properties, habitats fragmentation or paleo-climate conditions and have updated the references for each of the aforementioned factors.

C6: Ln43 - "Limited work on roles of geomorphology". The two cited references (10, 12) on diversification are on freshwater fishes. It seems to suggest that geomorphology modelling of this paper is only applicable to freshwater taxa that were affected by drainage changes.

We have added a new paragraph in the section named "*Geomorphically derived cost surfaces for lowland evergreen rainforests species*" from line 111 to 121 where we explain which species our approach is applicable to. Our geomorphically derived cost surfaces have been designed to evaluate connectivity pathways for lowland evergreen rainforests species since these organisms would be impacted by barriers to migration created by flooding episodes during sea-level highstands. They would also be affected by changes associated to drainage basin reorganisation and river captures under the assumption of limited rainforest habitats.

C7: Ln48 - It is hard to tell what for which taxa this model of dispersal corridors is applicable. Please note comments under Overview. It appears that landscape resistance based primarily on physiography

is only applicable to a certain group of species and the authors need to qualify the generality of the connectivity model (or validate it across a wide variety of taxa). In other studies, multispecies resistance maps were made for species that share the same habitat requirements, eg. native forest- and wetland-dwelling species. Koen 2014 Methods in Ecol and Evol 5:626.

As mentioned in the answer to C6, we have added a paragraph to explain the group of species we are evaluating with our approach. We have also added in the same section (from line 100 to 108) some explanations regarding the use and limitations of the species-agnostic approach proposed in the study.

C7: Ln84 - Most researchers have a nuanced view of whether sea-level changes are a species pump. Many studies found deeply diverged E-W lineages, indicating that there were rainforest refugia / areas of endemism despite repeated land bridge connections. Eg Sabah often shows deeply divergent lineages despite its permanent connection to the rest of Borneo. This pattern was found in many taxa from birds to Macaranga plants (Banfer et al 2016 Mol Ecol 15:4409). Thus, it is overly simplistic to implicate that scientist consider sea-level fluctuations as the primary mechanisms of generating species in SE Asia, and they only drive diversification, not homogenization or dispersals.

We agree with reviewer's comment and have modified the conclusion of the section to reflect a more nuanced view on the role of sea-level fluctuations. We now state that the timing of the divergences for different species groups and between populations cannot be attributed to a single event or mechanism such as eustatic sea-level fluctuations and that the observed Late Pleistocene increased in diversification rate is more likely caused by a combination of different drivers. These changes applied to lines 61 to 70 in the revised manuscript.

C8: I am not sure how Husson et al (6) is considered to be the existing phylogeographic dataset. This meta-analysis looked mainly at vertebrates (only 1 plant species, Shorea) and most taxa are birds or mammals. Husson et al also seemed to cherry pick data, selecting only a subset of species to use in their meta-analysis. For example, Leonard et al (2015) looked at 18 species of birds and their divergence times within Sundaland, but Husson et al (2015) only cited five. Also, this paper is predisposed to find recent divergence times (ie supporting Late Pleistocene increase in diversification rate) because it focused only on divergence times within recognized species. If sister species or congenerics were studied, it might find similar diversification rates during and before Pleistocene.

Our study primary looks at geomorphological changes across Sundaland over the past 500 kyr and evaluates how these changes might have impacted on species diversity by influencing migration pathways and habitats fragmentation. We do compare these results to the earlier compilation of Husson et al. (2020), but clearly, this article should not be regarded as a tribute to Husson et al., 2020! Our main focus is methodological and theoretical, only afterwards do we combine available data. In addition, as in Husson et al. (2020), we restricted our analysis to terrestrial organisms from evergreen forests (added paragraph from line 109 to 120). The phylogeographic dataset has been therefore chosen to evaluate diversification rates during this time interval. The choice of species is indeed limited in sample size and restricted to vertebrates. As mentioned in Husson et al. (2020), studies of plants and arthropods exist in the region but "*estimates of divergence times between intraspecific lineages that are vicariant across landmasses of Sundaland are, to our knowledge, virtually non-existent*". Husson et al. (2020) have compiled 36 unambiguous vicariant sister-lineage pairs, consisting of 21 mammals, 13 birds, one lizard and one plant pair from which 21 have divergence times within our study timeframe. In addition, we have added estimated time of divergence and confidence interval for songbird species (Fig. 2c) from Cros et al. (2020) and age estimates of population splits within vertebrate species between Borneo, Sumatra, and the Malay Peninsula from Leonard et al. (2015).

C9: Ln89 - I don't think paleo-drainage systems have been invoked to explain spatial distribution of SE Asia biota much. Voris 2000 only gave a series of bathymetric maps (no biogeographic studies). Molengraaf looked at coral reefs and freshwater fishes, and Sholihah looked at freshwater fishes. Thus, it seems to be relevant to only to freshwater aquatic species.

Following reviewer's comment, we have modified line 72 and 73.

C10: Ln103 - Does catchment characteristics mean catchment areas? Most the correlation coefficients have intermediate negative values, but no p-values. It makes tautological sense that increased sea-level meant smaller basins, but how do the correlation coefficients tell us that changes in basin boundaries and basin capture events were correctly modelled as well. In other words, what else do these correlation coefficients tell us other than that basin became smaller when sea-level rose.

For this study, we evaluate mean catchment areas, main river lengths, erosion/deposition patterns and distances between river outlets. We have calculated the correlation values for the basin area and for the erosion/deposition patterns across the shelf. As mentioned in the manuscript and by the reviewer, there is a clear relationship between drainage areas, river lengths and sea-level fluctuations which is directly related to flooding history of the region. In addition to this correlation, the analysis reveals several phases of basins reorganisation and rivers captures. During glacial periods, the main drainage systems are rerouted by both the action of tectonic forcing and the sedimentation patterns. Deposition on the shelf occurs during transgression and regression episodes and modifies local slopes distribution which in turns changes river paths over time.

C11: Ln121 - Woodruff 2010 talked about future climate change caused by increased CO2 emission (pg 929) and did not focus on paleoclimatic variation and is thus not a suitable citation.
Check Lim et al (2011) Evolution 65, 321-334, Lim et al (2015) Current Zoology 61, 922-934 and other papers as examples of papers that used environmental niche modelling and paleoclimatic models.

This part of the manuscript has been rewritten from line 94 to 99.

C12: Ln 125-131 "…our simulations demonstrate that [physiographic changes of river basins] are likely critical to some species.". The main support for this appears to have come from ED Fig 4. This figure shows a series of marine transgressions, and connection or disconnection of basins. Superimposed are some estimates of intraspecies divergence times. It is not clear how having divergences and physiographic changes both occurring within the last 500kya means that physiographic changes of river basins are critical to some species. In my opinion, these data from Husson et al do not constitute strong evidence for intraspecific divergences times being driven by geomorphological changes rather than by sea-level oscillations or other processes.

