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PROCEEDINGS B

Species packing and the latitudinal gradient in beta-diversity

Ke Cao, Richard Condit, Xiangcheng Mi, Lei Chen, Haibao Ren, Wubing Xu, David F. R. P. Burslem, Chunrong Cai, Min Cao, Li-Wan Chang, Chengjin Chu, Fuxin Cui, Hu Du, Sisira Ediriweera, C. S. V. Gunatilleke, I. U. A. N. Gunatilleke, Zhanqing Hao, Guangze Jin, Jinbo Li, Buhang Li, Yide Li, Yankun Liu, Hongwei Ni, Michael J. O'Brien, Xiujuan Qiao, Guochun Shen, Songyan Tian, Xihua Wang, Han Xu, YaozHan Xu, Libing Yang, Sandra L. Yap, Juyu Lian, Wanhui Ye, Mingjian Yu, Sheng-Hsin Su, Chia-Hao Chang-Yang, Yili Guo, Xiankun Li, Fuping Zeng, Daoguang Zhu, Li Zhu, I-Fang Sun, Keping Ma and Jens-Christian Svenning

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Final acceptance:	17 March 2021

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-3045.R0 (Original submission)

Review form: Reviewer 1 (Gabriel Arellano)

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
No

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
Review of RSPB-2020-3045, "Species packing and the latitudinal gradient in local beta diversity"

My opinion about journals and the pre-publication review process: We do not need to work for free for the journals, or pay them to publish our work. As authors, we can distribute our work with a few clicks in many ways. As readers, we can use Google etc. to find any piece of work relevant to us, regardless of it being published in journals or not. The "stamp of quality" implicit in the pre-publication peer review process is a fallacy. Journals fail at that, both in a myriad of individual cases, and at a deep level. Journal filters are biased to the point that most current published research findings may be false, and we face an obvious replication crisis. I don't know why we remain hostages of this system. Post-publication peer review exists, and people can build on previous work according to its merits, correctness, and interest for the broader community. Time put each work into its place. Too much energy is invested in trying to convince some editors/referees about the novelty and interest of a given piece of work. It is a painful waste of time and talent, and a source of bias in itself. I think scientist should focus on science, and not on the publication/acceptance process.

I hope the authors find my comments useful to improve their work.

GENERAL COMMENTS

(1) Effect of under-sampling of local communities vs. effect of random colonization from the pool of species

I describe how I understand your approach. Confirm that I understood it correctly before taking my comments into account.

The method you use is called "corrected beta-Shannon diversity". It uses the partitive approach: alpha diversity is calculated, gamma diversity is calculated, and beta diversity is derived from

alpha and gamma diversities. It is interpreted as true beta diversity sensu Tuomisto 2010. The difference from the standard approach is that alpha and gamma diversities are extrapolated from the sample to the whole system, and therefore the beta diversity is theoretically not biased by under-sampling. It could be seen as "asymptotical beta diversity".

You state "the bias arising in beta-diversity metrics is a dependence on sample size that interacts with gamma-diversity". I am not sure if the bias that worry those who study beta diversity is just due to a (necessarily) small local sample size. The effect of gamma on beta that is discussed in much of the literature refers to local assembly mechanisms more than local under-sampling. The null models simulate random sampling from a regional pool of species. If local communities do not differ from that, there are no local assembly mechanisms. If local communities differ from that, there are local assembly mechanisms (e.g. spatial or environmental). This is the approach taken by:

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- Etc.

Maybe I don't fully understand how your asymptotic approach and the null model approach compare with each other. This is a complex issue. I can imagine that if a local community (a sample) is just a random sample from the region, its species accumulation curve will be just the initial section of the regional species accumulation curve. And the same with any number of plots combined. If individuals there are just random samples from the regional species pool, many plots combined will accumulate more species, but the curvature of their species accumulation curve will be exactly the same as for a single plot. They will cover more portion of the regional species accumulation curve but the extrapolation will reach the same asymptote. In other words, there would be zero beta diversity. If there are local processes involved filtering out certain species from local communities, the extrapolation from a plot will not reach the whole species pool in the region. The gap between the asymptotic/extrapolated alpha and the asymptotic/extrapolated gamma would reflect beta-diversity not due to random sampling from the whole species pool. I think the approach is valid and conceptually equivalent to the null model approach, with the advantage of considering unseen species, but I would need to read reference 25.

The null model approach is limited in the sense that most of the times it does not incorporate unseen species neither locally (e.g. Condit et al. 2005) or regionally (e.g. Myers and LaManna 2016). The null model approach involves the simulation of the colonization process, which in turn requires a good deal of subjectivity, decisions taken by the researcher, etc. The definition of the species pool is, in general, a major practical inconvenient. The extrapolations of alpha and gamma diversities, in contrast, seems more process-agnostic and robust.

To understand this method better I would need to read reference 25 (Cao K., Svenning J.-C., Yan C., Zhang J., Ma K., Mi X. 2020 Undersampling correction methods to control γ-dependence for comparing β-diversity between regions. Ecology, (Under review)). I cannot access it. Even if that paper is accepted and published by the time you publish this work, it would be better if you include a summary of the approach in this manuscript, so the reader doesn't need to read two papers instead of one.

There is another method mentioned (Jaccard-Chao index, reference 32) that removes the effect of under-sampling from pairwise dissimilarity metrics. This method is not used. It could be mentioned in Discussion but it is not appropriate to mention it in Methods.
(2) Scales

Avoid using "local" in the text. It is very confusing when it refers to gamma diversity. Use alpha or quadrat-level and gamma or plot-level.

In a homogeneous system (perfect mix, no beta-diversity) alpha and gamma diversities are just arbitrary points of observation along the system-level species accumulation curve. I recommend using quadrat-level and plot-level diversity, more than alpha and gamma. It is more explicit.
In any case, in your work, beta-diversity and the processes generating it will refer to the scales between the local sample (a quadrat, in this manuscript) and the region (a big plot). Alpha diversity measured at the quadrat level is obviously nothing more than beta-diversity within the quadrat, the turnover of species identity from one tree to the other at those small scales. Statements like "higher/lower beta diversity at high/low latitudes" are scale-dependent.

You could improve the text a bit by polishing statements that are scale-dependent and make them more explicit.

(3) Causality
I think the "asymptotic approach" that you adopt does not require causality in any given direction. The gap between asymptotic/extrapolated alpha and asymptotic/extrapolated gamma reflects beta-diversity. It can be seen both as (a) the emergent diversity of pooling together more than one locality or (b) the incompleteness of the sampling/colonization from the species pool. This is nice, I like it.

However, in your Discussion and some other places, you imply that gamma diversity influences beta diversity, and not the other way around. This is the causal direction implied or assumed by those working with null models that "control for" the influence of gamma diversity. This assumption makes more sense at small extents than at large extents. At large extents, the pool of species results from the combination of multiple habitats/assemblages, and the causality goes in the opposite direction: it is the change in composition between habitat and along environmental gradients the cause of the region-level diversity (beta diversity causes gamma diversity). Both things can happen simultaneously and I have no idea at what scales one model is better than the other. Expression like "deviations from the expected", "controlling for", etc. could be revisited having this in mind.
Examples: lines 62-65, 105-107, 113, 270-271, 279.

(4) Grains

What do we learn by comparing grains? Your "region" is the big plot, and it seems reasonable to keep that fixed. Your "localities" can be any partition of the region, from many localities of few trees in size to 2 localities of ½ region in size. The 3 grains are not discussed, there is nothing in these 3 extents that make them particularly relevant for the readers. Why don't you use just one grain?

SPECIFIC COMMENTS

Line 63. Don't use "local species richness" to refer to gamma diversity, it is not intuitive.

Lines 81-82: beta-diversity more important than alpha diversity: Just say that it is key for conservation, there is no need to compete.

Line 86: "and more abiotically" □ "as more abiotically"?

Lines 86-87: it is not clear what "greater packing" means. More heterogeneous habitats imply more room for species, but does not obviously help for a tighter packing of species. This applies to other places in the text, in general you want to make a clear distinction between the amount of available niche space and how tightly species are packed within that niche space.

Line 87: Remove "alternatively".

Line 88: productivity conditions. Productivity is also the result of the species' niches and diversity through complementary effects.

Line 91: remove "local". Beta diversity could happen at any scale. There is beta diversity between 5x5m quadrats within a 25 ha plot, and there is beta diversity between countries in a continent.

Line 92: "latitudinal gradient" "latitunidal gradient in beta diversity"

Line 92: "abiotic environment" "abiotic heterogeneity". The environment does change with the latitude. I agree there is no reason why heterogeneity itself should change with latitude.

Lines 98-101: I suggest to make the example with two sites of exactly the same composition. Otherwise it is not that intuitive. And polish the statements more, as they are key. Example: "Small samples never capture all local species. Two small samples from two sites that have exactly the same composition will appear to differ by randomly capturing different subsets of the local composition. The more incomplete the sampling is, the greater the beta diversity will seem to be. As a result, high species richness will artificially inflate metrics of beta-diversity".

Line 104: "richer communities". It is not clear whether it refers to alpha or gamma scales.

Line 107: "packing": does it refer to (a) the size of the available niche space or (b) how tightly species partition that space?

Lines 110-113, 159-162, 249-252: Don't use "we" for reference 25. The first author is the same, but there are different authors. Besides, the reader will think that "we" refers to a simulation conducted in this particular manuscript, and not past work of the same team. Use "they". It is a different work. In the Discussion, don't try to earn points here based on the merits of that other work.

Line 117: niche specialization and niche marginality. These are species-level metrics but at the end of the day you summarize them into community-level metrics. At the community level, niche marginality is a measure of the size of the available niche space, and niche specialization is a measure of how tight the packing is. From my point of view it is more intuitive to present the available space first (marginality) and the tightness of the packing later (specialization). Using "community-wide niche marginality" as a metric equivalent to "total niche volume" is not very direct or intuitive but it is correct.

Line 130, after mentioning table S1 and before "we divided plots into quadrats" you should incorporate how you calculated two important attributes of the plots: the corrected latitude (moving text from lines 498-499) and the topographic heterogeneity (moving the text from lines 164-168 and 184-186).

