

## Fluctuating fortunes: genomes and habitat reconstructions reveal global climate-mediated changes in bats' genetic diversity

Balaji Chattopadhyay, Kritika M. Garg, Rajasri Ray and Frank E. Rheindt

### Article citation details

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### Review timeline

Original submission: 5 February 2019  
1st revised submission: 15 June 2019  
2nd revised submission: 23 August 2019  
Final acceptance: 23 August 2019

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

## Review History

RSPB-2019-0304.R0 (Original submission)

Review form: Reviewer 1 (Michela Leonardi)

### Recommendation

Accept with minor revision (please list 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?**

Good

**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.**

Yes

**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?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

No

**Do you have any ethical concerns with this paper?**

No

#### **Comments to the Author**

Revision for the manuscript "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity"

#### COMMENTS

Page 6, line 148. GBIF data may have different degrees of coordinates uncertainty (detailed in the column "coordinateUncertaintyInMeter"), did you check your records to avoid too great uncertainty? And, if so, which threshold did you use for inclusion?

Page 7, line 165-174: The procedure for the variable choice is sound, but the populations that you are analysing present great geographic and ecological variability, both in terms of environment occupied and type of resources used. I suggest to subset the sample by region or by ecological characteristics for the variable selection and use for each group of species the variables found to explain better the variation in the group itself. This procedure may not lead to significantly different results when compared to the one you followed. At the same time, given the great variety of species analysed, choosing variables based on their effect on all the occurrences as a whole is an assumption that needs to be tested.

Page 9, line 198-200: missing reference detailing the use of ROC (or comparing different methods for model evaluation) in Ecological Niche Modelling.

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Figure 1: I appreciate the use of small symbols to detail the diet of each species, it is very effective. The layout should be adjusted as the different boxes are not aligned, and the mustard and green

boxes borders are too close to the border of the figure (e.g. an easy way to avoid it would be to colour the outer box of each plot instead of adding a box all around).

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Figure 2 does not appear to use a colour scale easily readable for colour-blind. I suggest using <http://colorbrewer2.org/> or any similar software to generate a palette that is colour-blind safe. For the same reason it could be better to add a colour scale within the figure itself (e.g. a colour bar on one side or below).

Also, the layout can be improved increasing the size of the species names and the chronological periods and moving the latter to the top side of each column. On a minor note, you may also consider removing the outer line for each map and (eventually) moving the species name on the left side of each row of plots.

Supplementary table 2: for each species please add the references to the GBIF download (in the form of "GBIF.org (date) GBIF Occurrence Download <https://doi.org/xxxxxx>" as requested by the site, and any other reference for the occurrences used.

## 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?

Good

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

Good

### 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

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**Is it adequate?**

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### **Comments to the Author**

Overall, I really enjoyed reading your manuscript "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity". I liked the approaches you took and think the data was interesting. I think your methods were sound and think interpretations of results were reasonable. This said I do have some minor comments which I think would be nice to see addressed.

1) I am a little uncomfortable with your use of genetic diversity in this paper - more specifically in the introduction and discussion. Your technique does not really measure diversity per se. It is really focused on looking at effective population size. And although I recognize that there is a correlation between the two, they are not equivalent. If you could address this - either by replacing genetic diversity with Effective Population size or making a clear statement about the assumption you are making, an outline the caveats of making this assumption. I particularly struggle since measuring genetic diversity using a single genome is not really an accurate measure of actual diversity. This will address the big limitation of your analysis, that you are hoping the individual that is genotyped actually reflects species-wide processes.

a. In the introduction where your argument is that loss of habitat equates to a loss of diversity (line 60 and Lines 69-72). Do species with smaller habitats have less diversity? Not sure that is a generalizable statement, although likely, but I think you need a bridge statement which makes it clear that there is a relationship. Although if you just say population size, then that would be fine.

2) I struggle a little with the variation in scales and how that reflects the magnitude of changes you are seeing. For both area and numbers of individuals, there are large differences between species. This makes me wonder if some of the changes are a reflection of units not scale. For example, small changes in area, will produce larger % changes in small ranges species compared to species with large ranges. I realize this is a reality of species dynamics, however, I wonder if using "% of Maximum" would eliminate the differences in magnitude... One example, that demonstrates my difficulty - *Rhinolophus sinicus* area dropped massively in Late Glacial Max and then bounced back. YET, when you look at the numbers you say the drop was -99%, but bounce back was +24,300% - I realize why these numbers are what they are but they are confusing. They are also interesting as you cannot have a negative number greater than -100%, so positive is not the same scale as negative. I also think it would allow people to view species in term of where they are in their evolutionary timeline - when were they at maximum or are they at end of a decline over long time scale.

a. The scale is especially relevant in Figure 1... When I imagine each of these on the same scale and my interpretation would be very different - a drop of 1,000 compared to drop 10,000 seems dramatic but when we talk about that as a product of maximum, we are speaking at common

scale across species. This also addresses the issue of different generation times (Supplemental) which all have different scales, but the same pattern.

b. I also think this would then allow you to compare the patterns by a number rather than just “constant” increase or decrease”. I think if all species are on a similar scale you might have a reasonable value for fair comparison across species.