We have nuanced the claims made from former ED fig. 4 (which is now fig. 2). From all our models with active tectonics (uniform or variable tectonic maps), sea-level oscillations do not impact Sundaland before 200 ka. This suggests that other parameters are likely driving diversification prior to this. After 200 ka, we find several episodes of flooding as well as several periods of basin reorganisations and river captures. Our study shows that these changes have modified the connectivity across the Sunda Shelf and might be an additional driver along with sea-level, vegetation change, climate… that might have influenced biodiversity in the region. Rather than attributing solely the observed diversification patterns to any specific factor, this study draws the attention on the potential role of overlooked physiographic changes. The study of Husson et al. (2020) only serves as a basis of comparison. The current study is not reliant on this study, results hold regardless. We have modified the manuscript to convey this message more clearly.

C13: Ln137 - The authors are not explicit about what types of species the LEC+river closeness+local slope model is suitable for. In other words, it is hard to envision what species or species groups this model is useful for. Many species would have very different habitat and dispersal requirements (eg volant vs non-volant animals). For example, a bird species can have a large elevational range (ie not restricted to one elevation band), find rivers to be barriers rather than corridors and are not affected by steepness of local slopes. Is this model applicable to aquatic or terrestrial species? It seems like this model may be applicable for frogs and amphibians (eg Funk et al 2005 Mol Ecol 14:483) and not as

general as the authors claim it to be. Many multispecies resistances models (Koen et al 2014) rely on species requiring the same vegetation/habitat type (eg. closed forests, edge habitats, open prairie).

As mentioned in our previous answers, we have modified the manuscript and now explicitly described the species more suited to our cost surfaces. The geomorphically derived cost surfaces have been designed to evaluate connectivity pathways for lowland evergreen rainforests species since these organisms would be impacted by barriers to migration created by flooding episodes during sea level highstands and would also be affected by changes associated to drainage basin reorganisation and river captures under the assumption of limited rainforest habitats. In addition, and depending on considered species, rivers network is viewed either as corridor or as barrier to migration. Following reviewer's comment, we have also provided some explanations regarding the species-agnostic approach following suggested work from Koen et al. (2014).

C14: Ln292 - The PaleoClim database presumably simulated paleo-climatic conditions while treating Sundaland as not having experienced subsidence (the previous paradigm). A permanently subaerial Sunda shelf should reduce maritime impact in the region. How will this affect estimates of rainfall?

Several studies (Bush and Fairbanks (2003), DiNezio et al. (2016) and Sarr et al. (2019)) have investigated the effect of the exposure of the Sunda Shelf on climate dynamics using a set of numerical simulations with atmosphere-land surface and fully coupled general circulation models. Those studies highlight the lack of consensus on the effect of the shelf on annual precipitation pattern within different models that may simulate either drier or wetter climate. Alongside, Sarr et al. (2019) study shows that subaerial Sunda Shelf enhances moisture convergence and local convection, which fosters local precipitations during wet seasons, thereby increasing seasonality. Unfortunately, impact on local precipitation (*i.e.*, at the resolution of our landscape evolution simulations) is unknown due to lack of studies with exposed Sunda Shelf at ultra-high resolution. While increasing precipitation over the shelf is likely to impact vegetated surface properties and freshwater export into seawater its role on changing the geomorphology of Sundaland could be limited due to the shelf physiography (low elevation and relief) which implies a limited change in sediment erosion and deposition in our landscape evolution simulations. To test the effect of rainfall on geomorphological changes in the revised manuscript, we ran an additional model (scenario 4) with uniform rainfall over the simulated period and evaluated the responses of shelf in terms of drainage basins reorganisation.

C15: Ln330 - Reference 13 is Voris 2000. It shows a series of bathymetric maps but does not study freshwater taxa directly.

It has been changed to de Bruyn, M. et al. (2013).

Point-by-point responses to reviewer 2

Major comments

GC1: The authors state that "Two main scientific software are used in this study; Badlands and Circuitscape. In addition, a series of Python libraries are required and provided in a Docker container (geodels/gospl:bio)." This is nice, but I am interested in the software used to produce the results in the paper, not the collection of libraries composed to generate that software. A docker container with a script that generates the output figures shown in the paper would be ideal.

Response: As mentioned by the reviewer, 2 main scientific software are used in this study: Badlands and Circuitscape. Following reviewer's comment, a GitHub repository containing the required data (*e.g.*, precipitation, paleo-topography and tectonic maps as well as eustatic sea-level curves) has been created and is available from **badlands-sundaland**. In addition, the repository includes seven Jupyter Notebooks which have been designed to (1) run the landscape evolution simulations; (2) extract and visualise the information relative to catchment dynamics, erosion-deposition patterns across the Sunda Shelf as well as shelf exposure evolution; (3) compute cost surfaces used in the connectivity model (from the LEC index to cost associated to elevation, distance to rivers or slope values); (4) evaluate and plot statistical significance of computed connectivity (based on current flow) using z-score and Getis-Ord indices. We have also rebuilt the Docker container **geodels/gospl:bio**) that includes all the libraries required to run and analyse the simulations discussed in the manuscript as well as plot most of the presented graphs. The 3D figures in the paper are plotted with **ParaView** using the outputs obtained with the above notebooks. Using the Docker container allows the full reproducibility of the tested scenarios.

GC 2: What species are the authors talking about? It takes until Line 411 to get this basic modelling detail. For a long time, I was very confused.

Response: Following reviewer's comment, we have revised the manuscript to clearly explain which species our approach is applicable to (in the section named "*Geomorphically derived cost surfaces for lowland evergreen rainforests species*" from line 111 to 121). Our geomorphically derived cost surfaces have been designed to evaluate connectivity pathways for lowland evergreen rainforests species since these organisms would be impacted by barriers to migration created by flooding episodes during sea-level highstands and would also be affected by changes associated to drainage basin reorganisation and river captures under the assumption of limited rainforest habitats.

GC 3: What are the different scenarios and what are they testing? In the paper proper the authors refer obliquely to a variety of scenarios, but without much if any detail about what they are and why they are chosen. The supplemental doesn't provide much additional enlightenment. I see different sea level models and tectonic forcings, but how are these coupled to produce a realization? Is it a full-factorial design or something more judicious? What scenario are the results based on (or set of scenarios for judging sensitivity)?

Response: In this study, we are showing 5 scenarios. Following reviewer's comment, we have explicitly stated the different forcings used in each simulation (line 37 to 49 in the section *Sensitivity of Sundaland flooding history to tectonic and sea-level conditions* and ED Tab. 2). Our simulations mainly test the role of tectonic forcing by looking at 3 scenarios (without tectonic – which is the base case scenario from previous paradigm; uniform subsidence based on recent findings from Sarr et al. (2019) and variable tectonic map based on available dataset from the region). In addition, we evaluate the role of eustatic sea-level fluctuations using 2 different sea-level curves as well as the role of climate by imposing two rainfall conditions (either uniform precipitation or precipitation maps from the PaleoClim database).