Line 155: you use "true beta diversity" sensu Tuomisto 2010, but that name has not been widely applied. The reader will think you mean "correct" or "corrected" or "adjusted" or something like that. I would remove "true".

Line 157-159: if both methods are not used or discussed consistently, don't mention it and don't use it. It is not clear why you would do this comparison. It is not clear what we would learn by using two methods. If the asymptotic approach to true beta diversity is correct and valid, use it

and nothing else.

Lines 165-166: surface to planimetric area ratio. In a strict sense this means nothing. Surfaces are fractal. One planimetric hectare of forest may include 1 hectare of surface or 1 million km^2, depending on how tiny your measurement tool is. Be explicit on the resolution of your DEM.

Line 169: Use some mathematical notation to clarify this statement, like SD(available habitat)/SD(habitat used).

Line 169 etc. What is "habitat"?

Line 171: what is "ecological distance"?

Line 177, 189-190: Why is normality important? Why did you use Box-Cox transformation? What are the consequences of these transformations?

Lines 179-181: be explicit regarding the precise mapping of all individuals in these plots.

Line 186: "topographic variables were strongly correlated" □ "topographic variables are typically strongly correlated". You said that you had no other information but topographic variables.

Lines 190-192: these seem a repetition of lines 179-181.

Line 200: it is more intuitive to write (x – mean(x))/sd(x)

Lines 201-202: Box-Cox and min-max are not statistical analyses. Why is this necessary, anyway?

Line 212 etc.: before presenting the results for the asymptotic beta diversity you could present the results of the un-corrected beta diversity.

Lines 220-221: if we haven't read the caption of the figure we don't know what "adjusted latitude" means. Explain it when talking about the study sites and their properties, before explaining the division into quadrats.

Line 238: don't use LDG here or anywhere else, just use full words.

Lines 249-252: this refers to a different work, not this one. This is not appropriate. It seems this applies until the end of the paragraph. This is not appropriate for Discussion, you should explain and justify the asymptotic approach in Methods.

Lines 258: "more stable productivity" □ "greater stability"

Lines 258 etc. It is not fully discussed why species may have tighter packing in the same niche space in the tropics. I have worked on a related topic along an elevational gradient and we found lower niche overlap between species at higher elevation, where productivity and diversity are lower. Arellano, G., M. N. Umaña, M. J. Macía, M. I. Loza, A. Fuentes, V. Cala, P. M. Jørgensen. 2017. The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon-Andes gradient. Global Ecology and Biogeography 26: 191-202. DOI: 10.1111/geb.12531

Line 266: you conclude that beta diversity is driven by local processes. Why? You study a very local scale, small quadrats within large plots. You cannot conclude anything about beta diversity at the 1, 10, 100 km scale.

Lines 285-289: Open data is required for reproducibility of results. Open data also destroys the incentive to install and maintain permanent forest plots as those used here. I don't have a solid

opinion on this, but the journal may have one. In any case, the data availability statement, as it is ow, means almost nothing. It means that data exist somewhere, and that through some dozens of e-mails and weeks/months of conversations with plot PI's someone may gather the same or similar dataset. There is no guarantee that the whole dataset will be shared as a package upon reasonable request. Therefore, there is no guarantee of reproducibility.

Figure 1: this is a map with the true location of the plots. The adjusted latitude is relevant for the analyses and should be presented in Methods. Additionally, you could project these latitudes on the vertical axis and show there some arrows or something like that to represent the latitude adjustment. It is not necessary.

Panels in figures: 2c, 3b, 3d: their Y axes mean nothing, these should not be figures. These numbers should be presented in the text or in a table.

Line 508: check double spaces.

Good luck with this work and your other ongoing projects.
Sincerely yours,

Gabriel Arellano, gabriel.arellano.torres@gmail.com

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?

N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
Cao et al. found evidence for latitudinal gradient of beta-diversity even after correcting the effects of topographic heterogeneity, sample sizes and gamma-diversity. Since the latitudinal gradient of beta-diversity is still a hot topic, this manuscript will attract broad readers. I only have a few comments to improve readability.

Conceptual figure for niche specialization and niche marginality like Fig. S1 is a must. If there is no enough space for the main text, I would suggest to replace the current Fig. 1 showing maps with Fig. 1S. It would be more helpful for most of the readers. Related with this, Fig. S1A is hard to understand. How did you estimate (c) the favorable but uncolonized area due to competitive exclusion? How is this related with Fig. S1B-D? If Fig. S1A is not that important in explaining the key idea of this manuscript, I would suggest to delete Fig. S1A.

The relationship between niche space and marginality is unclear. One of the main analyses in this manuscript assumes that higher community-level niche marginality indicates a larger niche space (L184), however according to Fig. S1D, higher community-level niche marginality doesn't have to indicate a larger niche space. If the niche space means the length of x-axis in Fig. S1D, both communities have the same niche space but different marginality. If the niche space means the width of the bell shaped curve in Fig. S1D, the bottom figure with lower marginality looks to have larger niche space to me. I would suggest to explain the term "niche space" in line with niche marginality more clearly.

Topographic heterogeneity is not explained. The topographic factors used in the study are listed but how did you calculate or define topographic heterogeneity from those factors?

The discussion look a bit descriptive. I feel there are some contents that could be discussed, such as the differences in the effect sizes between latitude and topographic heterogeneity and the differences in the effect sizes among grain sizes.

Minor comments:
L93-94: Please rephrase this sentence. The second clause doesn't explain why the alternatives remain unresolved. It just repeats the same meaning.

L98-101: These two sentences are a bit unclear to me, although I understand that small sample sizes (alpha scales) inflate beta diversity in the absence of controlling gamma diversity (Sreekar et al. 2018, Kraft et al. 2011).

L109-110: It would be better to delete "in East Asia" because it's duplicated.

L178: How did you choose the scale parameters (usually lambda) for Box-Cox transformation?

L201: Finally? I thought you used Box-Cox transformed niche specialization for linear regressions.

L266-277: I guess the key message here is that topographic heterogeneity itself alone doesn't explain latitudinal beta-diversity, but topographic heterogeneity is important for maintaining beta-diversity. It's a bit hard to grasp at the first glance. Please explain this in a more clear way in

this paragraph and the previous paragraph.

L260-263: It would be also better to mention the result of multiple regression that suggests the existence of latitudinal gradient in beta-diversity after controlling topographic heterogeneity.

Fig. S1: Caption letter "C" is missing in the figure. Caption letters are capital in the figure but lower case in the caption text. Please fix them. In Fig. S1C, does each point indicate each quadrat? If so, which grain size?

Fig. 3: It would be better to mention that niche specialization is scaled to 0 to 1 after Box-Cox transformation in the legend.

Please check the values in Table S4 and Fig 3C. The significance for the grain size 50m is different between the figure and the table.

Decision letter (RSPB-2020-3045.R0)

11-Jan-2021

Dear Dr Mi:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Maurine Neiman
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
The two reviewers and I are positive about the data and results being presented in this MS, although Reviewer 1 rightly draws attention to the fact that some of the methods are only available in a second MS that is not publicly available (Cao et al, Ecology, in review). You'll need to either provide a precis of those missing details in the MS along with a more detailed explanation in the Supplement, or make the other MS available through a preprint server. Beyond that, there is quite a list of clarifications that are needed to make the MS easier to interpret for the readers.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
Review of RSPB-2020-3045, "Species packing and the latitudinal gradient in local beta diversity"

My opinion about journals and the pre-publication review process: We do not need to work for free for the journals, or pay them to publish our work. As authors, we can distribute our work with a few clicks in many ways. As readers, we can use Google etc. to find any piece of work relevant to us, regardless of it being published in journals or not. The "stamp of quality" implicit in the pre-publication peer review process is a fallacy. Journals fail at that, both in a myriad of individual cases, and at a deep level. Journal filters are biased to the point that most current published research findings may be false, and we face an obvious replication crisis. I don't know why we remain hostages of this system. Post-publication peer review exists, and people can build on previous work according to its merits, correctness, and interest for the broader community. Time put each work into its place. Too much energy is invested in trying to convince some editors/referees about the novelty and interest of a given piece of work. It is a painful waste of time and talent, and a source of bias in itself. I think scientist should focus on science, and not on the publication/acceptance process.

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· Mori et al. 2013. Community assembly processes shape an altitudinal gradient of forest biodiversity. Global Ecology and Biogeography 22: 878–888
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The null model approach is limited in the sense that most of the times it does not incorporate unseen species neither locally (e.g. Condit et al. 2005) or regionally (e.g. Myers and LaManna 2016). The null model approach involves the simulation of the colonization process, which in turn requires a good deal of subjectivity, decisions taken by the researcher, etc. The definition of the species pool is, in general, a major practical inconvenient. The extrapolations of alpha and gamma diversities, in contrast, seems more process-agnostic and robust.

To understand this method better I would need to read reference 25 (Cao K., Svenning J.-C., Yan C., Zhang J., Ma K., Mi X. 2020 Undersampling correction methods to control γ-dependence for comparing β-diversity between regions. Ecology, (Under review)). I cannot access it. Even if that paper is accepted and published by the time you publish this work, it would be better if you include a summary of the approach in this manuscript, so the reader doesn't need to read two papers instead of one.

There is another method mentioned (Jaccard-Chao index, reference 32) that removes the effect of under-sampling from pairwise dissimilarity metrics. This method is not used. It could be mentioned in Discussion but it is not appropriate to mention it in Methods.

(2) Scales

Avoid using "local" in the text. It is very confusing when it refers to gamma diversity. Use alpha or quadrat-level and gamma or plot-level.

In a homogeneous system (perfect mix, no beta-diversity) alpha and gamma diversities are just arbitrary points of observation along the system-level species accumulation curve. I recommend using quadrat-level and plot-level diversity, more than alpha and gamma. It is more explicit.

In any case, in your work, beta-diversity and the processes generating it will refer to the scales between the local sample (a quadrat, in this manuscript) and the region (a big plot). Alpha diversity measured at the quadrat level is obviously nothing more than beta-diversity within the quadrat, the turnover of species identity from one tree to the other at those small scales. Statements like "higher/lower beta diversity at high/low latitudes" are scale-dependent.