3) On a similar note, when looking at figure 1, I realize that 1) you are going backward in time, and your graphs extend beyond the time scale you are using for habitat. Although this in nature of the analysis, it can be a little confusing. We usually think about increasing time, and we think the data is showing only the time frame you are talking about. If you could make these just the range of time you focused on it would help a lot - unless you want to talk about long term trajectory, OR maybe make predictions about periods when habitat was considerably larger or smaller. Also if you could make it increasing time, it would help when trying to compare fig 1 to Fig 2 - which is showing increasing time scales (Left to Right). Not sure if possible but it would be awesome if it was possible to combine Fig1 and Fig2. Show changes in genetics and changes in habitat in one figure would allow direct comparisons. Not sure if possible but something to think about.

4) This is minor thing, but I wonder if it is possible to give a little more information about the assumptions that the models are making and how they might impact your interpretations. All the models you use have limitations and make some important assumption. It is unlikely that your reader will be familiar with both models and so might need some hand holding. They are relying on you (and us the reviewer) being upfront about limitations, but I think the reader should have access to this so they can be critical. I am not saying, I think your results would change dramatically with different parameters, but I think the reader would appreciate more reflection of how your assumptions and parameters might change the end results. I think this could easily be done by expanding your limitations paragraph or few sentences in methods clarifying these assumptions, but more importantly how changes in the parameters can alter outcome (if at all). To be clear, I am not asking for a long rewrite or considerable just more direct or detailed focus on limitations. I think all can be done in the limitations section but also could be scattered throughout. I am also fine with mentioning them and referring the reader to papers/ reviews which deal with this issue. .

a. For example, PSMC modeling it is well known is heavily influenced by your selection of mutation rates, generation time, population structure and the individual you used. I recognize you discuss some of these, such as species being from range edge (population structure/individual choice) and different generation time - and you mentioned how these had an important impact on the outcomes - one extremely low  $N_e$  and the other large fluctuation in total  $N_e$  respectively. You do not really do the same of mutation rate or the fact you are choosing a single individual as representative of the whole species. (although I know you said it should be repeated with multiple individuals).

b. Likewise, I also know there are quite a few criticisms of distribution models, especially ones which only use climate data as the sole parameters to develop the models.

Like I said, I think these are minor issues, but I think clarity on some of these issues might help with the reception of the paper. Great jon.

Other minor comments

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Table 1 – It would be nice to see current on this graph as a reference point (Extra column with current Ne)

Table 3 – I struggle with the scale of these numbers - +2,000% versus -99% (which is maximum change short of extinction)

Fig 1 – I could not really make out the light blue, dark blue and orange in the pdf. Am I missing something?

## Decision letter (RSPB-2019-0304.R0)

12-Apr-2019

Dear Dr Rheindt:

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. 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=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document%20not%20available)), 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,  
Proceedings B  
<mailto:proceedingsb@royalsociety.org>

Associate Editor  
Board Member: 1  
Comments to Author:

Despite the reviewer's ranking of "minor revisions," some of the issues that they raise are substantive and speak to the paper's statistical analyses and interpretation. I think that these critiques can be addressed with a revision, but I will likely send a revised draft back out to reviewers for a second look.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Revision for the manuscript "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity"

COMMENTS

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Referee: 2

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## Author's Response to Decision Letter for (RSPB-2019-0304.R0)

See Appendix A.

## RSPB-2019-0304.R1 (Revision)

### Review form: Reviewer 1 (Michela Leonardi)

#### **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?**

Good

#### **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.**

Yes

**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?**

Yes

#### **Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

Most of the comments that I suggested have been addressed in a satisfactory way and the (already very high) quality of the manuscript has increased. The manuscript is clear and pleasant to read. The problem tackled is very interesting, the analyses are sound and both methods and data are clearly referenced in order to allow replication, if needed. The figures are now clear and beautiful, and their appearance and quality are good for publication. On the other hand, I still have two concerns that, if clarified, I believe would further enhance the quality of the paper. I am convinced that answering such concerns should not be very time-consuming as it does not require additional analyses, but just presenting a different set of results, and I tried to include in my answer as much information as possible to make the process easier to perform.

First of all, the calculation of the area still does not appear correct to me.

When using a geographic data file (e.g. a raster), the cells do not represent an area on the land that is a square, because of the Earth being a spheroid. While the latitudinal sides (the north-south sides) of the cells are always constant, the longitudinal ones decrease from the Equator going north (leading to the cell becoming a triangle when reaching the poles).

The method you use to calculate the area is based on the assumption of the cells being squared and hence overestimate cell areas in regions far from the equator (this is the reason why it gives the same results as counting the cells).

This problem can be solved in two different ways. The first one is projecting the raster/geographic file using any equal-area projection (a non-exhaustive list:

[https://en.wikipedia.org/wiki/Map\\_projection#Equal-area](https://en.wikipedia.org/wiki/Map_projection#Equal-area)) which can be easily done in R or any GIS software, and then report the number of cells covered. The second one (if using a non-projected map) is to explicitly correct for latitude when calculating the area of the cell, for example using the area function within the raster package in R

<https://www.rdocumentation.org/packages/raster/versions/2.9-5/topics/area>.

I also have a concern about variable choice.