Full comments

C1: L79: Perhaps this is just the Nature style, but the sudden introduction of scenarios here catches me off-guard. Additionally, I don't see a clear list of scenarios anywhere in the paper or supplement. See Barnes and Clark (2017, "Sixty-Five Million Years of Change in Temperature and Topography Explain Evolutionary History in Eastern North American Plethodontid Salamanders") p 3-5 for a good example of explaining scenarios.

As mentioned previously, we have revised the paper and now present the different scenarios in first section of the Main from line 37 to 49 (*Sensitivity of Sundaland flooding history to tectonic and sea-level conditions*) as well as in a new table (ED Tab. 2).

C2: Extended Data Figure 1: Figure b here looks as though uplift data does not necessarily follow topographic boundaries. As a result, I think, the fitted surface's lower right blue line cuts directly through a swath of topography that appears, to me, as though it might reasonably be thought of as uplifting. Have you experimented with adding or dropping points to shape this poorly-constrained surface to see how this affects your results?

We agree that our tectonic map is constrained based on the limited number of uplift rates available for the region for the considered time interval. We were unsure about the lower right blue line the reviewer is referring to in his question. Nevertheless, we acknowledge that the map presented here is regional and does not account for several more local rates found across the simulated domain.

C3: Figure 2: how are these basin boundaries generated? Is it appropriate that their out boundaries remain unchanged over 500ka?

Basins edges are not stationary. They are generated from our landscape evolution model based on flow accumulation and direction. The overall shape of basin boundaries is controlled by erosion from the stream power law and the position of the drainage divide over time. The simulation resolution is about 5 km and drainage divide positions are changing over time but these changes, expect during reorganisations and captures, are quite limited mainly due to the limited tectonic rates (uplift/subsidence) and shelf physiography (low elevation and relief).

C4: L107-119: Is the evidence for these capture events derived solely from simulation, or is there empirical data to support it as well?

The river capture events in our study are derived from our simulation results. There are studies reporting evidence of river captures in the region (Woodruff et al., 2010; Morley et al., 2017). Other have proposed river captures across Sundaland as a driver for freshwater taxa (deBruyn et al, 2013; Bolotov et al., 2020). However, these events remain poorly understood, dated and could not be directly related to the simulated events in our study.

C5: L123: "drainage basin connectivity [...] physiographic changes of river basins unaccounted for". These statements seem to contradict each other. Is the implication that drainage basin connectivity is static in the other models you're referring to? Stokes and Perron (2020, "Modeling the Evolution of Aquatic Organisms in Dynamic River Basins") might be a useful counterexample here.

The sentence was referring explicitly to analysis conducted for the Sundaland region, but we agree with the reviewer's suggestion, Stokes and Perron (2020) or Lyons et al. (2020) have proposed models accounting for freshwater taxa evolution under different physiographic changes. In the revised version of the manuscript the suggested sentence has been modified.

C6: L561: "With these forcing conditions" Which forcing conditions? "For the other forcing conditions"

Which ones? It's hard to follow what's going on in this figure with respect to the argument you're making.

The caption of Fig. ED 3 has been rewritten and additional explanations on the different tested scenarios are provided in the main manuscript.

C7: Extended Data Figure 5: It looks as though the river model you're using has a static river network which is cropped by the coastline at any given point. That is, the rivers' streambed locations remain unchanged over the 75,000 years between the two images. Could you confirm that this is correct? Could you comment on whether it is appropriate?

The main rivers remain relatively static over time, but this is not an imposed choice. This is mainly related to small regional changes in tectonic regime across Sundaland. In addition, between the two time steps the Sunda Shelf has not experienced any flooding for this scenario and therefore marine sedimentation has not modified local slopes. In the method section, we present some of the limitations of our modelling approach and suggest that a multiple flow direction (D-8 / D-inf) could be used in future studies to allow for a better representation of river network across the shelf region.

C8: Figure 3: I find it the mottled landscape towards the center right of these images interesting. I presume this is from an area with varied topography, but I don't understand why the whole region wouldn't be black: living on a ridge can be as much an impediment to travel as living in a valley... for some species. Perhaps the mottled nature is true for some species and I'm just thinking of the wrong ones. This raises a general point with the paper, "species" seems to be used in a generic way but the connectivity and other landscapes look vastly different depending on what species you are. For instance, in L126, you refer specifically to "lowland freshwater biotas", but Figure 3 shows corridors for migration that seem only loosely constrained by any freshwater river networks (which, after all, seem to be static in your model). Is it possible to draw conclusions for a broad ensemble of species all at once? It seems to me that multiple model runs might be needed depending on the assumed characteristics of the species in question.

This comment relates to comments made by reviewer #1. To address it, we have first defined more clearly the species we were looking at with our cost surfaces and we have run a series of new analysis not only using rivers as corridor enhancing migration but also making them as barriers therefore fostering habitat fragmentation. Even though species-agnostic methods do not rely on any particular species, they are often used to predict functional connectivity across large regions for multispecies favouring a similar type of habitat (*e.g.*, closed forests, edge habitats, open prairies). Here we designed our cost surfaces to look at lowland rainforest species. As noted in the revised manuscript (lines 140 to 146), our choice of resistance and weight values implies assumptions about species movement ability and many examples can be found where a natural topographic feature may act as a barrier for one species but not for another. As a result, our geomorphically derived cost surfaces have been designed to evaluate connectivity pathways and investigate the potential role of geomorphology in affecting species migration across the exposed Sundaland.

C9: Extended Data Figure 6: What's that big spike at 235m in Panel A?

The spike at 235 m is within the shelf elevation range but corresponds to regions outside the shelf and relates to flood plains and plateaus found in the northern part of the simulated domain (i.e., Chao Phraya flood plain as well as the Khorat Basin in Thailand and to a lesser extent the Tonle Sap Lake in Cambodia). This has been added to the Main text in section *Geomorphically derived cost surfaces for lowland evergreen rainforests species*.

C10: L185: "from landscape evolution simulations" - I'm concerned at this point that the static river

network layout discussed above seems to indicate that the landscape itself is unchanged. Given that, I'm unsure what you mean by landscape evolution simulation.

The landscape changes over time with more than 500 m erosion across the mountain range and several tens of metres of deposition on the shelf (e.g., Gulf of Thailand). As shown in our different simulations, there are several basin reorganisations and river captures happening during the last 500 kyr. These changes might not be seen as drastic by the reviewer, but they are large enough to change the overall connectivity patterns across the Shelf. The apparent stability of the landscape is mostly related to the large-scale tectonic rates which does not account for more local changes induced for example by fault activity. Yet considering these local changes will likely increase the number of reorganisations and captures in the region. It is also worth noting that even though the major drainages which are limited by relatively stable divides do not change much, sub-catchments within each basin are subject to more variations. In the last section of the Methods, we suggest that additional work could be done to evaluate over a smaller region (such as the Siam or Johore basins) the implication of these variations in more details.