You could improve the text a bit by polishing statements that are scale-dependent and make them more explicit.

(3) Causality

I think the "asymptotic approach" that you adopt does not require causality in any given direction. The gap between asymptotic/extrapolated alpha and asymptotic/extrapolated gamma reflects beta-diversity. It can be seen both as (a) the emergent diversity of pooling together more than one locality or (b) the incompleteness of the sampling/colonization from the species pool. This is nice, I like it.

However, in your Discussion and some other places, you imply that gamma diversity influences beta diversity, and not the other way around. This is the causal direction implied or assumed by those working with null models that "control for" the influence of gamma diversity. This assumption makes more sense at small extents than at large extents. At large extents, the pool of species results from the combination of multiple habitats/assemblages, and the causality goes in the opposite direction: it is the change in composition between habitat and along environmental gradients the cause of the region-level diversity (beta diversity causes gamma diversity). Both things can happen simultaneously and I have no idea at what scales one model is better than the other. Expression like "deviations from the expected", "controlling for", etc. could be revisited having this in mind.

Examples: lines 62-65, 105-107, 113, 270-271, 279.

(4) Grains

What do we learn by comparing grains? Your "region" is the big plot, and it seems reasonable to keep that fixed. Your "localities" can be any partition of the region, from many localities of few trees in size to 2 localities of ½ region in size. The 3 grains are not discussed, there is nothing in these 3 extents that make them particularly relevant for the readers. Why don't you use just one grain?

SPECIFIC COMMENTS

Line 63. Don't use "local species richness" to refer to gamma diversity, it is not intuitive.

Lines 81-82: beta-diversity more important than alpha diversity: Just say that it is key for conservation, there is no need to compete.

Line 86: "and more abiotically" □ "as more abiotically"?

Lines 86-87: it is not clear what "greater packing" means. More heterogeneous habitats imply more room for species, but does not obviously help for a tighter packing of species. This applies

to other places in the text, in general you want to make a clear distinction between the amount of available niche space and how tightly species are packed within that niche space.

Line 87: Remove “alternatively”.

Line 88: productivity conditions. Productivity is also the result of the species’ niches and diversity through complementary effects.

Line 91: remove “local”. Beta diversity could happen at any scale. There is beta diversity between 5x5m quadrats within a 25 ha plot, and there is beta diversity between countries in a continent.

Line 92: “latitudinal gradient” “latitunidal gradient in beta diversity”

Line 92: “abiotic environment” “abiotic heterogeneity”. The environment does change with the latitude. I agree there is no reason why heterogeneity itself should change with latitude.

Lines 98-101: I suggest to make the example with two sites of exactly the same composition. Otherwise it is not that intuitive. And polish the statements more, as they are key. Example: “Small samples never capture all local species. Two small samples from two sites that have exactly the same composition will appear to differ by randomly capturing different subsets of the local composition. The more incomplete the sampling is, the greater the beta diversity will seem to be. As a result, high species richness will artificially inflate metrics of beta-diversity”.

Line 104: “richer communities”. It is not clear whether it refers to alpha or gamma scales.

Line 107: “packing”: does it refer to (a) the size of the available niche space or (b) how tightly species partition that space?

Lines 110-113, 159-162, 249-252: Don’t use “we” for reference 25. The first author is the same, but there are different authors. Besides, the reader will think that “we” refers to a simulation conducted in this particular manuscript, and not past work of the same team. Use “they”. It is a different work. In the Discussion, don’t try to earn points here based on the merits of that other work.

Line 117: niche specialization and niche marginality. These are species-level metrics but at the end of the day you summarize them into community-level metrics. At the community level, niche marginality is a measure of the size of the available niche space, and niche specialization is a measure of how tight the packing is. From my point of view it is more intuitive to present the available space first (marginality) and the tightness of the packing later (specialization). Using “community-wide niche marginality” as a metric equivalent to “total niche volume” is not very direct or intuitive but it is correct.

Line 130, after mentioning table S1 and before “we divided plots into quadrats” you should incorporate how you calculated two important attributes of the plots: the corrected latitude (moving text from lines 498-499) and the topographic heterogeneity (moving the text from lines 164-168 and 184-186).

Line 155: you use “true beta diversity” sensu Tuomisto 2010, but that name has not been widely applied. The reader will think you mean “correct” or “corrected” or “adjusted” or something like that. I would remove “true”.

Line 157-159: if both methods are not used or discussed consistently, don’t mention it and don’t use it. It is not clear why you would do this comparison. It is not clear what we would learn by using two methods. If the asymptotic approach to true beta diversity is correct and valid, use it and nothing else.

Lines 165-166: surface to planimetric area ratio. In a strict sense this means nothing. Surfaces are fractal. One planimetric hectare of forest may include 1 hectare of surface or 1 million km^2, depending on how tiny your measurement tool is. Be explicit on the resolution of your DEM.

Line 169: Use some mathematical notation to clarify this statement, like SD(available habitat)/SD(habitat used).

Line 169 etc. What is "habitat"?

Line 171: what is "ecological distance"?

Line 177, 189-190: Why is normality important? Why did you use Box-Cox transformation? What are the consequences of these transformations?

Lines 179-181: be explicit regarding the precise mapping of all individuals in these plots.

Line 186: "topographic variables were strongly correlated" □ "topographic variables are typically strongly correlated". You said that you had no other information but topographic variables.

Lines 190-192: these seem a repetition of lines 179-181.

Line 200: it is more intuitive to write (x – mean(x))/sd(x)

Lines 201-202: Box-Cox and min-max are not statistical analyses. Why is this necessary, anyway?

Line 212 etc.: before presenting the results for the asymptotic beta diversity you could present the results of the un-corrected beta diversity.

Lines 220-221: if we haven't read the caption of the figure we don't know what "adjusted latitude" means. Explain it when talking about the study sites and their properties, before explaining the division into quadrats.

Line 238: don't use LDG here or anywhere else, just use full words.

Lines 249-252: this refers to a different work, not this one. This is not appropriate. It seems this applies until the end of the paragraph. This is not appropriate for Discussion, you should explain and justify the asymptotic approach in Methods.

Lines 258: "more stable productivity" □ "greater stability"

Lines 258 etc. It is not fully discussed why species may have tighter packing in the same niche space in the tropics. I have worked on a related topic along an elevational gradient and we found lower niche overlap between species at higher elevation, where productivity and diversity are lower. Arellano, G., M. N. Umaña, M. J. Macía, M. I. Loza, A. Fuentes, V. Cala, P. M. Jørgensen. 2017. The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon-Andes gradient. Global Ecology and Biogeography 26: 191-202. DOI: 10.1111/geb.12531

Line 266: you conclude that beta diversity is driven by local processes. Why? You study a very local scale, small quadrats within large plots. You cannot conclude anything about beta diversity at the 1, 10, 100 km scale.

Lines 285-289: Open data is required for reproducibility of results. Open data also destroys the incentive to install and maintain permanent forest plots as those used here. I don't have a solid opinion on this, but the journal may have one. In any case, the data availability statement, as it is ow, means almost nothing. It means that data exist somewhere, and that through some dozens of

e-mails and weeks/months of conversations with plot PI's someone may gather the same or similar dataset. There is no guarantee that the whole dataset will be shared as a package upon reasonable request. Therefore, there is no guarantee of reproducibility.

Figure 1: this is a map with the true location of the plots. The adjusted latitude is relevant for the analyses and should be presented in Methods. Additionally, you could project these latitudes on the vertical axis and show there some arrows or something like that to represent the latitude adjustment. It is not necessary.

Panels in figures: 2c, 3b, 3d: their Y axes mean nothing, these should not be figures. These numbers should be presented in the text or in a table.

Line 508: check double spaces.

Good luck with this work and your other ongoing projects.

Sincerely yours,

Gabriel Arellano, gabriel.arellano.torres@gmail.com

Referee: 2

Comments to the Author(s)
Cao et al. found evidence for latitudinal gradient of beta-diversity even after correcting the effects of topographic heterogeneity, sample sizes and gamma-diversity. Since the latitudinal gradient of beta-diversity is still a hot topic, this manuscript will attract broad readers. I only have a few comments to improve readability.

Conceptual figure for niche specialization and niche marginality like Fig. S1 is a must. If there is no enough space for the main text, I would suggest to replace the current Fig. 1 showing maps with Fig. 1S. It would be more helpful for most of the readers. Related with this, Fig. S1A is hard to understand. How did you estimate (c) the favorable but uncolonized area due to competitive exclusion? How is this related with Fig. S1B-D? If Fig. S1A is not that important in explaining the key idea of this manuscript, I would suggest to delete Fig. S1A.

The relationship between niche space and marginality is unclear. One of the main analyses in this manuscript assumes that higher community-level niche marginality indicates a larger niche space (L184), however according to Fig. S1D, higher community-level niche marginality doesn't have to indicate a larger niche space. If the niche space means the length of x-axis in Fig. S1D, both communities have the same niche space but different marginality. If the niche space means the width of the bell shaped curve in Fig. S1D, the bottom figure with lower marginality looks to have larger niche space to me. I would suggest to explain the term "niche space" in line with niche marginality more clearly.

Topographic heterogeneity is not explained. The topographic factors used in the study are listed but how did you calculate or define topographic heterogeneity from those factors?

The discussion look a bit descriptive. I feel there are some contents that could be discussed, such as the differences in the effect sizes between latitude and topographic heterogeneity and the differences in the effect sizes among grain sizes.

Minor comments:
L93-94: Please rephrase this sentence. The second clause doesn't explain why the alternatives remain unresolved. It just repeats the same meaning.

L98-101: These two sentences are a bit unclear to me, although I understand that small sample sizes (alpha scales) inflate beta diversity in the absence of controlling gamma diversity (Sreekar et al. 2018, Kraft et al. 2011).

L109-110: It would be better to delete "in East Asia" because it's duplicated.

L178: How did you choose the scale parameters (usually lambda) for Box-Cox transformation?

L201: Finally? I thought you used Box-Cox transformed niche specialization for linear regressions.