The Authors previously performed the variable choice by merging together species from different macroregions (America, Palearctic, Australasia and Africa) (from now on I will refer to those analyses as “full dataset analyses”). My previous concern was that species living in such different areas would likely be driven by different variables (e.g. minimum temperature is likely to play a different role for Palearctic versus Australasian species).

The Authors did a great job in expanding the description of the methods, the discussion and the limitations on this topic, and they provided clear and referenced reasons to support their choices. Furthermore the Authors followed my suggestion by subsetting the data and selecting different sets of statistics grouping the data by species or continental groups (from now respectively “species analyses” and “continental analyses”).

The Authors explicitly test for idiosyncrasy, following Junior and Nobrega 2018, but they do not answer the concern I raised about the variables not being equally representative in all regions considered. In order to answer to my concern it could have been sufficient for example to show (if so) that the variables estimated for each continental group were in most cases included in the variables estimated based on the full dataset.

Moreover, when looking at idiosyncrasy, I do not agree with the choice of the Authors to compare the different analyses looking at how much the extent estimated with the species and continental analyses is in accord with trends estimated with the full dataset. In my view this

procedure would be correct if the estimates based on the full dataset were clearly unbiased (as the simulated data in the Junior and Nobrega 2018 reference, that use the same procedure to test for idiosyncrasy), but, as I previously explained, so far I am still not convinced that considering different continental subgroups could not be a better choice.

In my opinion this issue could be solved easily if the Author would accept to compare the three datasets (“Full”, “continental groups” and “species”) with a different method able to identify idiosyncrasy (e.g. comparing the variance of TSSs as detailed by Junior and Nobrega 2018). If following this, both the “species” and “continental” datasets show convincing signals of idiosyncrasy all Authors’ choices will be shown to be fully justified (and the results based on such datasets can then be removed from the paper because shown to be biased).

I also found a couple of typos that you could correct: “Ne” should be written with the “N” in italic and in line 237 you find “earth” instead of “Earth”.

## 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?**

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?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

You have addressed all most of my concerns and think the paper is much approved. I hope you agree. I have two minor additional suggestion but otherwise, I think your manuscript looks great and enjoyed reading.

Abstract; Line 28 - replace "genetic diversity" with "population sizes"

Methods: Line 240-244 - for classifying  $N_e$  as Zero - what range did you have around Zero (I am assuming they were not EXACTLY the same. Likewise, what was the range of change for +1 and -1

**Decision letter (RSPB-2019-0304.R1)**

05-Aug-2019

Dear Dr Rheindt

I am pleased to inform you that your Review manuscript RSPB-2019-0304.R1 entitled "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity" has been accepted for publication in Proceedings B.

The referee(s) do not recommend any further changes. Therefore, please proof-read your manuscript carefully and upload your final files for publication. 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 me know immediately.

To upload your manuscript, 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.

You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, upload a new version through your Author Centre.

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. Please note that PowerPoint files are not accepted.
- 3) Electronic supplementary material: this should be contained in a separate file from the main

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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 see: <https://royalsociety.org/journals/authors/author-guidelines/>

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

5) 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 final version. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Dr Sasha Dall  
 Editor, Proceedings B  
<mailto:proceedingsb@royalsociety.org>

Associate Editor Board Member: 1  
 Comments to Author:

Thank you for your revised paper. The paper is much improved. I would like to see one more minor revision, however, that responds to two important issues raised by reviewer #2. I will be evaluate the response and shouldn't need to send the paper out for further review.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s)

You have addressed all most of my concerns and think the paper is much approved. I hope you agree. I have two minor additional suggestion but otherwise, I think your manuscript looks great and enjoyed reading.

Abstract; Line 28 – replace “genetic diversity” with “population sizes”

Methods: Line 240-244 – for classifying Ne as Zero – what range did you have around Zero (I am assuming they were not EXACTLY the same. Likewise, what was the range of change for +1 and -1

Referee: 1

#### Comments to the Author(s)

Most of the comments that I suggested have been addressed in a satisfactory way and the (already very high) quality of the manuscript has increased. The manuscript is clear and pleasant to read. The problem tackled is very interesting, the analyses are sound and both methods and data are clearly referenced in order to allow replication, if needed. The figures are now clear and beautiful, and their appearance and quality are good for publication. On the other hand, I still have two concerns that, if clarified, I believe would further enhance the quality of the paper. I am convinced that answering such concerns should not be very time-consuming as it does not require additional analyses, but just presenting a different set of results, and I tried to include in my answer as much information as possible to make the process easier to perform.

First of all, the calculation of the area still does not appear correct to me.

When using a geographic data file (e.g. a raster), the cells do not represent an area on the land that is a square, because of the Earth being a spheroid. While the latitudinal sides (the north-south sides) of the cells are always constant, the longitudinal ones decrease from the Equator going north (leading to the cell becoming a triangle when reaching the poles).

The method you use to calculate the area is based on the assumption of the cells being squared and hence overestimate cell areas in regions far from the equator (this is the reason why it gives the same results as counting the cells).