C12: L283: I see you're using the Braun and Willet method. A couple of notes on this. Campforts et al (2017, "Accurate simulation of transient landscape evolution by eliminating numerical diffusion: the TTLEM 1.0 model") criticize the Braun and Willet method for having too much numerical diffusion, leading to the fast degradation of knickpoints. If your landscape features sharp changes in elevation, this may be important. Barnes (2019, "Accelerating a fluvial incision and landscape evolution model with parallelism") demonstrates that the stack-based method used by Braun and Willet is inefficient in parallel sets and provides a fast alternative. This would be useful if you were propagating uncertainty in your model, though it doesn't seem you are. Anand et al (2020, "Linear layout of multiple flow-direction networks for landscape-evolution simulations") discuss ways of extending Braun and Willet's approach to multiple flow methods.

Following reviewer's suggestions, we have added a section in the Method regarding our modelling approach limitations and assumptions where we discuss the Braun & Willet method, its limitations and existing alternatives to MFD algorithms.

C13: L293-315: There's a "wall of text" effect going on here. Is it possible to succinctly summarize somewhere the different scenarios that were run?

We have rewritten this part which is now part of the Main text and where we explicitly stated the different forcings used in each simulation (line 37 to 49 in the section *Sensitivity of Sundaland flooding history to tectonic and sea-level conditions* and ED Tab. 2).

C14: L317: Can submerged sediments be swept away by the ocean?

Our landscape evolution model allows marine sediment transport by longshore drift, but this capability has not been turned on in this study. In our simulations, submerged sediments are transported by diffusion processes defined with a constant marine diffusion coefficient (Ln 214).

C15: L369: Note that the path costs are symmetric so it may be possible to leverage memorization to accelerate this algorithm. Since you're considering all-pairs, Floyd–Warshall would be another approach to consider.

Thanks for the proposition, this is something we will be looking into in future studies.

C16: L387: Barnes and Clark (2017, "Sixty-Five Million Years of Change in Temperature and Topography Explain Evolutionary History in Eastern North American Plethodontid Salamanders") see a similar result owing, essentially, to climate change alone. It's unclear to me whether climate is incorporated into the

model you're discussing at this point, but it seems like a more likely explanation for a mid-elevation clustering than sea-level change alone since the latter would affect species living in the lowlands, but only have a direct impact on those at higher elevations whereas climate affects species across the entire elevation gradient and occurs in sync with sea level changes.

Climate is incorporated in the model based on available rainfall maps from PaleoClim dataset for the considered time intervals. The approach is rather simple and does not explicitly account for local orographic changes. In the Method section we discuss the assumptions and limitations of the proposed approach. Simple paleo-climatic regimes, along with tectonic rates and other constraints are fed into the landscape evolution model, which then drives the LEC calculations. Therefore, LEC distribution is resulting from the interactions between these different forcing mechanisms.

C17: L411: "to represent [...] of non-volant terrestrial species" I feel (as evidenced by the above comments) like this statement is really buried deeply in the paper and should be expressed earlier to orientate readers. It's especially confusing given earlier statements about freshwater biota in the paper proper.

We have added a new paragraph in the section named "*Geomorphically derived cost surfaces for lowland evergreen rainforests species*" from line 111 to 121 where we explain which species our approach is applicable to.

Point-by-point responses to reviewer 3

Major comments

GC: The conclusions seem supported by the work presented here, but it is difficult to comment on how much this is the case, since important information regarding the experiment setup and propagation of errors cannot be found in adequate detail in the manuscript. Despite my experience in palaeoclimate models and their use as constraints for landscape evolution models (LEMs) and other models, I would not be able to reproduce the study from the descriptions provided here. Furthermore, if my interpretations of the palaeoclimate constraints are correct, the coupling to palaeoclimate may be oversimplified and overstated.

Response: Following reviewer's comment, we have added a new section at the end of the Methods to outline some of the assumptions and limitations of our approach as well as some potential methodological avenues for future work. We answer to some of the specific comment regarding experimental setup and imposed climatic conditions with more details in our responses below. To allow the full reproducibility of tested scenarios and also to help others willing to perform similar studies and analysis, we have put together a Github repository **badlands-sundaland** and a Docker image **geodels/gospl:bio** containing the Jupyter notebooks used to run and analyse the model presented in our manuscript.

Specific comments

C1: Given the many processing steps (even beyond this modelling chain), a visualisation and/or very clear communication of the processing chain would be very beneficial. These are of particular importance when multiple methods are applied to address a specific problem.

Following reviewer's comment, a GitHub repository containing the required data (*e.g.*, precipitation, paleo-topography and tectonic maps as well as eustatic sea-level curves) has been created and is available from **badlands-sundaland**. In addition to better document the processing chain, the repository includes seven Jupyter Notebooks which have been designed to (1) run the landscape evolution simulations; (2) extract and visualise the information relative to catchment dynamics, erosion-deposition patterns across the Sunda Shelf as well as shelf exposure evolution; (3) compute cost surfaces used in the connectivity model (from the LEC index to cost associated to elevation, distance to rivers or slope values); (4) evaluate and plot statistical significance of computed connectivity (based on current flow) using z-score and Getis-Ord indices. We have also rebuilt the Docker container **geodels/gospl:bio** that includes all the libraries required to run and analyse the simulations discussed in the manuscript as well as plot most of the presented graphs. The 3D figures in the paper are plotted with **ParaView** using the outputs obtained with the above notebooks.

C2: The reason for the choice of time slices in the presented figures is unclear:
Figure 1: Is there a reason for this particular/uneven temporal spacing in the presentation of results in Figure 1? These time slices are not mentioned as any particularly meaningful ones for the problem. Is the choice made due to technical constraints or scientific merit? What happens between the time slices? Are these 3 particularly representative of the modelled changes?
Figure 2: Same as Figure 1.

The choice has been made to represent some particular time intervals representative of the modelled changes. The landscape evolution model uses an explicit scheme to solve sediment transport from source to sink. The length of the time steps is determined from a Courant–Friedrichs–Lewy (CFL) like condition to ensure numerical stability and is usually in the order of tens to hundreds of years. In our simulations, the

outputs are generated every 1,000 years and over the last million year 1,000 outputs are created. Thus, maps like the ones used for Figs. 1 and 2 are available every 1,000 years. For example, Fig. 1 shows different phases of flooding across the Shelf from fully exposed to pervasive flooding. In Fig. 2, we chose time steps highlighting different phases of basins organisation and river captures.

C3: Comment on parameterisations and assumptions in "Methods – surface processes model and forcing mechanisms":
Multiple decisions and assumptions are made here, such as assumptions about soil properties. The reason for those is oftentimes unclear and it is equally unclear how sensitive results may be to different parameterisation, such as not treating regolith and bedrock the same. Furthermore, it is unclear if the experiments comprise transient or time slice specific simulations. The modelling intervals are not presented clearly either. These items need to be communicated very clearly to allow reproduction and is especially important since the manuscript is relevant to a diverse audience of scientists that may be used to very different type of modelling.