L266-277: I guess the key message here is that topographic heterogeneity itself alone doesn't explain latitudinal beta-diversity, but topographic heterogeneity is important for maintaining beta-diversity. It's a bit hard to grasp at the first glance. Please explain this in a more clear way in this paragraph and the previous paragraph.

L260-263: It would be also better to mention the result of multiple regression that suggests the existence of latitudinal gradient in beta-diversity after controlling topographic heterogeneity.

Fig. S1: Caption letter "C" is missing in the figure. Caption letters are capital in the figure but lower case in the caption text. Please fix them. In Fig. S1C, does each point indicate each quadrat? If so, which grain size?

Fig. 3: It would be better to mention that niche specialization is scaled to 0 to 1 after Box-Cox transformation in the legend.

Please check the values in Table S4 and Fig 3C. The significance for the grain size 50m is different between the figure and the table.

Author's Response to Decision Letter for (RSPB-2020-3045.R0)

See Appendix A.

RSPB-2020-3045.R1 (Revision)

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is my second time to review this manuscript. The authors clarified the concerns that the reviewers pointed out. I still found two minor things that will not affect the conclusions.

Please check the values for niche specialization in Fig. 3 and 4. Did you apply Box-Cox transformation but didn't scale to [0-1] this time? The text says values were scaled to the range [0, 1] (line 189).

L193-195 and Fig.2:
Having a larger niche marginality still doesn't look a necessary condition for a greater niche space. If each species has very flat fat-tailed distribution but has similar mean values, this community will show a smaller niche marginality with a greater niche space (see the attached figure). It would be better to state that a high niche marginality generally suggests a greater niche space because the extreme case like the fig in bottom left are not likely to happen in the nature.

Decision letter (RSPB-2020-3045.R1)

10-Mar-2021

Dear Dr Mi

I am pleased to inform you that your manuscript RSPB-2020-3045.R1 entitled "Species packing and the latitudinal gradient in local beta-diversity" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your

manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
- DNA sequences: Genbank accessions F234391-F234402
- Phylogenetic data: TreeBASE accession number S9123
- Final DNA sequence assembly uploaded as online supplemental material
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311

NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr Maurine Neiman
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:
Referee: 2
Comments to the Author(s)
This is my second time to review this manuscript. The authors clarified the concerns that the reviewers pointed out. I still found two minor things that will not affect the conclusions.

Please check the values for niche specialization in Fig. 3 and 4. Did you apply Box-Cox transformation but didn't scale to [0-1] this time? The text says values were scaled to the range [0, 1] (line 189).

L193-195 and Fig.2:
Having a larger niche marginality still doesn't look a necessary condition for a greater niche space. If each species has very flat fat-tailed distribution but has similar mean values, this community will show a smaller niche marginality with a greater niche space (see the attached figure). It would be better to state that a high niche marginality generally suggests a greater niche space because the extreme case like the fig in bottom left are not likely to happen in the nature.

Author's Response to Decision Letter for (RSPB-2020-3045.R1)

See Appendix B.

Decision letter (RSPB-2020-3045.R2)

17-Mar-2021

Dear Dr Mi

I am pleased to inform you that your manuscript entitled "Species packing and the latitudinal gradient in local beta-diversity" has been accepted for publication in Proceedings B. We consulted with the Associate Editor about the data and we are happy with your explanation.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

11-February-2021

Dear Dr Neiman:

Thank you for your handling our manuscript (MS RSPB-2020-3045) entitled “Species packing and the latitudinal gradient in local beta-diversity”. We are happy to accept your kind invitation for an opportunity to thoroughly revise the MS and resubmit it to Proceedings of the Royal Society B for possible publication. We have rewritten the major parts of our manuscript following your and two reviewers’ comments and suggestions.

If you recall, the work attempt to resolve a current debate whether local beta-diversity along latitudinal gradient contributes to global species richness in East Asian tree communities. We present an unprecedented study to detect the latitudinal beta-diversity pattern, using data from 21 permanent dynamic plots spanning 55 degrees of latitude in East Asian forests. As we identified metrics of beta-diversity that are independent of gamma-diversity and sample size (under review in Ecology). With the unbiased metrics, we demonstrate that the significant decline in beta-diversity from tropical toward boreal forests of East Asia remains. Beyond that, our large forest plots detect stronger niche specialization and marginality in tropical relative to temperate forests, supporting the notion that tighter species packing and larger niche space at low latitude enables species to specialize on narrower habitats.

In this revised version, we first added a detailed explanations of the beta-Shannon diversity undersampling corrections in the electronic supplementary material so that readers can understand this method easily. We also made our MS of beta-diversity methods available on a preprint server, BioRxiv (https://biorxiv.org/cgi/content/short/2021.01.24.427952v1). Second, we focused on results at grain size of 20 m × 20 m, and put the results of grain size of 10 m × 10 m and 50 m × 50 m into electronic supplementary material. Third, we revised almost every paragraphs following two reviewers’ comments and suggestions. We find our manuscript much improved, which is great news.

Below you will find our point-by-point response to the first reviews and manuscript with tracked changes. Thank you again for your encouragement and we are looking forward to your assessment of the revised version of the MS.

Sincerely,

Xiangcheng

Dr. Xiangcheng Mi

Associate Professor,

Institute of Botany, Chinese Academy of Sciences,

Beijing, 100093,

China

Associate Editor

Board Member: 1

Comments to Author:

The two reviewers and I are positive about the data and results being presented in this MS, although Reviewer 1 rightly draws attention to the fact that some of the methods are only available in a second MS that is not publicly available (Cao et al, Ecology, in review). You'll need to either provide a precis of those missing details in the MS along with a more detailed explanation in the Supplement, or make the other MS available through a preprint server. Beyond that, there is quite a list of clarifications that are needed to make the MS easier to interpret for the readers.

Response: We thank you, Dr. Neiman, and the reviews for the positive feedback and constructive responses. We understand the importance of accessibility and now include detailed explanations of the beta-Shannon diversity undersampling corrections in the electronic supplementary material (*S1*). We also made our MS of beta-diversity methods available on a preprint server, BioRxiv (https://biorxiv.org/cgi/content/short/2021.01.24.427952v1).

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Review of RSPB-2020-3045, “Species packing and the latitudinal gradient in local beta diversity”

My opinion about journals and the pre-publication review process: We do not need to work for free for the journals, or pay them to publish our work. As authors, we can distribute our work with a few clicks in many ways. As readers, we can use Google etc. to find any piece of work relevant to us, regardless of it being published in journals or not. The "stamp of quality" implicit

in the pre-publication peer review process is a fallacy. Journals fail at that, both in a myriad of individual cases, and at a deep level. Journal filters are biased to the point that most current published research findings may be false, and we face an obvious replication crisis. I don't know why we remain hostages of this system. Post-publication peer review exists, and people can build on previous work according to its merits, correctness, and interest for the broader community. Time put each work into its place. Too much energy is invested in trying to convince some editors/referees about the novelty and interest of a given piece of work. It is a painful waste of time and talent, and a source of bias in itself. I think scientist should focus on science, and not on the publication/acceptance process.

I hope the authors find my comments useful to improve their work.

Response: Thanks for sharing your opinion about publication and review processes. We usually find that the insights of reviewer comments greatly improve our work, and are indeed grateful for this part of the process. On the other hand, we have also experienced situations where anonymity provided reviewers avenues to be less than tactful, or reject work for what we believed were irrelevant reasons. We believe that the peer review process, in general, should lead to better science, despite its many pitfalls.

GENERAL COMMENTS

(1) Effect of under-sampling of local communities vs. effect of random colonization from the pool of species

I describe how I understand your approach. Confirm that I understood it correctly before taking my comments into account.

The method you use is called “corrected beta-Shannon diversity”. It uses the partitive approach: alpha diversity is calculated, gamma diversity is calculated, and beta diversity is derived from alpha and gamma diversities. It is interpreted as true beta diversity sensu Tuomisto 2010. The

difference from the standard approach is that alpha and gamma diversities are extrapolated from the sample to the whole system, and therefore the beta diversity is theoretically not biased by under-sampling. It could be seen as "asymptotical beta diversity".

You state "the bias arising in beta-diversity metrics is a dependence on sample size that interacts with gamma-diversity". I am not sure if the bias that worry those who study beta diversity is just due to a (necessarily) small local sample size. The effect of gamma on beta that is discussed in much of the literature refers to local assembly mechanisms more than local under-sampling. The null models simulate random sampling from a regional pool of species. If local communities do not differ from that, there are no local assembly mechanisms. If local communities differ from that, there are local assembly mechanisms (e.g. spatial or environmental). This is the approach taken by:

• Kraft et al. 2011. Disentangling the drivers of beta diversity along latitudinal and elevational gradients. Science 333: 1755–1758.

• Caceres et al. 2012. The variation of tree beta diversity across a global network of forest plots. Global Ecology and Biogeography 21: 1191–1202.

• Mori et al. 2013. Community assembly processes shape an altitudinal gradient of forest biodiversity. Global Ecology and Biogeography 22: 878–888

• Myers et al. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecology Letters 16: 151–157.

• Tello et al. 2015. Elevational gradients in β-diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. PloS one 10: e0121458.

• Etc.

Response: Thank you for taking the time to understand our method in detail; we agree that it can be interpreted as an "asymptotical beta diversity". When we compare beta-diversities from species-poor regions with species-rich regions, the species pool size and sample size jointly

affect the magnitude of beta-diversity regardless of ecological and evolutionary processes. Small samples can capture most of species in a site of species-poor regions, and observed beta-diversity among samples is approximately the real beta-diversity. In contrast, small samples often greatly underestimate the shared species of species-rich regions, and thus inflate the beta-diversity. This inflated beta-diversity from species-rich region sampling is caused by the interaction of species pool size and sample size. This effect of sampling is called sampling effect by Kraft et al. (2011), Mori et al. (2013) and Myers et al. (2013), gamma-diversity dependence by Bennett and Gilbert (2016), and undersampling by Beck et al. (2013) and Chao et al. (2014).