This problem can be solved in two different ways. The first one is projecting the raster/geographic file using any equal-area projection (a non-exhaustive list:

[https://en.wikipedia.org/wiki/Map\\_projection#Equal-area](https://en.wikipedia.org/wiki/Map_projection#Equal-area)) which can be easily done in R or any GIS software, and then report the number of cells covered. The second one (if using a non-projected map) is to explicitly correct for latitude when calculating the area of the cell, for example using the area function within the raster package in R

<https://www.rdocumentation.org/packages/raster/versions/2.9-5/topics/area>.

I also have a concern about variable choice.

The Authors previously performed the variable choice by merging together species from different macroregions (America, Palearctic, Australasia and Africa) (from now on I will refer to those analyses as “full dataset analyses”). My previous concern was that species living in such different areas would likely be driven by different variables (e.g. minimum temperature is likely to play a different role for Palearctic versus Australasian species).

The Authors did a great job in expanding the description of the methods, the discussion and the limitations on this topic, and they provided clear and referenced reasons to support their choices. Furthermore the Authors followed my suggestion by subsetting the data and selecting different sets of statistics grouping the data by species or continental groups (from now respectively “species analyses” and “continental analyses”).

The Authors explicitly test for idiosyncrasy, following Junior and Nobrega 2018, but they do not answer the concern I raised about the variables not being equally representative in all regions considered. In order to answer to my concern it could have been sufficient for example to show (if so) that the variables estimated for each continental group were in most cases included in the variables estimated based on the full dataset.



Moreover, when looking at idiosyncrasy, I do not agree with the choice of the Authors to compare the different analyses looking at how much the extent estimated with the species and continental analyses is in accord with trends estimated with the full dataset. In my view this procedure would be correct if the estimates based on the full dataset were clearly unbiased (as the simulated data in the Junior and Nobrega 2018 reference, that use the same procedure to test for idiosyncrasy), but, as I previously explained, so far I am still not convinced that considering different continental subgroups could not be a better choice.

In my opinion this issue could be solved easily if the Author would accept to compare the three datasets ("Full", "continental groups" and "species") with a different method able to identify idiosyncrasy (e.g. comparing the variance of TSSs as detailed by Junior and Nobrega 2018). If following this, both the "species" and "continental" datasets show convincing signals of idiosyncrasy all Authors' choices will be shown to be fully justified (and the results based on such datasets can then be removed from the paper because shown to be biased).

I also found a couple of typos that you could correct: "Ne" should be written with the "N" in italic and in line 237 you find "earth" instead of "Earth".

## Author's Response to Decision Letter for (RSPB-2019-0304.R1)

See Appendix B.

## Decision letter (RSPB-2019-0304.R2)

23-Aug-2019

Dear Dr Rheindt

I am pleased to inform you that your manuscript entitled "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity" has been accepted for publication in Proceedings B.

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.

If you have any queries regarding the production of your final article or the publication date please contact [procb\\_proofs@royalsociety.org](mailto:procb_proofs@royalsociety.org)

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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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.

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,

Editor, Proceedings B

mailto:proceedingsb@royalsociety.org

## Appendix A

### Response to Referees

In the following, we will outline in detail the ways in which we have accommodated the comments and suggestions by each individual board member and reviewer. Our responses are in **bold**.

#### **Board Member: 1**

Comment 1: Despite the reviewer's ranking of "minor revisions," some of the issues that they raise are substantive and speak to the paper's statistical analyses and interpretation. I think that these critiques can be addressed with a revision, but I will likely send a revised draft back out to reviewers for a second look.

**Response: We thank the reviewers for the constructive and helpful comments on our manuscript. We have undertaken an extensive review, addressing each of the comments and suggestions for improvement individually, as outlined below.**

#### **Referee 1:**

Comment 2: Page 6, line 148. GBIF data may have different degrees of coordinates uncertainty (detailed in the column "coordinateUncertaintyInMeter"), did you check your records to avoid too great uncertainty? And, if so, which threshold did you use for inclusion?

**Response: We thank the reviewer for this comment. We acknowledge that we did not take coordinate uncertainty into account in our submitted manuscript. However, to account for potential errors, we adopted an alternative approach that had not previously been detailed: We removed any location points marked within GBIF as being associated with a "geospatial issue". Furthermore, we manually checked all location points to ensure that any points not within the known range of a species or incorrectly mapped onto a water body had been removed. We have taken the opportunity to update the Methods to outline these safeguards to the reader, and hope that this sufficiently addresses the reviewer's criticism (line numbers: 154–156).**

Comment 3: Page 7, line 165-174: The procedure for the variable choice is sound, but the populations that you are analysing present great geographic and ecological variability, both in terms of environment occupied and type of resources used. I suggest to subset the sample by region or by ecological characteristics for the variable selection and use for each group of species the variables found to explain better the variation in the group itself. This procedure may not lead to significantly different results when compared to the one you followed. At the same time, given the great variety of species analysed, choosing variables based on their effect on all the occurrences as a whole is an assumption that needs to be tested.

**Response: We are glad the reviewer agreed with the soundness of our approach of selecting appropriate bioclimatic variables based on the distribution points of all samples across the 11 species. The reviewer encouraged us to additionally divide the dataset into ecological or geographic subgroups and re-run the bioclimatic variables to**

test the soundness of this approach. The reviewer then remarked that rerunning our dataset for individual subgroups of samples should not lead to very different results.