As previously mentioned, the landscape evolution model simulates transient evolution of morphological changes over the 1 Myr interval. Following reviewer's suggestion, we have added to the Methods a section on model assumptions and limitations. In the first paragraph, we discuss assumptions related to the transient landscape evolution simulations focussing on the flow direction algorithm used to simulate temporal changes in river pathways, erosion/deposition approach based on a detachment-limited erosion law and the use of uniform and invariant soil erodibility coefficient. Regarding the erodibility coefficient, its value has been calibrated independently for each simulation (Extended Data Tab. 3). We acknowledge that soil cover and properties vary notably between Borneo, Sumatra, Java and the Malay Peninsula and soil conditions for the exposed sea floor would have changed significantly over successive flooding events. Badlands software allows for multiple erodibility coefficients representing different soil compositions to be defined and this functionality could be used to evaluate the impact of differential erosion on physiographic changes. Similarly, several transport-limited laws are also available and could be compared against our detachment-limited simulations.

C4: Comment on palaeoclimate constraints in "Methods – surface processes model and forcing mechanisms":
If I understand the manuscript correctly, the authors simulate from the Calabrian (1Ma) onward. Given that the palaeoclimate model results from Brown et al. (2016) are used, the authors should consequently be restricted to the time periods published. Only one of the 3 simulations published in the cited literature, namely MIS19, falls into the time span investigated here (i.e., the last 1 million years). The mid-Pliocene and Late Pliocene are irrelevant. However, the authors mention that they have used 9 simulations. The same project (PaleoClim) includes palaeoclimate simulations from Fordham et al. (2017), Otto-Biesner et al. (2006) and others, but the authors of this study do not cite them. Neither do they mention the time periods they used as constraints for modelling. The PaleoClim simulations that match the investigated time period in this study add up to 8 (not 9). This needs to be addressed and appropriate credit needs to be given to these other studies if they were used.
This is essential to uphold high standards in publishing and referencing, as well as to allow others to reproduce this study.
The second concern I have regarding the palaeoclimate simulations is the temporal spacing. If indeed the 8 simulations are used, i.e., 1 by Brown et al. (2017), 1 by Otto-Bliesner et al. (2006) and 6 by Fordham et al. (2017), 6/8 simulations fall into the time period after the LGM (21ka) and 4/8 between 1Ma and 13ka. The presentation of results focuses primarily on results prior to the LGM (and up to 13ka including the highlighting of migrational corridors). There is no information on how the authors attempted to integrate the different contraints for LEM modelling. Were palaeoclimates interpolated over time? If so, how was this done when only 2 simulations prior to 21ka exist and no further palaeoclimate information was considered?
Beyond these points, I am unable to comment on the merits of this aspect of the work, because it is not described in sufficient detail.

We agree with reviewer's comment but sadly are limited by the temporal extent and resolution of the existing and publicly available paleo-climate datasets. Following reviewer's comment, we have added to the Methods a section on model assumptions and limitations. One of the main simplifications lies in the climatic conditions (*i.e.,* rainfall regimes) used to force our simulations. We relied on the PaleoClim database which contains nine high-resolution paleo-climate datasets (Otto-Bliesner et al., 2006; Fordham et al., 2017 and Brown et al., 2018) corresponding to specific time periods (4.2-0.3 ka, 8.326-4.2 ka, 11.7-8.326 ka, 12.9-11.7 ka, 14.7-12.9 ka, 17.0-14.7 ka, ca. 130 ka, ca. 787 ka and 3.205 Ma). In our simulations, we oversimplified the climatic conditions by assuming that precipitation distribution and intensity remain constant between two consecutive intervals. Recent work (Sarr et al., 2019) suggests clear regional responses induced by the emerged Sunda Shelf with seasonal enhancement of moisture convergence and continental precipitation induced by thermal properties of the land surface. This could significantly impact our simulation results. However, the outputs from Sarr et al. (2019) are from low-resolution climate models that usually fail at reproducing the local precipitation patterns in the region, as they cannot represent the small islands that span the archipelago. Therefore, at the time of writing, the use of the PaleoClim data base appeared to be the more convincing option as more continuous high-resolution paleo-climatic reconstructions considering the shelf as an emerged continental platform were still unavailable. It will surely represent a significant advance for future studies.

C5: In more complex approaches like employed for this study, uncertainties accumulate over the different processing steps, time and models. This ought to be adequately acknowledged. Palaeoclimate simulations, esp. those conducted with GCMs (the Hadley Centre GCM for Brown et al.) come with significant uncertainties due to (a) uncertainties in palaeoevironmental boundary conditions, (b) GCM specific parameterisations that may even be propagated when nesting RCMs into GCMs for downscaling. There is no adequate discussion of what these uncertainties are for the study region and how these would propagate through this study's experiments and compromise the study's results. I cannot comment much about the tectonic (and other) constraints, but the same may apply there. Such discussions (and sensitivity experiments where possible) are important.

We acknowledge that the paleoClim database comes with uncertainties related for example to vegetation cover or paleogeography reconstructions to cite a few, that can have big impact on local precipitation amount, as well as to model-inherent biases which result to incorrect representation of precipitation over land in the maritime continent region (*e.g.,* Toh et al., 2018). We are aware of those bias but did not have better alternative than the PaleoClim climate maps we are using currently. We acknowledge that such sensitivity experiments are important, and as mentioned above, we have discussed some of the limitations and assumptions in the Method section. To evaluate the physiographic responses on the Sunda Shelf to precipitation, we ran an additional experiment with uniform rainfall over 1 Myr (scenario 4). Despite changes in basins reorganisation timing and extent (Extended Data Fig. 2 and Fig. 3b), we found limited differences in terms of flooding history and erosion/deposition patterns when compared with scenario 5 (Extended Data Fig. 1c, d and Extended Data Tab 2). One approach would have consisted in using the orographic rainfall capability (Smith and Barstad, 2004) available in Badlands. The method is better suited to run generic simulations but falls short when applied to real cases as it relies on imposing paleo-environmental boundary conditions (e.g., temporal changes in wind direction and speed, moist stability frequency or depth of moist layer) difficult to obtain for Earth-like model applied over geological time scales.

C6: What are the implications of the biological connectivity model being species agnostic? How relevant are species specific traits and how much of it is lost in the analysis? Furthermore, how are non-external pressures for species dispersal considered? Are such mechanisms relevant for this particular study?

Connectivity maps are sensitive to the way connectivity models are conceptualized and implemented. The most common approach to modelling connectivity is the focal species approach which considers one or a few species that serve as surrogates to characterize connectivity for a larger suite of species. However, because species differ, e.g., in habitat requirements, body size, dispersal ability, or lifespan, the

effect of habitat fragmentation on functional connectivity can differ importantly. For this reason, the effectiveness of such an approach to evaluate connectivity for a suite of species is highly debated. In addition, large-scale analyses such as the one performed in our study, may require large numbers of focal species to represent diverse habitat types. To overcome these limitations, a species-agnostic approach is often used. Here, our approach is solely based on quantifying the degree of changes in the landscapes. Both focal-species and species-agnostic approaches are known to be sensitive to cost values. Parameterization and optimization of these cost values for connectivity mapping across species remains a nontrivial challenge. Given a cost surfaces, connectivity can be evaluated either by least cost path analysis or by quantifying current density based on circuit theory. The latter approach is used in this study as it allows for multiple movement pathways and varying degrees of corridor use across the landscape. This makes it possible to investigate multiple corridor routing options.