Ecologists have tried to use individual randomization null models to remove sampling effects, but there is debate about the success of these heuristics. While Kraft et al. (2011), Mori et al. (2013), and Myers et al. (2013) found that null model-corrected beta-diversity revealed more effects of ecological processes, Bennett and Gilbert (2016) and Ulrich et al. (2017) found that the null model approach was inadequate to remove sampling effects. Our other paper by Cao et al. (2020, BioRxiv 2021: doi: 10.1101/2021.01.24.427952) showed that beta-Shannon diversity is more robust in removing sampling effects than other metrics adjusted by the null model approach.

Maybe I don't fully understand how your asymptotic approach and the null model approach compare with each other. This is a complex issue. I can imagine that if a local community (a sample) is just a random sample from the region, its species accumulation curve will be just the initial section of the regional species accumulation curve. And the same with any number of plots combined. If individuals there are just random samples from the regional species pool, many plots combined will accumulate more species, but the curvature of their species accumulation curve will be exactly the same as for a single plot. They will cover more portion

of the regional species accumulation curve but the extrapolation will reach the same asymptote. In other words, there would be zero beta diversity. If there are local processes involved filtering out certain species from local communities, the extrapolation from a plot will not reach the whole species pool in the region. The gap between the asymptotic/extrapolated alpha and the asymptotic/extrapolated gamma would reflect beta-diversity not due to random sampling from the whole species pool. I think the approach is valid and conceptually equivalent to the null model approach, with the advantage of considering unseen species, but I would need to read reference 25.

The null model approach is limited in the sense that most of the times it does not incorporate unseen species neither locally (e.g. Condit et al. 2005) or regionally (e.g. Myers and LaManna 2016). The null model approach involves the simulation of the colonization process, which in turn requires a good deal of subjectivity, decisions taken by the researcher, etc. The definition of the species pool is, in general, a major practical inconvenient. The extrapolations of alpha and gamma diversities, in contrast, seems more process-agnostic and robust.

To understand this method better I would need to read reference 25 (Cao K., Svenning J.-C., Yan C., Zhang J., Ma K., Mi X. 2020 Undersampling correction methods to control γ-dependence for comparing β-diversity between regions. Ecology, (Under review)). I cannot access it. Even if that paper is accepted and published by the time you publish this work, it would be better if you include a summary of the approach in this manuscript, so the reader doesn't need to read two papers instead of one.

Response: Thank you for your detailed and constructive suggestion. The merit of the asymptotic beta-diversity (i.e., the corrected beta-Shannon diversity) is based on its prediction of the unseen species using diversity-accumulation curves, thus avoiding non-independence in the randomization of null model approach. In contrast, Bennett and Gilbert (2016) found that the

null model-corrected beta-diversity is still dependent on gamma-diversity, perhaps because of the interlink between gamma- and beta-diversity during the randomization (Ulrich et al. (2017)).

We agree with you that it would be easier for readers to understand the undersampling correction method by including a summary of the approach. We now include a summary of the undersampling correction method for beta-Shannon diversity in an electronic supplementary material (*S1*) (Lines 12-45 in electronic supplementary material), while posting our other beta-diversity method paper to BioXriv (BioRxiv 2021, doi: 10.1101/2021.01.24.427952)

There is another method mentioned (Jaccard-Chao index, reference 32) that removes the effect of under-sampling from pairwise dissimilarity metrics. This method is not used. It could be mentioned in Discussion but it is not appropriate to mention it in Methods.

Response: As you suggested for results from the Jaccard-Chao index, we agree that it would be more intuitive for readers to focus on the best metric we selected. Therefore, the results from Jaccard-Chao index were removed from the manuscript.

(2) Scales

Avoid using "local" in the text. It is very confusing when it refers to gamma diversity. Use alpha or quadrat-level and gamma or plot-level.

In a homogeneous system (perfect mix, no beta-diversity) alpha and gamma diversities are just arbitrary points of observation along the system-level species accumulation curve. I recommend using quadrat-level and plot-level diversity, more than alpha and gamma. It is more explicit.

Response: Thanks for your constructive suggestions, and we now understand how these terms may be confused. There has been debate surrounding the contribution of beta-diversity to latitudinal species richness gradients at different scales. Our work here was aimed at this debate, and agree that "local" is very confusing when it refers to gamma- diversity at plot level.

However, the terms “quadrat-level” and “plot-level” diversity may be unintuitive to readers who are not familiar with this topic. We define “quadrat level” as alpha level, and “plot level” as gamma level (Line 140) in the “methods” section, and use “alpha-“ and “gamma-diversity” in “results” and “discussion” sections. We thus revised “local beta-diversity” as “beta-diversity” and “local overall species richness” as “overall species richness” and so on throughout the manuscript. We hope this is more clear and intuitive for readers.

In any case, in your work, beta-diversity and the processes generating it will refer to the scales between the local sample (a quadrat, in this manuscript) and the region (a big plot). Alpha diversity measured at the quadrat level is obviously nothing more than beta-diversity within the quadrat, the turnover of species identity from one tree to the other at those small scales. Statements like “higher/lower beta diversity at high/low latitudes” are scale-dependent.

You could improve the text a bit by polishing statements that are scale-dependent and make them more explicit.

Response: Thank you again for your constructive suggestions. Diversity is well-known scale-dependent. However, this topic is not key point of the current work. For clarity, we presented only results at grain size of 20 m × 20 m so that we could focus on key questions regarding whether there are latitudinal gradient in beta-diversity and its potential mechanisms. So we moved the results at grain sizes of 20 m × 20 m and 50 m × 50 m to electronic supplementary materials (Tables S2, S3, Figures S2, S6).

(3) Causality

I think the “asymptotic approach” that you adopt does not require causality in any given direction. The gap between asymptotic/extrapolated alpha and asymptotic/extrapolated gamma reflects beta-diversity. It can be seen both as (a) the emergent diversity of pooling together more

than one locality or (b) the incompleteness of the sampling/colonization from the species pool. This is nice, I like it.

However, in your Discussion and some other places, you imply that gamma diversity influences beta diversity, and not the other way around. This is the causal direction implied or assumed by those working with null models that "control for" the influence of gamma diversity. This assumption makes more sense at small extents than at large extents. At large extents, the pool of species results from the combination of multiple habitats/assemblages, and the causality goes in the opposite direction: it is the change in composition between habitat and along environmental gradients the cause of the region-level diversity (beta diversity causes gamma diversity). Both things can happen simultaneously and I have no idea at what scales one model is better than the other. Expression like "deviations from the expected", "controlling for", etc. could be revisited having this in mind.

Examples: lines 62-65, 105-107, 113, 270-271, 279.

Response: Thank you for pointing out this problem. However, we do not mean to imply that gamma-diversity influences beta diversity directly, but rather that gamma-diversity affects beta-diversity *indirectly through sampling*. That is, small samples in high diversity regions may inflate beta-diversity, leading to problematic inferences of ecological processes. Even at large extents, undersampling still affects beta-diversity (e.g., Xing and He, 2019, Ecology Letters), and this is the central question explored in our work. We understand the confusion associated with expressions like "small samples in areas with high gamma-diversity" (Lines 62-65 in previous manuscript), "gamma-diversity dependence" (Lines 105-107, 270-271 in previous manuscript), "dependence on gamma-diversity and sample size" (Lines 113 in previous manuscript), "controlling for gamma-diversity" (Lines 279 in previous manuscript), and we have revised these phrases where appropriate.

"We identified the corrected beta-Shannon diversity index and other similar metrics as highly effective at removing dependence on gamma-diversity and sample size" as "Cao et al. identified that the corrected beta-Shannon diversity index is highly effective at removing the bias arising from beta-diversity metrics in small samples of high gamma-diversity communities" (Lines 116-118).

"We suggest that the effect of local processes have been obscured by gamma-diversity dependence in previous studies" as "We suggest that the effect of local processes have been obscured by the biases in beta-diversity metrics of small samples from high gamma-diversity communities in previous studies" (Lines 272-274).

"In conclusion, we inferred that a latitudinal gradient in beta-diversity contributes to the broad latitudinal pattern of species richness after separately controlling for gamma-diversity and local topographic heterogeneity" as "In conclusion, our results support that a latitudinal gradient in beta-diversity contributes to the latitudinal gradient in tree species richness after separately controlling for local topographic heterogeneity and the bias in beta-diversity metrics in small samples of high gamma-diversity areas." (Lines 283-286).

(4) Grains

What do we learn by comparing grains? Your "region" is the big plot, and it seems reasonable to keep that fixed. Your "localities" can be any partition of the region, from many localities of few trees in size to 2 localities of ½ region in size. The 3 grains are not discussed, there is nothing in these 3 extents that make them particularly relevant for the readers. Why don't you use just one grain?

Response: Thank you for your comments, and we have added more on grain size following your suggestion. Diversity measurements are well-known to be scale-dependent, and this is not the focal conclusion of our work. For clarity, we presented only results at grain size of 20 m ×

20 m so that we could focus on key questions regarding whether there are latitudinal gradient in beta-diversity and its potential mechanisms. So we moved the results at grain sizes of 20 m × 20 m and 50 m × 50 m to electronic supplementary materials (Tables S2, S3, Figures S2, S6).

SPECIFIC COMMENTS

Line 63. Don't use "local species richness" to refer to gamma diversity, it is not intuitive.

Response: Revised as "overall species richness" to refer to gamma-diversity (Line 66).

Lines 81-82: beta-diversity more important than alpha diversity: Just say that it is key for conservation, there is no need to compete.

Response: We revised here as "Beta-diversity is the variation of species composition across space, and it is a key element of conservation planning because it indicates whether diversity is concentrated within a few sites or spread across many sites" (Lines 84-86).

Line 86: "and more abiotically" ◊ "as more abiotically"?

Response: We deleted this sentence, so this problem does not exist.

Lines 86-87: it is not clear what "greater packing" means. More heterogeneous habitats imply more room for species, but does not obviously help for a tighter packing of species. This applies to other places in the text, in general you want to make a clear distinction between the amount of available niche space and how tightly species are packed within that niche space.