We agree with the reviewer that bioclimatic variable selection is an important and active field of current enquiry, and we seized the opportunity to add text to the Results and Discussion outlining in detail why we have taken this particular approach. In brief, we follow multiple studies (Dormann 2007; Galante 2015; Naimi and Araújo 2016; Júnior and Nobrega 2018) that attest to the bias introduced by collinearity of variables, justifying an approach that selects a set of meaningful bioclimatic variables rather than including all of them. However, we don't necessarily agree with the reviewer that adopting his/her "subgroup approach" would lead to similar results: Júnior and Nobrega (2018) showed that data idiosyncrasy can be an important source of bias if parameter choice hinges on input data from few species, which led us to adopt a global approach incorporating all species in the first place.

To test whether our data would bear out the reviewer's predictions or ours, we additionally reconstructed ancient distributions of species using environmental variables selected on the basis of distribution points of four geographic species groups: (1) American species, (2) Palaearctic species, (3) Australasian species, and (4) African species, rather than combining all species. We also reconstructed distributions based on each species' individual data points. These analyses showed that a partitioning of our data points into subgroups – whether by individual species or by continental group – only leads to a ~56-63% agreement in expansion versus contraction trends as compared with the predictions that are based on the global dataset, reinforcing previous findings that smaller datasets heavily suffer from idiosyncratic biases (Júnior and Nobrega 2018), and that our global approach is warranted.

We have appended details about these analyses to the Methods and Results section and added discussion of these points to our manuscript. We hope that this substantial expansion of these discussion points satisfies the reviewer's concerns (line numbers: 182–190; 279–284; 386–397).

Comment 4: Page 9, line 198-200: missing reference detailing the use of ROC (or comparing different methods for model evaluation) in Ecological Niche Modelling.

**Response: We thank the reviewer for this comment. We have included references for the use of receiver operating characteristics (ROC) plot analysis for model evaluation in the revised version of the manuscript (line number: 215).**

Comment 5: Page 9, line 208-210: the number of occupied cells should be translated into the physical space covered by each of them (e.g. square km). As the cell size decreases going from the equator towards the poles, counting the number of cells instead of the surface covered overestimates the surface occupied the farthest from the Equator.

**Response: We thank the reviewer for this comment. We have now corrected the area calculation in the revised version of the manuscript according to the reviewer's suggestions. Our conclusions have remained identical after the recalculation (line numbers: 223–230).**

Comment 6: Figure 1: I appreciate the use of small symbols to detail the diet of each species, it is very effective.

The layout should be adjusted as the different boxes are not aligned, and the mustard and green boxes borders are too close to the border of the figure (e.g. an easy way to avoid it would be to colour the outer box of each plot instead of adding a box all around). I find the use of colours hard to follow, given that it is defined only in the figure description. Moreover, the orange/blue/green shadings are very light, I would consider adding some contrast or use instead lines and/or labels. In general a legend in the figure detailing the meaning of each colour (green/mustard box, blue/green/orange shadings, blue line) would improve readability, or otherwise, you could consider replacing some of them with labels within the plots themselves. Another possibility would be to plot the variation in the habitat estimates next (or on top) of the genetic estimates. As an example, you can check figure 2 in Lorenzen et al, Species-specific responses of Late Quaternary megafauna to climate and humans, *Nature* 2011 Nov 2;479(7373):359-64. doi: 10.1038/nature10574 <https://www.nature.com/articles/nature10574>.

**Response: Based on comments from both reviewers, we have completely reworked our two previous figures and combined them into one figure, showing PSMC graphs adjacent to habitat reconstructions for all species. We have followed this reviewer's advice and made sure that a legend, embedded within the figure, provides information on any colors and symbols used in the figure.**

Comment 7: Figure 2 does not appear to use a colour scale easily readable for colour-blind. I suggest using <http://colorbrewer2.org/> or any similar software to generate a palette that is colour-blind safe. For the same reason it could be better to add a colour scale within the figure itself (e.g. a colour bar on one side or below). Also, the layout can be improved increasing the size of the species names and the chronological periods and moving the latter to the top side of each column. On a minor note, you may also consider removing the outer line for each map and (eventually) moving the species name on the left side of each row of plots.

**Response: We have taken this reviewer's suggestions on board and made our color scheme color-blind safe, while embedding the legend for the color scheme within the figure itself. The font for all species names has been considerably increased. Our chronological scale is no longer as crowded because we have removed parts of the time scale in response to Referee 2 (see below). Species names and figure items have been completely rearranged following our merger of former figures 1 and 2.**

Comment 8: Supplementary table 2: for each species please add the references to the GBIF download (in the form of "GBIF.org (date) GBIF Occurrence Download <https://doi.org/xxxxxx>") as requested by the site, and any other reference for the occurrences used.

**Response: We have added references for the GBIF locations to Supplementary table S2, as requested by the reviewer. However, given that we had extracted these localities from GBIF using the R package `rgbif` rather than through the GBIF portal, we appended the citations following `rgbif` format.**

## **Referee 2:**

Comment 9: Overall, I really enjoyed reading your manuscript "Fluctuating fortunes: genomes and habitat reconstructions reveal global climate mediated changes in bats' genetic diversity". I liked the approaches you took and think the data was interesting. I think your methods were sound and think interpretations of results were reasonable. This said I do have some minor comments which I think would be nice to see addressed.