C7: Presentation: The figures are of high quality. However, font size is too small in most cases. For example, in Fig. 2 b, some font sizes seem half of that in the figure caption (or less). This makes the figures hard to read in places. I recommend adjustments wherever it is possible.

We have increased the font sizes in many of our figures.

18th Oct 21

Dear Dr Salles,

Please allow me to sincerely apologise for the long delay in sending a decision on your manuscript titled "Quaternary landscape dynamics boosted species dispersal across Southeast Asia". It has now been seen again by two of our reviewers, whose comments appear below. In light of their advice I am delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License).

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. In particular, please either remove your claim of an increase in diversification rate in the Late Pleistocene or conduct the statistical comparisons to other periods that are necessary to support this statement. (Depending on your responses we may need to consult briefly with a reviewer again). At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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We hope to hear from you within two weeks; please let us know if you need more time.

Best regards,

Joe Aslin

Associate Editor,
Communications Earth & Environment
https://www.nature.com/commsenv/
Twitter: @CommsEarth

REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

Main comments
This is an important article shedding light on detailed geomorphological changes in Sundaland through time, and their implications for population connectivity and divergence. The authors considered tectonic, eustatic and atmospheric forcing, and various scenarios (eg no subsidence vs variable subsidence). The modeling is detailed, substantial and well-calibrated and will be an important resource for geographers and biologists alike.

It shows, with broad brushes, areas in Sundaland that were important for maintaining gene flow among populations. How well the calculated current density maps reflect past gene flow potentials of various species depends on whether LEC, proximity to rivers and local slope are equally important (they received equal weightage), and the importance of unmodeled factors (eg vegetation type). Given the broad similarities between the top and bottom panels of Fig 5, it appears that LEC sets the broad patterns and rivers affect current density at a more local scale, whether rivers are considered barriers or corridors. This is somewhat curious to me given that it is well known that large rivers (eg the Amazon) are known to play a significant role in separating species since the time of Wallace, either through vicariance or by delineating zones of secondary contacts (eg Capparella, A. (1988) Genetic variation in Neotropical birds: implication for the speciation process. Acta XIX Congr. Intern. Ornith. vol. 2, 1658-64). Finding out whether currently submerged rivers (eg N Sunda river) played a

significant role in species diversification will be an interesting future area of research.

The authors made various improvements to the previous version of the manuscript:
The authors provided better explanations on why they expect the gene flow models to be applicable for a broad swath of lowland forest species.

The authors strengthened the introduction by adding appropriate key citations related to various aspects of Sundaland biogeography and geologic history.

The authors provided a more nuanced take on the relationship between marine incursion events and observed phylogeographic patterns and diverging times. I think additional (supplemental) text and table are needed to tell readers which splits the various bars and intervals in Fig 2 are referring to (see comments below). For example, the Piciforms paper looked at a total 26 barbet species.

Finally, the authors added a useful section in Methods detailing modeling caveats pertaining to landscape evolution, climatic conditions and gene flow analysis. This makes the assumptions much more transparent and will help other researchers who would like to tweak aspects of the analyses in order to conduct sensitivity analyses.

Specific comments

L29-30
Fragmentation is a double-edged sword; it may favor local endemism but can also increase extinction rate (due to smaller effective population sizes and lack of demographic rescues).

L41
Nice detailed exploration of scenarios related to having different assumptions (rainfall, vertical movement and sea-level changes).

L47-48
The authors did a nice job calibrating their models against inferred positions of paleo-rivers (based on phylogeographic patterns), borehole data and sediment accumulation data.

L54
Given that scenario 1 (no subsidence) is likely to be wrong, why not report sediment accumulation in the Gulf of Thailand under other scenarios?

L57-58
“highly variable”. Does this mean that different scenarios show very different results, or that the level of incursion was highly variable across time?

The statement that there was <20% flooding (or >80% exposure) even during sea-level high stands (ie interglacials) is not clear. Based on Fig 1c, the penultimate (~100 ka, mainly blue) interglacial period shows an average of ~40% land exposure (ie ~60% flooding).

L68
It’s unclear what evidence is provided to show that there is an “increase in diversification rate” in

Late Pleistocene. To show this, the authors need to show that early Pleistocene and even Pliocene periods have lower diversification rate. Simply demonstrating that divergence events happened in late Pleistocene is not sufficient (cf Fig 2b and 2c). To demonstrate a change in diversification rate through time, it is usual to conduct "lineage-through-time" analyses and show (statistically) that a time period has higher or lower rate compared to another (e.g., comparing periods with climatic fluctuations vs stability). Using results from other papers, the authors showed that divergences did happen in late Pleistocene. But I don't think we can confidently state that divergence rate in late Pleistocene was higher than other periods.

L94
Ref 53 (den Tex and Leonard) is a paper on barbets (birds), not aquatic species.

L99
"…we found that many of the Johore, Siam and West Borneo reorganisations often predate measured divergence times and population splits"
This point was touched upon in the previous review. Based on my general understanding of the phylogeographic literature of Sundaland, population splits of terrestrial species often predate 400 kyr, which is opposite of what is claimed by this statement. This means that factors other than basin reorganization (eg formation of forest refugia) were important for driving phylogeographic patterns / divergence histories in this region. A case in point is from Table 1 of the Leonard et al (2015) review paper cited in this paper. Out of the 16 within-species Malay Peninsula-Borneo split times they reported in Table 1, 11 (69%) were older than 400 kyr. Therefore, by and large, population divergence events were initiated and driven by factors other than basin reorganizations described in this manuscript. Of course, there could be nuances such as how basin rearrangements affected post-divergence flow, etc, and this is a point that could segue well with the next section.

L171-172
The point that yellow areas in Fig 5 (especially during 13 ka) being essential areas for migration due to lack of alternatives is well made (these are called pinch or choke points). For the sake of some readers, I think it is worth emphasizing that gray areas in Fig. 5 are not areas that did not support gene flow. It is just that these areas (eg between Java and Borneo) had low resistance in general and so there were no pinch points showing up as high current density areas (yellow).
Similarly, in Fig 6, the area between Java and Borneo appears mainly as blue (cold spots). Again, these areas may be misinterpreted as ones with little gene flow (ie high resistance corridors that do not favor species migration, cf L184 which talks about hotspots as being the opposite: "a network of preferential, well-connected, biodiversity corridors that favour species migration"). My understanding is that these "cold spots" are cold because there was a big area for gene flow to occur, hence current density can be "diffused". But it doesn't mean that resistance was high, it's just that gene flow was not constrained. Again, this is a point that's worth mentioning.

L179
"We then stack all time slices to evaluate persistent corridors over geological time scales..."
This suggests that the hotspot analysis evaluates both spatial clustering of areas with high current density, as well the persistence/occurrence of these clusters over time. Thus, please mention which time slices are used to conduct the hot spot analysis.