Response: Thanks for this insightful suggestion. We revise "High levels of beta-diversity at local scales could be caused by higher habitat heterogeneity, as more abiotically variable habitats allow greater packing of species" as "One factor enhancing beta-diversity should be

large niche space, i.e., more species sharing more available niches, perhaps associated with either high productivity or abiotic habitat heterogeneity" (Lines 86-88).

Line 87: Remove "alternatively".

Response: removed.

Line 88: productivity ◊ conditions. Productivity is also the result of the species' niches and diversity through complementary effects.

Response: We agree with you that productivity is the result of the species' niches and diversity through complementary effects. However, stable conditions may not be productive conditions (like tropical dry forests). "stable climate and higher productivity" may be more appropriate.

Line 91: remove "local". Beta diversity could happen at any scale. There is beta diversity between 5x5m quadrats within a 25 ha plot, and there is beta diversity between countries in a continent.

Response: removed.

Line 92: "latitudinal gradient" ◊ "latitunidal gradient in beta diversity"

Response: revised as you suggested (Lines 92).

Line 92: "abiotic environment" ◊ "abiotic heterogeneity". The environment does change with the latitude. I agree there is no reason why heterogeneity itself should change with latitude.

Response: revised as you suggested (Lines 92).

Lines 98-101: I suggest to make the example with two sites of exactly the same composition. Otherwise it is not that intuitive. And polish the statements more, as they are key. Example: "Small samples never capture all local species. Two small samples from two sites that have exactly the same composition will appear to differ by randomly capturing different subsets of the local composition. The more incomplete the sampling is, the greater the beta diversity will seem to be. As a result, high species richness will artificially inflate metrics of beta-diversity".

Response: Thank you for your suggestions; we have revised our example to make it more intuitive as following:

"Small samples rarely (if ever) capture all local species. Two small samples from two sites that have exactly the same composition will appear to differ by randomly capturing different subsets of the local communities. The fewer the species sampled, the greater this artifactual beta-diversity will appear. A crucial aspect of the sample size bias is the dependence on gamma-diversity it engenders, since small samples underestimate diversity more severely in species-rich sites than in species-poor sites" (Lines 99-104).

Line 104: "richer communities". It is not clear whether it refers to alpha or gamma scales.

Response: Here we refer to gamma scales. We revised the previous sentence "Crucial in the sample size bias is the dependence on gamma-diversity it engenders, since larger samples are needed in richer communities" as "A crucial aspect of the sample size bias is the dependence on gamma-diversity it engenders, since small samples underestimate diversity more severely in species-rich sites than in species-poor sites" (Lines 102-104).

Line 107: "packing": does it refer to (a) the size of the available niche space or (b) how tightly species partition that space?

Response: Species packing refers to how tightly species partition this space. Following your suggestion, we added "larger niche space" here (Line 110-111).

Lines 110-113, 159-162, 249-252: Don't use "we" for reference 25. The first author is the same, but there are different authors. Besides, the reader will think that "we" refers to a simulation conducted in this particular manuscript, and not past work of the same team. Use "they". It is a different work. In the Discussion, don't try to earn points here based on the merits of that other work.

Response: Following your suggestion, we deleted the second paragraph in the Discussion section. Instead, we provided more detailed explanation of the asymptotic approach in the Electronic Supplementary material *S1*, and we posted our beta-diversity method paper to BioRxiv ((https://biorxiv.org/cgi/content/short/2021.01.24.427952v1).

Line 117: niche specialization and niche marginality. These are species-level metrics but at the end of the day you summarize them into community-level metrics. At the community level, niche marginality is a measure of the size of the available niche space, and niche specialization is a measure of how tight the packing is. From my point of view it is more intuitive to present the available space first (marginality) and the tightness of the packing later (specialization). Using "community-wide niche marginality" as a metric equivalent to "total niche volume" is not very direct or intuitive but it is correct.

Response: Thank you for your helpful suggestions. Following them, we moved "marginality" ahead of "specialization" (Lines 121-122). In addition, we agree that "community-wide marginality" is not a direct metric of "total niche volume", so we use "large niche space" in the Discussion.

Line 130, after mentioning table S1 and before "we divided plots into quadrats" you should incorporate how you calculated two important attributes of the plots: the corrected latitude (moving text from lines 498-499) and the topographic heterogeneity (moving the text from lines 164-168 and 184-186).

Response: Following your suggestion, we moved the latitude correction methods and the topographic heterogeneity methods here lines 141-146.

Line 155: you use "true beta diversity" sensu Tuomisto 2010, but that name has not been widely applied. The reader will think you mean "correct" or "corrected" or "adjusted" or something like that. I would remove "true".

Response: We deleted "true" according to your advice in Line 170.

Line 157-159: if both methods are not used or discussed consistently, don't mention it and don't use it. It is not clear why you would do this comparison. It is not clear what we would learn by using two methods. If the asymptotic approach to true beta diversity is correct and valid, use it and nothing else.

Response: Thanks for your constructive suggestions. We removed the Jaccard-Chao index throughout the entire manuscript, including Lines 157-159 in "**Materials and Methods"**, and Lines 221-224 in **"Results"** in previous manuscript, and supplementary results in *Table S3* and *Figure S3* were removed from the electronic supplementary material.

Lines 165-166: surface to planimetric area ratio. In a strict sense this means nothing. Surfaces are fractal. One planimetric hectare of forest may include 1 hectare of surface or 1 million km^2, depending on how tiny your measurement tool is. Be explicit on the resolution of your DEM.

Response: Thank you for your suggestion; we have clarified the resolution of DEMs in Lines 143-145: "we used the ratio of surface area to planimetric as a metric of topographic heterogeneity, calculating at grain sizes of 10 m × 10 m, 20 m × 20 m, and 50 m × 50 m".

Line 169: Use some mathematical notation to clarify this statement, like SD(available habitat)/SD(habitat used).

Response: Following your suggestions, we revised this sentence as "Niche specialization was defined as *SD(available habitat)/SD(habitat used)*, in which *SD(available habitat)* represented the standard deviation of environmental conditions for a community and *SD(habitat used)* represented the standard deviation of environmental conditions occupied by a species" (Lines 178-182).

Line 169 etc. What is "habitat"?

Response: To avoid ambiguity, we have substituted "habitat" for "environmental conditions". Specifically, we revised "available habitat for a community" as "environmental conditions for a community", and "habitat used by a species" as "environmental conditions occupied by a species" (Lines 180-182).

Line 171: what is "ecological distance"?

Response: As described in *Figure S1c*, the quadrats where the focal species was observed constitute a subset of the global distribution for a community, and are plotted as a smaller hyper-ellipsoid within the global one. The species marginality is the distance between these centroids. For clarity, "ecological" was deleted.

Line 177, 189-190: Why is normality important? Why did you use Box-Cox transformation? What are the consequences of these transformations?

Response: Two key assumptions of linear regression model are: 1) linear relationship between response variable and explanatory variables; 2) the normal distribution of residual of linear regression model. For example, plot latitude and topographic heterogeneity are normally distributed, but niche specialization are not normal distribution. This may leads to violation of assumptions of linear regression model. Without Box-Cox transform, the residuals of linear regression model of niche specialization against latitude is not normally distributed (Fig. 1a, c, e in the following). However, this problem could be greatly improved after Box-Cox transformation of niche specialization (Fig. 1b, d, f below). Therefore, we used the Box-Cox transformed niche specialization in linear models.

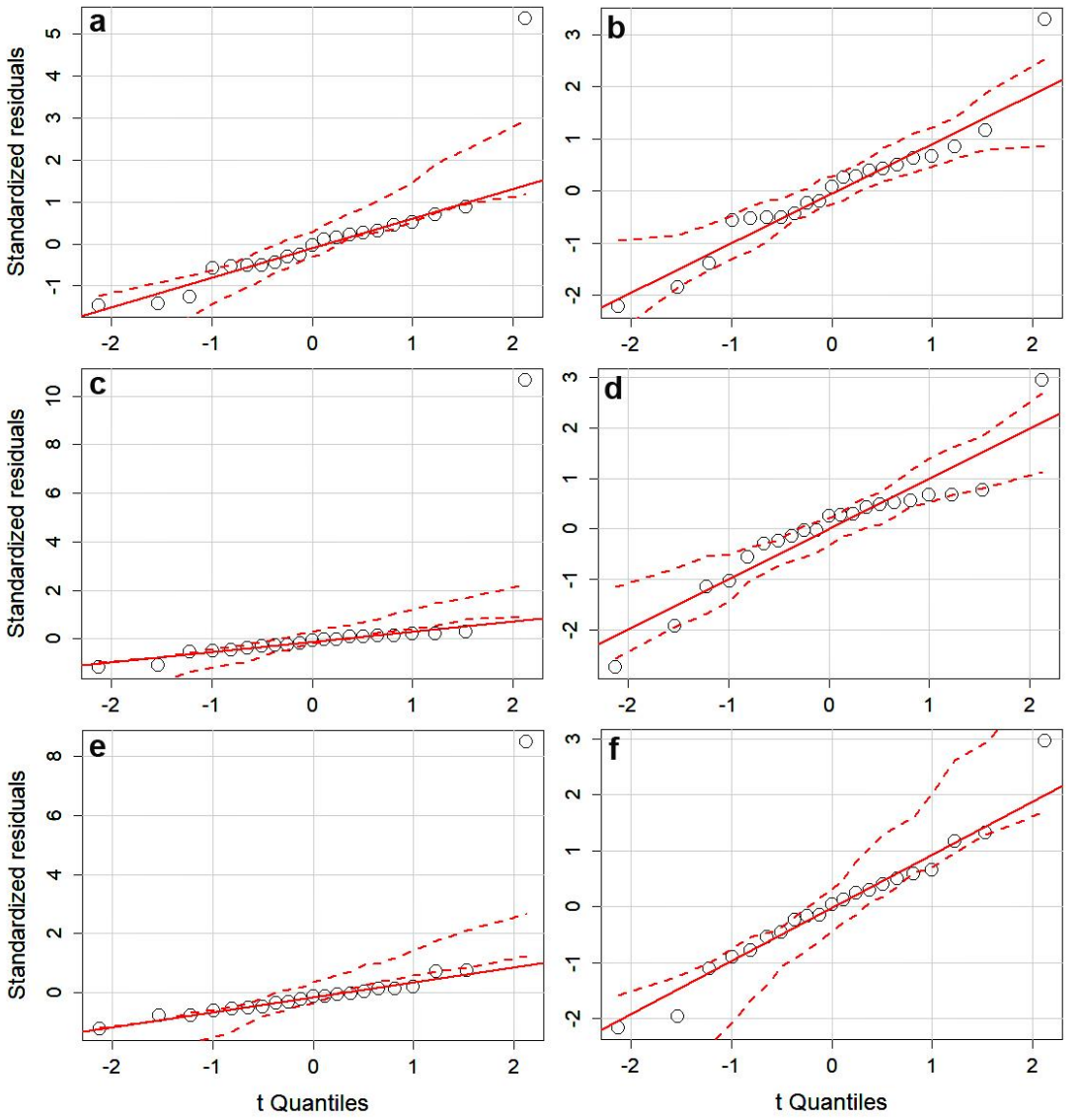

Fig. 1. QQ-plot from a linear model (niche specialization~latitude) before (a, c, e) and after (b, d, f) Box-Cox transformation of niche specialization at grain size of 10 m × 10 m (a, b), 20 m × 20 m (c, d) and 50 m × 50 m (e, f).