**Response: We are genuinely grateful to the reviewer for the resounding praise of our approach. We have addressed his/her specific comments in detail below.**

Comment 10: 1) I am a little uncomfortable with your use of genetic diversity in this paper - more specifically in the introduction and discussion. Your technique does not really measure diversity per se. It is really focused on looking at effective population size. And although I recognize that there is a correlation between the two, they are not equivalent. If you could address this - either by replacing genetic diversity with Effective Population size or making a clear statement about the assumption you are making, an outline the caveats of making this assumption. I particularly struggle since measuring genetic diversity using a single genome is not really an accurate measure of actual diversity. This will address the big limitation of your analysis, that you are hoping the individual that is genotyped actually reflects species-wide processes.

**Response: We acknowledge the reviewer's discomfort with considering effective population size as equivalent to genetic diversity. We have taken this concern into account by replacing "genetic diversity" and similar expressions with "effective population size" in the majority of occurrences throughout the text – whenever appropriate. Additionally, we have added a cautionary statement to the Introduction raising awareness that effective population size calculated on the basis of a single genome does not always perfectly reflect the genetic diversity of the whole species (line numbers: 78–81). Despite these changes, however, we do concur with the reviewer's previous comment that all our study's main conclusions remain sound.**

a. In the introduction where your argument is that loss of habitat equates to a loss of diversity (line 60 and Lines 69-72). Do species with smaller habitats have less diversity? Not sure that is a generalizable statement, although likely, but I think you need a bridge statement which makes it clear that there is a relationship. Although if you just say population size, then that would be fine.

**Response: As also outlined in response to the previous comment, we have changed the wording (including in the lines referred to in this comment) to make sure that we are no longer referring to "genetic diversity", but instead to "population size", as requested by the reviewer (line numbers: 60; 70).**

Comment 11: 2) I struggle a little with the variation in scales and how that reflects the magnitude of changes you are seeing. For both area and numbers of individuals, there are large differences between species. This makes me wonder if some of the changes are a

reflection of units not scale. For example, small changes in area, will produce larger % changes in small ranges species compared to species with large ranges. I realize this is a reality of species dynamics, however, I wonder if using "% of Maximum" would eliminate the differences in magnitude... One example, that demonstrates my difficulty - *Rhinolophus sinicus* area dropped massively in Late Glacial Max and then bounced back. YET, when you look at the numbers you say the drop was -99%, but bounce back was +24,300% - I realize why these numbers are what they are but they are confusing. They are also interesting as you cannot have a negative number greater than -100%, so positive is not the same scale as negative. I also think it would allow people to view species in term of where they are in their evolutionary timeline – when were they at maximum or are they at end of a decline over long time scale.

**Response: We acknowledge the difficulties surrounding the most appropriate representation of differences in suitable habitat between time periods, and we thank the reviewer for his/her valuable suggestion of an alternative way to present these results. We have followed suit and adopted the reviewer's approach of rendering habitat fluctuations as percentages of the maximum habitat extent for each species. Table 2 has been completely redone to reflect these changes.**

a. The scale is especially relevant in Figure 1... When I imagine each of these on the same scale and my interpretation would be very different – a drop of 1,000 compared to drop 10,000 seems dramatic but when we talk about that as a product of maximum, we are speaking at common scale across species. This also addresses the issue of different generation times (Supplemental) which all have different scales, but the same pattern.

**Response: We agree with the reviewer's previous comment that fluctuations in habitat extent should be scaled, and we have implemented his/her suggested solution. As regards fluctuations in effective population size ( $N_e$ ), we point to Table 1, which provides the actual raw population sizes. We have further revised this table and added  $N_e$  values for the Last Interglacial to ensure that readers will not be misled by dimensions. We do not believe that a scaling exercise is necessary, practicable or even desirable for the actual PSMC plots. We note that our mode of displaying temporal fluctuations in  $N_e$  follows established standards in the PSMC literature (e.g. Nadachowska-Brzyska et al. 2015; Nadachowska-Brzyska et al. 2016; Kim et al. 2016; Kozma et al. 2016), and that an equal scale of  $N_e$  would lead to the indecipherability of trends for most species as many bats have population sizes that are orders of magnitude smaller than those of other bats. We hope the reviewer agrees that our present rendition of PSMC plots is appropriate and suitable.**

b. I also think this would then allow you to compare the patterns by a number rather than just "constant" increase or decrease". I think if all species are on a similar scale you might have a reasonable value for fair comparison across species.

**Response: As mentioned, we have adjusted and scaled trends in habitat fluctuations according to the reviewer's suggestion. As for trends in effective population size, Table 1 provides raw values and our characterizations are invariably qualitative ("increase versus decrease") rather than quantitative, which should address any concerns about scalability.**

Comment 12: 3) On a similar note, when looking at figure 1, I realize that 1) you are going backward in time, and your graphs extend beyond the time scale you are using for habitat. Although this in nature of the analysis, it can be a little confusing. We usually think about increasing time, and we think the data is showing only the time frame you are talking about. If you could make these just the range of time you focused on it would help a lot - unless you want to talk about long term trajectory, OR maybe make predictions about periods when habitat was considerably larger or smaller. Also if you could make it increasing time, it would help when trying to compare fig 1 to Fig 2 – which is showing increasing time scales (Left to Right). Not sure if possible but it would be awesome if it was possible to combine Fig1 and Fig2. Show changes in genetics and changes in habitat in one figure would allow direct comparisons. Not sure if possible but something to think about.