Figures
Fig 1c

Given the central importance of the Sunda shelf, make it more front and center that it's delineated by the white contour in 1b. Right now, it's mentioned in parenthesis in 1c.
Explain how the various periods delineated by different colors (cream, green and blue) are quantitatively defined.

Fig 2a.
This is a nice way of portraying the various physiographic changes/events in the past 500 ka based on different simulations.

I suggest numbering the five rows as scenarios 1-5 for easy reference to the text.

The extent of flooding is given in terms of the area of Sundaland (gray boxes are >50% flooding of Sundaland), while Fig 1c and most of the text describe flooding in terms of the shelf, which is a part of Sundaland (ie white contour in 1b). I think it's important to keep it consistent since Sundaland has landmasses that have always been subaerial (ie current Sumatra, Borneo, Malay Peninsula, etc.).

For the caption of Fig 2a, refer to Fig 3 since the readers have not been introduced to the various basins in Sundaland.

Fig 2b
Which splits (eg Borneo vs Malay Peninsula? Between various subspecies?) do the divergence times refer to? The studies referred to in Fig 2b covered a plethora of species, subspecies and geographic populations. It is hard to tell which phylogeographic splits the vertical lines are referring to. A supplemental table and some supplemental text explaining which splits were being referred to will be useful.

For example:
den Tex et al – 26 species of barbets (Piciforms) were studied, each with 1 or multiple geographic populations sampled.
Molye et al – Looked at subspecies of Enicurus leschenaultia in Java, mainland Asia, Sundaland, etc.
Sheldon – Looked at Copsychus saularis complex in Asia (including the Philippines) and C. albospecularis in Madagascar.
Lohman et al – This is a review paper. It has a phylogenetic tree for the yellow-vented bulbul but no specific timescale for the tree.
Steiner et al – Subspecies of Dicerorhinus sumatrensis (Sumatra rhinos) from Sumatra, Malay Peninsula and Borneo were covered.

Fig 2c
It is not clear why there are 4 bars but five confidence intervals. It is also not clear which interval goes with which point estimate. Specify that 2 of the time estimates overlap and form 1 bar visually (P. simplex and T. rostratum).

Fig 3a
I am curious, and did not pick it up in the previous version, as to why the Siam basin is south of the Johore basin. Are these conventional names for the various paleo-river systems? More commonly used paleo-river names I have seen are: Chao/Thai/Siam river (=Johore river in this paper), N Sunda river (=Siam river in this paper) and Malacca Straits river (=Singapore river).

ED Fig 5
Shouldn’t the current flow fields correspond to 250 ka (cf L185 in main text), instead of 280 ka?

Methods
L320
Provide a citation for the Getis Ord statistic.

Reviewer #2 (Remarks to the Author):

Having read the revised paper, I'm happy to recommend it for publication.

A difficulty with any study like this is that a significant amount of work needs to go into merely describing the model, much less the science coming out of it. The authors have handled this well enough in the paper, but supported their written work with the release of Jupyter notebooks and docker images for full reproducibility. This is commendable and a standard that all such papers should be held to.

GC1: The Jupyter notebooks the authors have added look to be in order and have nice explanations and pre-generated figures. This is good work. The article seems more reproducible now - thanks!

GC2: Thanks, this is a useful addition.

G3: Extended Data Table 2 is great. I wish it could be included in the main paper. I still find it challenging to see how the various scenarios are used to elucidate the point. It took several readings of this paragraph to fully understand it. I'm not sure off-handedly how to improve this, but suggest looking at it again. I was expecting something like: "Since Scenario 1 omits tectonics it can be used as a control to help isolate the effects of tectonics in the other scenarios while Scenario 4 can be used as a control for rainfall. [...]" Note that the idea of using scenarios as controls is challenging since there are more variable combinations than scenarios, but the above should give you the idea.

C1: Thanks.

C2: Okay.

C3: Great, thanks. Perhaps a note about this should be added to the paper?

C4: Okay.

C5: Okay.

C6: The caption is very readable now, thank you.

C7: Okay.

C8: Okay.

C9: Okay.

C10: Thank you for your explanation; perhaps the changes, though significant at the local level don't plot well at a zoomed-out level.

C12: Thanks.

C13: Okay.

C14: Okay.

C15: Okay.

C16: Okay.

C17: Okay.

Rebuttal letter

We would like to thank the two reviewers for their comments and feedbacks on the revised version of the manuscript.

Point-by-point responses to reviewer 1

Specific comments

SC1: Fragmentation is a double-edged sword; it may favor local endemism but can also increase extinction rate (due to smaller effective population sizes and lack of demographic rescues).

We agree with reviewer's comment and have modified the sentence accordingly (ln 39-40).

SC2: Given that scenario 1 (no subsidence) is likely to be wrong, why not report sediment accumulation in the Gulf of Thailand under other scenarios.

We provide in extended table 3, the sediment accumulation for the 5 different scenarios and presented results in Fig. 1b are for scenario 5 which is forced with variable tectonic regime.

SC3: "highly variable". Does this mean that different scenarios show very different results, or that the level of incursion was highly variable across time ?
The statement that there was <20% flooding (or >80% exposure) even during sea-level high stands (ie interglacials) is not clear. Based on Fig 1c, the penultimate (~100 ka, mainly blue) interglacial period shows an average of ~40% land exposure (ie ~60% flooding).

Following reviewer's comment, we have changed the sentence to "variable" and specified that the variability was relative to the level of incursion between the different scenarios. We also thank the reviewer for pointing out the error when reporting the percentage during sea-level high stands where we mistakably inverted the % of shelf flooded with the exposed one. It should have been *<80% of the shelf flooded* or *>20% of the shelf exposed* and *not <20% of the shelf flooded*. We have corrected the error.

SC4: It is unclear what evidence is provided to show that there is an "increase in diversification rate" in Late Pleistocene. To show this, the authors need to show that early Pleistocene and even Pliocene periods have lower diversification rate. Simply demonstrating that divergence events happened in late Pleistocene is not sufficient (cf Fig 2b and 2c). To demonstrate a change in diversification rate through time, it is usual to conduct "lineage-through-time" analyses and show (statistically) that a time period has higher or lower rate compared to another (e.g., comparing periods with climatic fluctuations vs stability). Using results from other papers, the authors showed that divergences did happen in late Pleistocene. But I don't think we can confidently state that divergence rate in late Pleistocene was higher than other periods.

We agree with the reviewer and have updated the manuscript to lower the claim made in this section. As pointed out by the reviewer, evaluating the increase in diversification rate in Late Pleistocene will require to evaluate the evolution over a much longer period than the one studied here. We have modified the sentence accordingly (Ln 68) where we now state that "*the divergences that did happen in late Pleistocene were more likely caused by a combination of different drivers*".

SC5: Ref 53 (den Tex and Leonard) is a paper on barbets (birds), not aquatic species.

We thank the reviewer for picking this reference mistake and we have now moved the reference to its correct place in the figure legend.