Lines 179-181: be explicit regarding the precise mapping of all individuals in these plots.

Response: Following your advice, we revised this sentence to "Based on the precise mapping of all individuals in these plots, the community-level niche marginality and specialization were respectively quantified as species-level niche marginality and specialization, weighted by relative species abundance" (Lines 190-193).

Line 186: “topographic variables were strongly correlated” ◊ “topographic variables are typically strongly correlated”. You said that you had no other information but topographic variables.

Response: We revised as you suggested (Lines 196-198).

Lines 190-192: these seem a repetition of lines 179-181.

Response: This sentence was deleted.

Line 200: it is more intuitive to write (x – mean(x))/sd(x)

Response: As you suggested, we revised “*(x-x´)/SD(x)*” as “*(x – mean(x))/SD(x)*” (Line 207-208).

Lines 201-202: Box-Cox and min-max are not statistical analyses. Why is this necessary, anyway?

Response: As we mentioned above, the Box-Cox transformation was used to better meet the assumption of normality of residuals in linear regression models. Moreover, as the range of values of niche specialization differed dramatically across grain sizes, for comparison, min-max transformation was used to plot these data from different grain sizes into one panel (electronic supplementary material, figure S3, S4, S6 now). As it is inappropriate to put these transformations in statistical analyses, we moved this text to the “Community-level niche differentiation” section and revised as: “To better meet the assumption of normality of residual in regression model and approximate the linear relationship between niche specialization and explanatory variables (Supplementary material, figure S1a), the log- and Box-Cox

transformations were applied for niche specialization (Supplementary material, figures S1)." (Lines 185-189).

Line 212 etc.: before presenting the results for the asymptotic beta diversity you could present the results of the un-corrected beta diversity.

Response: Being consistent with your previous suggestion ("If the asymptotic approach to true beta diversity is correct and valid, use it and nothing else."), we thought it would be clearer to focus on the results of the best metric we selected: the corrected Shannon beta-diversity. For example, when we plotted the un-corrected (Figure 2a and 2b below) and corrected metrics (Figure 2c and 2d below) with latitude, the difference were not very intuitive. Now we only present the results of the corrected Shannon beta-diversity in the article.

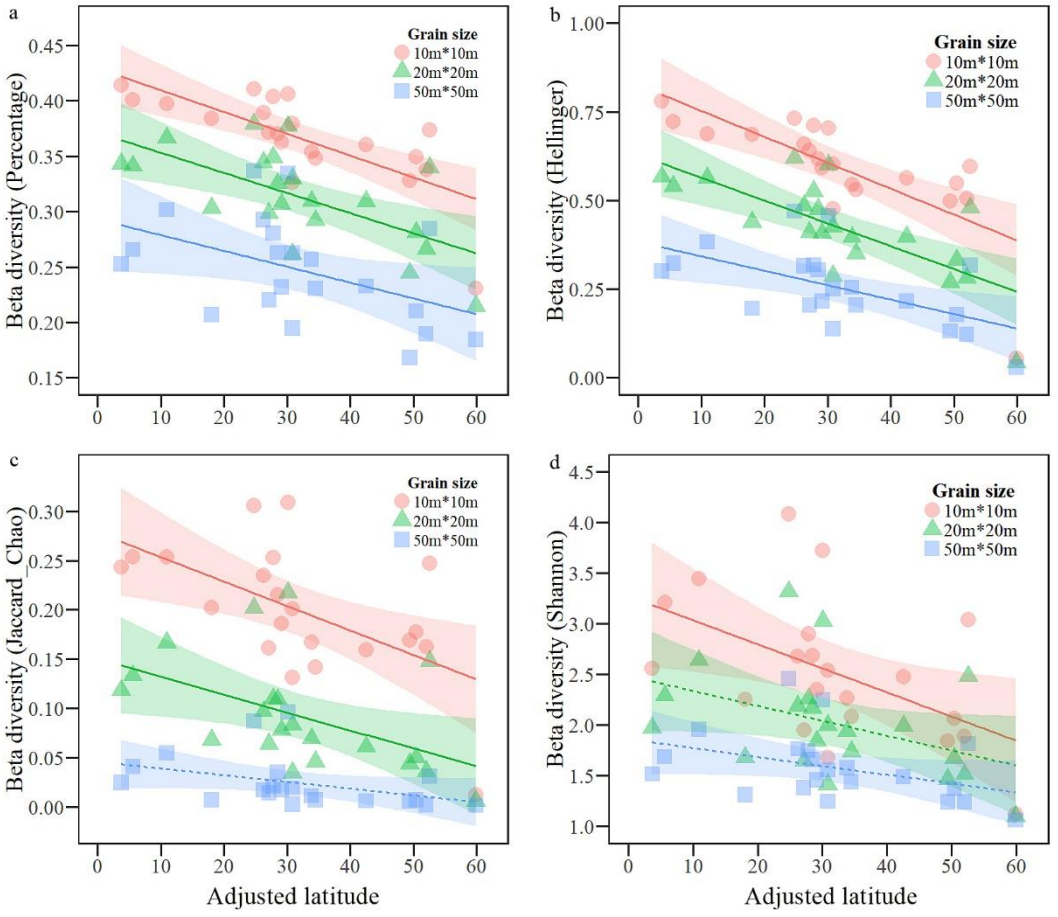

Figure 2. The latitudinal gradient of un-corrected (a, Bray-Curtis (also percentage); b, Hellinger) and corrected beta-diversity metrics (c, Jaccard-Chao; d, corrected Shannon beta-diversity) across grain sizes. Dashed lines show non-significant relationships, while solid lines show significant relationships.

Lines 220-221: if we haven't read the caption of the figure we don't know what "adjusted latitude" means. Explain it when talking about the study sites and their properties, before explaining the division into quadrats.

Response: Sorry for the confusion and inconvenience. Following your advice, we added a sentence "Plot latitudes were adjusted for mean elevation: an upward shift of 100 m equal to a poleward shift of 100 km." (Lines 141-142).

Line 238: don't use LDG here or anywhere else, just use full words.

Response: "LDG" was deleted throughout the article.

Lines 249-252: this refers to a different work, not this one. This is not appropriate. It seems this applies until the end of the paragraph. This is not appropriate for Discussion, you should explain and justify the asymptotic approach in Methods.

Response: Thanks for your insightful suggestions. Following your suggestion, we deleted the second paragraph in the Discussion. Instead, a more detailed explanation of the asymptotic approach was provided in the Electronic Supplementary material *S1*.

Lines 258: "more stable productivity" ◊ "greater stability"

Response: We agree with you that "greater stability" is better than "more stable productivity". So we used "stable climate and higher productivity" (Line 258).

Lines 258 etc. It is not fully discussed why species may have tighter packing in the same niche space in the tropics. I have worked on a related topic along an elevational gradient and we found lower niche overlap between species at higher elevation, where productivity and diversity are lower. Arellano, G., M. N. Umaña, M. J. Macía, M. I. Loza, A. Fuentes, V. Cala, P. M. Jørgensen. 2017. The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon-Andes gradient. Global Ecology and Biogeography 26: 191-202. DOI: 10.1111/geb.12531

Response: Thanks for sharing this excellent work, we found it helpful in supplementing a key aspect missed in this study: niche overlap. In places where species had high niche overlap (e.g., temperate forests), few species dominate and most species are rare (Arellano *et al*., 2017). In this case, species have low niche filling efficiency, and thus few species co-occur (low packing). To clarify why species have tighter packing in tropics, we added one sentence in Lines 262-264: "These consequently reduce niche overlap and competition between co-occurring species and facilitates species coexistence (Arellano et al., 2017)".

Line 266: you conclude that beta diversity is driven by local processes. Why? You study a very local scale, small quadrats within large plots. You cannot conclude anything about beta diversity at the 1, 10, 100 km scale.

Response: We agree with you that studies focusing on beta-diversity at local scales may shed limited light on beta-diversity at large scales (Xing and He, 2019). In our work, with-plot beta-diversity (at extent of 15-52 ha) was driven by local topographic heterogeneity representing local processes more than by latitude representing climate variables and other factors at larger-scales. For clarity, we revised this sentence as "We also conclude that beta-diversity at extent

of 15-52 ha is largely driven largely by local processes—specifically, topographic heterogeneity and the niche differentiation it fosters" (Line 267-268).

Lines 285-289: Open data is required for reproducibility of results. Open data also destroys the incentive to install and maintain permanent forest plots as those used here. I don't have a solid opinion on this, but the journal may have one. In any case, the data availability statement, as it is ow, means almost nothing. It means that data exist somewhere, and that through some dozens of e-mails and weeks/months of conversations with plot PI's someone may gather the same or similar dataset. There is no guarantee that the whole dataset will be shared as a package upon reasonable request. Therefore, there is no guarantee of reproducibility.

Response: Thank you for this point. We will follow the journal requirements.