**Response: We thank the reviewer for these valuable comments. In response, we have merged both previous figures into one figure. We have also truncated all PSMC graphs to the time period that is considered in the habitat modelling, and we have made sure that the timeline in the PSMC graphs goes in the same direction as the timeline in the habitat reconstructions. To help the reader, we have juxtaposed these two timelines and connected the two time points of comparison with colored arrows. We hope these bold changes to the figure will be to the reviewer's satisfaction.**

Comment 13: 4) This is minor thing, but I wonder if it is possible to give a little more information about the assumptions that the models are making and how they might impact your interpretations. All the models you use have limitations and make some important assumption. It is unlikely that your reader will be familiar with both models and so might need some hand holding. They are relying on you (and us the reviewer) being upfront about limitations, but I think the reader should have access to this so they can be critical. I am not saying, I think your results would change dramatically with different parameters, but I think the reader would appreciate more reflection of how your assumptions and parameters might change the end results. I think this could easily be done by expanding your limitations paragraph or few sentences in methods clarifying these assumptions, but more importantly how changes in the parameters can alter outcome (if at all). To be clear, I am not asking for a long rewrite or considerable just more direct or detailed focus on limitations. I think all can be done in the limitations section but also could be scattered throughout. I am also fine with mentioning them and referring the reader to papers/reviews which deal with this issue.

**Response: This reviewer comment echoes one of the comments of Referee 1. In response to both these reviewers, we have substantially expanded the last section on “Limitations and Future Challenges” and additionally added sentences to the Introduction, Methods and Results to point out in detail some of the limitations involving our methodology, and how they can be overcome. We'll outline our specific responses regarding the population-genetic and ENM methodology below, under (a) and (b), respectively.**

a. For example, PSMC modeling it is well known is heavily influenced by your selection of mutation rates, generation time, population structure and the individual you used. I recognize you discuss some of these, such as species being from range edge (population structure/individual choice) and different generation time - and you mentioned how these had an important impact on the outcomes - one extremely low  $N_e$  and the other large fluctuation



in total  $N_e$  respectively. You do not really do the same of mutation rate or the fact you are choosing a single individual as presentative of the whole species. (although I know you said it should be repeated with multiple individuals).

**Response: We have added extensive commentary to the Introduction and Discussion to point out limitations of the PSMC approach relating to imprecisions based on the choice of mutation rates and the use of a single genome to infer species-wide population trends (line numbers: 78–81; 405–408).**

b. Likewise, I also know there are quite a few criticisms of distribution models, especially ones which only use climate data as the sole parameters to develop the models.

**Response: This point was raised by Referee 1 in greater detail, and we have added multiple sentences across the manuscript, including in the Methods, Results and Discussion, that go into great details about the challenges currently facing ENM analysis as relating to the choice of bioclimatic variables, and the choice of distribution points for ENM inference (line numbers: 182–190; 279–284; 386–397).**

Comment 14: Like I said, I think these are minor issues, but I think clarity on some of these issues might help with the reception of the paper. Great job.

**Response: We thank the reviewer for the positive comments.**

Other minor comments

Comment 15: Line 69 - delete “by now”

**Response: Done (line number: 68).**

Comment 16: Line 71 – replace “bats” with “their”

**Response: Done (line number: 70).**

Comment 17: Line 137 – don’t assume people are aware of the parameter codes for PSMC analysis. You should outline what each other parameter means. (t, r, p)

**Response: Done (line numbers: 138–140).**

Comment 18: Line 155 – first time you use Abbreviation spell it out. “ENM”

**Response: Done (line number: 161).**

Comment 19: Line 216 – I am not sure why you only used Constant, increasing and decreasing. Seems like if you scaled you can use relative numbers to look at relationship.

**Response: See our response to this reviewer under his/her comment 11 (see above).**

Comment 20: Table 1 – It would be nice to see current on this graph as a reference point (Extra column with current  $N_e$ )

**Response: There is no current  $N_e$  estimate. PSMC only provides  $N_e$  estimates up to 10,000 years ago.**

Comment 21: Table 3 – I struggle with the scale of these numbers - +2,000% versus -99% (which is maximum change short of extinction)

**Response: See our response to this reviewer under his/her comment 11 (see above).**

Comment 22: Fig 1 – I could not really make out the light blue, dark blue and orange in the pdf. Am I missing something?

**Response: We have completely revamped this figure in response to previous comments (see above).**

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## Appendix B

### Response to Referees

In the following, we will outline in detail the ways in which we have accommodated the comments and suggestions of the board member and reviewers. Our responses are in **bold**.

#### Board Member

Comments to Author:

Thank you for your revised paper. The paper is much improved. I would like to see one more minor revision, however, that responds to two important issues raised by reviewer #2. I will be evaluate the response and shouldn't need to send the paper out for further review.