SC6: "…we found that many of the Johore, Siam and West Borneo reorganisations often predate measured divergence times and population splits"
This point was touched upon in the previous review. Based on my general understanding of the phylogeographic literature of Sundaland, population splits of terrestrial species often predate 400 kyr, which is opposite of what is claimed by this statement. This means that factors other than basin reorganization (eg formation of forest refugia) were important for driving phylogeographic patterns / divergence histories in this region. A case in point is from Table 1 of the Leonard et al (2015) review paper cited in this paper. Out of the 16 within-species Malay Peninsula-Borneo split times they reported in Table 1, 11 (69%) were older than 400 kyr. Therefore, by and large, population divergence events were initiated and driven by factors other than basin reorganizations described in this manuscript. Of course, there could be nuances such as how basin rearrangements affected post-divergence flow, etc, and this is a point that could segue well with the next section.

We agree with reviewer's comment, indeed there are many evidence suggesting that population splits of terrestrial species predated the Late Pleistocene as shown in Leonard et al. (2015) and others. However, our sentence claims that basins reorganisations predate divergence times over the past 320 kyr and we specifically focus on this time interval (*i.e.,* the last 500 kyr) in this study. As pointed by the reviewer, geomorphological changes might not be the primary factor that triggered population splits in the region, but they might have contributed to it to some extent and our study try to quantify this potential contribution during the Late Pleistocene. We have modified the end of section *Sensivity of Sundaland flooding history* (Ln 70) to consider reviewer's suggestion.

SC7: The point that yellow areas in Fig 5 (especially during 13 ka) being essential areas for migration due to lack of alternatives is well made (these are called pinch or choke points). For the sake of some readers, I think it is worth emphasizing that gray areas in Fig. 5 are not areas that did not support gene flow. It is just that these areas (eg between Java and Borneo) had low resistance in general and so there were no pinch points showing up as high current density areas (yellow).
Similarly, in Fig 6, the area between Java and Borneo appears mainly as blue (cold spots). Again, these areas may be misinterpreted as ones with little gene flow (ie high resistance corridors that do not favor species migration, cf L184 which talks about hotspots as being the opposite: "a network of preferential, well-connected, biodiversity corridors that favour species migration"). My understanding is that these "cold spots" are cold because there was a big area for gene flow to occur, hence current density can be "diffused". But it doesn't mean that resistance was high, it's just that gene flow was not constrained. Again, this is a point that's worth mentioning.

We agree with the reviewer and have updated the manuscript to emphasize his point. Specifically, we have added a sentence in the Landscape connectivity section (relative to Fig. 5 - Ln 160) and in the Hotspot analysis section (for Fig. 6 - Ln 182) to clarify the fact that low resistance regions and cold spots do not reflect low support of gene flow but rather unconstrained ones.

SC8: "**We then stack all time slices to evaluate persistent corridors over geological time scales..."**
This suggests that the hotspot analysis evaluates both spatial clustering of areas with high current density, as well the persistence/occurrence of these clusters over time. Thus, please mention which time slices are used to conduct the hot spot analysis.

The considered time slices for the hotspot analysis are extracted from scenario 5 (our preferred model) during periods of marine regression where at least 50% of shelf is exposed. We have updated the manuscript adding this information in the first sentence of the section (Ln 177).

Figures comments

FC1: fig1c Given the central importance of the Sunda shelf, make it more front and center that it's delineated by the white contour in 1b. Right now, it's mentioned in parenthesis in 1c.
Explain how the various periods delineated by different colors (cream, green and blue) are

quantitatively defined.

We have modified Fig. 1b to highlight the Sunda Shelf by changing the contour colour from white to black and by adding the name in the figure. We have modified the caption to reflect these changes and also explained the approach used to compute shelf exposure over time.

FC2: fig2a This is a nice way of portraying the various physiographic changes/events in the past 500 ka based on different simulations.
I suggest numbering the five rows as scenarios 1-5 for easy reference to the text.
The extent of flooding is given in terms of the area of Sundaland (gray boxes are >50% flooding of Sundaland), while Fig 1c and most of the text describe flooding in terms of the shelf, which is a part of Sundaland (ie white contour in 1b). I think it's important to keep it consistent since Sundaland has landmasses that have always been subaerial (ie current Sumatra, Borneo, Malay Peninsula, etc.).

Following reviewer's comment, we have added each scenario number to Fig. 2a and we have also corrected the caption for the gray area which are actually representing time interval with flooding > 50% of Sunda Shelf and not of Sundaland.

FC3: fig2b Which splits (eg Borneo vs Malay Peninsula? Between various subspecies?) do the divergence times refer to? The studies referred to in Fig 2b covered a plethora of species, subspecies and geographic populations. It is hard to tell which phylogeographic splits the vertical lines are referring to. A supplemental table and some supplemental text explaining which splits were being referred to will be useful.

The studies referred to in Fig 2b mostly summarise for the considered time interval the ones defined in Husson et al. (2018). For now, we have (in ED Table 4) the genera for freshwater halfbeak fishes and corresponding paleo-drainage basins, and we have added the reference to Husson et al. paper at the end of Fig. 2 caption. If necessary, we could add a supplementary table as suggested by the reviewer in the supplementary information.

FC4: fig3a I am curious and did not pick it up in the previous version, as to why the Siam basin is south of the Johore basin. Are these conventional names for the various paleo-river systems? More commonly used paleo-river names I have seen are: Chao/Thai/Siam river (=Johore river in this paper), N Sunda river (=Siam river in this paper) and Malacca Straits river (=Singapore river).

As pointed out by the reviewer, different names have been proposed for these paleo-river systems and here we chose to use the naming convention defined in Darmadi et al. (2007), De Bruyn (2013) and Alqahtani et al. (2015).

FC5: ED fig5 Shouldn't the current flow fields correspond to 250 ka (cf L185 in main text), instead of 280 ka?

In the main text, we refer to Fig 5 that displays the current flow field at 250 ka and not ED Fig 5 that provided a display of current flow distribution at another time interval (280 ka).

Methods comments

MC1: Provide a citation for the Getis-Ord statistic.

As suggested by the reviewer, we have added a reference to the Getis-Ord statistic in the manuscript at line 320 (reference 67).

Responses to reviewer 2

Comments

GC 3: Extended Data Table 2 is great. I wish it could be included in the main paper. I still find it challenging to see how the various scenarios are used to elucidate the point. It took several readings of this paragraph to fully understand it. I'm not sure off-handedly how to improve this, but suggest looking at it again. I was expecting something like: "Since Scenario 1 omits tectonics it can be used as a control to help isolate the effects of tectonics in the other scenarios while Scenario 4 can be used as a control for rainfall. [...]" Note that the idea of using scenarios as controls is challenging since there are more variable combinations than scenarios, but the above should give you the idea.

Response: Following reviewer's comment, we have added a summary at the end of the paragraph (Ln 49) that summarise our choice of scenarios: *scenarios 1 and 2 are used to isolate the effects of tectonics, while scenario 4 is used as a control for rainfall regime. Scenarios 3 and 5 are used to evaluate the role of sea-level on flooding history of the shelf.*