Figure 1: this is a map with the true location of the plots. The adjusted latitude is relevant for the analyses and should be presented in Methods. Additionally, you could project these latitudes on the vertical axis and show there some arrows or something like that to represent the latitude adjustment. It is not necessary.

Response: Thank you for your suggestion. We added text as "Plot latitudes were adjusted for mean elevation: an upward shift of 100 m equal to a poleward shift of 100 km."(Lines 141-142).

Panels in figures: 2c, 3b, 3d: their Y axes mean nothing, these should not be figures. These numbers should be presented in the text or in a table.

Response: Thank you for the suggestion; however, we think it would be more intuitive for the readers to compare both the effect sizes of latitude relative to topographic heterogeneity and

the differences between grain sizes with figures (electronic supplementary material, figures S2, S6 now).

Line 508: check double spaces.

Response: revised.

Good luck with this work and your other ongoing projects.

Sincerely yours,

Gabriel Arellano, gabriel.arellano.torres@gmail.com

Referee: 2

Comments to the Author(s)

Cao et al. found evidence for latitudinal gradient of beta-diversity even after correcting the effects of topographic heterogeneity, sample sizes and gamma-diversity. Since the latitudinal gradient of beta-diversity is still a hot topic, this manuscript will attract broad readers. I only have a few comments to improve readability.

Response: Thank you for your positive comments on our manuscript. We believe our manuscript has been greatly improved following your and Reviewer 1's suggestions.

Conceptual figure for niche specialization and niche marginality like Fig. S1 is a must. If there is no enough space for the main text, I would suggest to replace the current Fig. 1 showing maps with Fig. 1S. It would be more helpful for most of the readers. Related with this, Fig. S1A is hard to understand. How did you estimate (c) the favorable but uncolonized area due to competitive exclusion? How is this related with Fig. S1B-D? If Fig. S1A is not that important in explaining the key idea of this manuscript, I would suggest to delete Fig. S1A.

Response: Thank you for your insightful suggestions. We created the conceptual figure in Fig. S1A by adopting the concept of realized niche from Soberon (2007) and Soberon and Nakamura (2009). We agree that it was difficult to understand and estimate each of the areas in Fig. S1A. We deleted Fig. S1A, and used Fig. S1B, S1C, and S1D to illustrate niche specialization and marginality of focal species. We have only three figures in the main text and agree that this figure is very helpful for readers, so we used it as Figure 2 in the main text (See Fig. 2 in the main text).

The relationship between niche space and marginality is unclear. One of the main analyses in this manuscript assumes that higher community-level niche marginality indicates a larger niche space (L184), however according to Fig. S1D, higher community-level niche marginality doesn't have to indicate a larger niche space. If the niche space means the length of x-axis in Fig. S1D, both communities have the same niche space but different marginality. If the niche space means the width of the bell shaped curve in Fig. S1D, the bottom figure with lower marginality looks to have larger niche space to me. I would suggest to explain the term "niche space" in line with niche marginality more clearly.

Response: Thank you for pointing out this problem. Yes, we assumed that higher community-level niche marginality indicated a larger niche space because species in a community had a larger average distance from average environmental conditions of a community. Fig. S1D did not clearly show the niche marginality, so in the new version of Fig. S1D (Fig. 2c now), we show niche marginality more clearly (see Fig. 2c for more details). Following your suggestion, we also explained the relationship between niche space and marginality in the legend of Fig. 2. Hopefully it is clear now.

Topographic heterogeneity is not explained. The topographic factors used in the study are listed but how did you calculate or define topographic heterogeneity from those factors?

Response: We explained the topographic heterogeneity as "we used the ratio of surface area to planimetric as a metric of topographic heterogeneity, calculating at grain sizes of 10 m × 10 m, 20 m × 20 m, and 50 m × 50 m, which provided a useful measure of the range and roughness of the overall plot, based on digital elevation models (DEMs) (Lines 143-146).", following the method in Brown et al. (2013).

Brown C., Burslem D.F., Illian J.B., Bao L., Brockelman W., Cao M., Chang L.W., Dattaraja H.S., Davies S., Gunatilleke C.V., et al. 2013 Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. P Roy Soc B-Biol Sci 280(1764), 20130502.

The discussion look a bit descriptive. I feel there are some contents that could be discussed, such as the differences in the effect sizes between latitude and topographic heterogeneity and the differences in the effect sizes among grain sizes.

Response: Thanks for your suggestion. It is well known that beta-diversity, niche specialization, and marginality are all scale-dependent, however, this topic is not our focus. Following your suggestion, we added more discussion regarding niche specialization and niche marginality to the second paragraphs of the Discussion (Lines 260-263).

Minor comments:

L93-94: Please rephrase this sentence. The second clause doesn't explain why the alternatives remain unresolved. It just repeats the same meaning.

Response: Thanks for your advice. We revised this sentence as "These alternatives remain unresolved and studies on the causes of the latitudinal gradient in beta-diversity appears to reach opposing conclusions" (Lines 93-95).

L98-101: These two sentences are a bit unclear to me, although I understand that small sample sizes (alpha scales) inflate beta diversity in the absence of controlling gamma diversity (Sreekar et al. 2018, Kraft et al. 2011).

Response: To clarify and follow Reviewer 1's suggestion, we revised these sentences as "Small samples rarely (if ever) capture all local species. Two small samples from two sites that have exactly the same composition will appear to differ by randomly capturing different subsets of the local communities. The fewer the species sampled, the greater this artifactual beta-diversity will appear. A crucial aspect of the sample size bias is the dependence on gamma-diversity it engenders, since small samples underestimate diversity more severely in species-rich sites than in species-poor sites." (Lines 99-104). We hope that it is easier to understand now.

L109-110: It would be better to delete "in East Asia" because it's duplicated.

Response: The first "in East Asia" was deleted.

L178: How did you choose the scale parameters (usually lambda) for Box-Cox transformation?

Response: We chose the value of lambda that provided the best approximation to a normal distribution of niche specialization using the standard procedure of the boxcox() function in the R package "MASS". In this procedure, we used the boxcox() function over a range of lambda values (for example, from -20 to 20) in steps of 0.01. The value of lambda was chosen to maximize the profile log-likelihood of a linear model with niche specialization fitted to 1 (boxcox(niche specialization~1)).

L201: Finally? I thought you used Box-Cox transformed niche specialization for linear regressions.

Response: Yes, we used Box-Cox transformed niche specialization in linear regressions. To be more explicit, we moved this sentence to Lines 185-189 and revised as “To better meet the assumption of normality of residual in regression model and approximate the linear relationship between niche specialization and explanatory variables, the log- and Box-Cox transformations were applied for niche specialization across grain sizes”

L266-277: I guess the key message here is that topographic heterogeneity itself alone doesn't explain latitudinal beta-diversity, but topographic heterogeneity is important for maintaining beta-diversity. It's a bit hard to grasp at the first glance. Please explain this in a more clear way in this paragraph and the previous paragraph.

Response: Yes, we agree on the key message of these statements and understand the ambiguity. We have revised these statements accordingly: “We also conclude that beta-diversity at extent of 15-52 ha is largely driven largely by local processes—specifically, topographic heterogeneity and the niche differentiation it fosters. However, topographic heterogeneity did not contribute to the latitudinal gradient in beta-diversity (figures 3 and 4).” (Lines 267-270). We hope that it is clear now.

L260-263: It would be also better to mention the result of multiple regression that suggests the existence of latitudinal gradient in beta-diversity after controlling topographic heterogeneity.

Response: Thank you for your constructive suggestion. We deleted the entire previous second paragraph, so this issue does not exist.

Fig. S1: Caption letter "C" is missing in the figure. Caption letters are capital in the figure but lower case in the caption text. Please fix them. In Fig. S1C, does each point indicate each quadrat? If so, which grain size?

Response: We changed the Figure S1, and this problem does not exist.

Fig. 3: It would be better to mention that niche specialization is scaled to 0 to 1 after Box-Cox transformation in the legend.

Response: According to your advice, we added one sentence in the caption text of Fig. 3 (Figure S6 now): "Community-level niche specialization was Box-Cox transformed and was subsequently scaled to the range [0, 1] for comparison across grain sizes."

Please check the values in Table S4 and Fig 3C. The significance for the grain size 50m is different between the figure and the table.

Response: We checked the simple regression model again for niche marginality at the grain size of 50m◊50m and found that the significance value in *Table S4* was incorrect. We have revised appropriately.

Appendix B

16-March-2021

Dear Dr Neiman:

Herewith, we resubmit the accepted manuscript with two additional changes requested by the referee 2. Specifically, we deleted the description about the scale of niche specialization. In addition, we agree with the referee 2 that large niche marginality generally suggest large niche space. We then revised the related sentences in “methods” section and figure legend. Thus, we believe we have complied with all requests. Please find below our reply to the reviewers' comments (reviewers' comments are in black; our replies are in blue) and final main document with tracked changes.

Sincerely Yours,

On behalf of all authors,

Xiangcheng Mi

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s)

This is my second time to review this manuscript. The authors clarified the concerns that the reviewers pointed out. I still found two minor things that will not affect the conclusions.

Please check the values for niche specialization in Fig. 3 and 4. Did you apply Box-Cox transformation but didn't scale to [0-1] this time? The text says values were scaled to the range [0, 1] (line 189).

Response: Thanks for your careful reading our MS. We have deleted this sentence because we have only one scale thus do not scale niche specialization in main text.

L193-195 and Fig.2:

Having a larger niche marginality still doesn't look a necessary condition for a greater niche space. If each species has very flat fat-tailed distribution but has similar mean values, this community will show a smaller niche marginality with a greater niche space (see the attached figure). It would be better to state that a high niche marginality generally suggests a greater niche space because the extreme case like the fig in bottom left are not likely to happen in the nature.

Response: Thank you for raising this point. We agree with you that a high niche marginality generally suggests a greater niche space. Thus we revised the sentence as “Higher community-level niche specialization indicates the fine partitioning of available niche space, while higher community-level niche marginality indicates a larger deviation from mean environmental conditions of a community, and thus suggesting a larger niche space.”