**Response: We thank the editor and the reviewers for the positive comments on the manuscript. We have addressed all comments raised by the reviewers in this revised version of the manuscript.**

#### Referee 2

Comments to the Author(s)

You have addressed all most of my concerns and think the paper is much approved. I hope you agree. I have two minor additional suggestion but otherwise, I think your manuscript looks great and enjoyed reading.

**Response: We thank the reviewer for the positive comments on our manuscript and have addressed the two remaining comments raised by this reviewer in the revised version of the manuscript.**

Abstract; Line 28 – replace “genetic diversity” with “population sizes”

**Response: We have replaced the word “genetic diversity” with “population sizes” in the revised version of the manuscript (line number: 28).**

Methods: Line 240-244 – for classifying  $N_e$  as Zero – what range did you have around Zero (I am assuming they were not EXACTLY the same. Likewise, what was the range of change for +1 and -1

**Response: We thank the reviewer for pointing out the lack of detailed explanation on our approach. We have taken the opportunity to rewrite the corresponding Methods paragraph to describe our approach more clearly. Briefly, we calculated percentage change in habitat and effective population size ( $N_e$ ) and generally classified trends as increasing or decreasing. For three species (*Eidolon helvum*, *Eptesicus fuscus* and *Rhinolophus sinicus*), there was no change in  $N_e$  from the last glacial maximum to the Holocene. Hence, we opted to characterize the change in  $N_e$  as “stable” (see Fig. 1 and Table 1). We have amended the Methods section of the revised manuscript to reflect this approach (line numbers: 209–213).**

## **Referee 1**

Comments to the Author(s)

Most of the comments that I suggested have been addressed in a satisfactory way and the (already very high) quality of the manuscript has increased. The manuscript is clear and pleasant to read. The problem tackled is very interesting, the analyses are sound and both methods and data are clearly referenced in order to allow replication, if needed. The figures are now clear and beautiful, and their appearance and quality are good for publication. On the other hand, I still have two concerns that, if clarified, I believe would further enhance the quality of the paper. I am convinced that answering such concerns should not be very time-consuming as it does not require additional analyses, but just presenting a different set of results, and I tried to include in my answer as much information as possible to make the process easier to perform.

**Response: We thank the reviewer for the positive comments on the manuscript. Detailed responses to comments raised by the reviewer are given below.**

First of all, the calculation of the area still does not appear correct to me.

When using a geographic data file (e.g. a raster), the cells do not represent an area on the land that is a square, because of the Earth being a spheroid. While the latitudinal sides (the north-south sides) of the cells are always constant, the longitudinal ones decrease from the Equator going north (leading to the cell becoming a triangle when reaching the poles).

The method you use to calculate the area is based on the assumption of the cells being squared and hence overestimate cell areas in regions far from the equator (this is the reason why it gives the same results as counting the cells).

This problem can be solved in two different ways. The first one is projecting the raster/geographic file using any equal-area projection (a non-exhaustive list: [https://en.wikipedia.org/wiki/Map\\_projection#Equal-area](https://en.wikipedia.org/wiki/Map_projection#Equal-area)) which can be easily done in R or any GIS software, and then report the number of cells covered. The second one (if using a non-projected map) is to explicitly correct for latitude when calculating the area of the cell, for example using the area function within the raster package in R (<https://www.rdocumentation.org/packages/raster/versions/2.9-5/topics/area>).

**Response: We appreciate the solutions pointed out by the reviewer, and would like to respond in two different ways:**

- (1) We believe we satisfactorily addressed this concern in our past revision by adopting an approach resembling the second suggestion pointed out by the reviewer. Briefly, we have used BIOCLIM data available in a non-projected latitude/ longitude coordinate reference system; the datum is WGS84 ([www.worldclim.org](http://www.worldclim.org)). We carried out corrections for cell size dimensions at higher latitudes according to available documents (Daac 2004). We had described these changes in the Methods section in our last revision, and have taken the opportunity to add further clarification in this revision to make sure the readers understand our approach (line numbers in supporting information: 51–62).**
- (2) Our implementation of cell size corrections notwithstanding, we do not believe that latitudinal cell size bias affects our analyses in any considerable way, given**

**that our habitat range comparisons are always carried out within the same species across epochs. We note that all our species are generally confined to one each out of the Earth's major biomes (tropical, subtropical, temperate zone etc). An equatorial cell size is not generally being contrasted to one at temperate latitudes across the vast majority of our comparisons.**

**In combination, we believe these two points address any biases that may be generated by latitudinal cell size differences.**

I also have a concern about variable choice.

The Authors previously performed the variable choice by merging together species from different macroregions (America, Palearctic, Australasia and Africa) (from now on I will refer to those analyses as “full dataset analyses”). My previous concern was that species living in such different areas would likely be driven by different variables (e.g. minimum temperature is likely to play a different role for Palearctic versus Australasian species).

The Authors did a great job in expanding the description of the methods, the discussion and the limitations on this topic, and they provided clear and referenced reasons to support their choices. Furthermore the Authors followed my suggestion by subsetting the data and selecting different sets of statistics grouping the data by species or continental groups (from now respectively “species analyses” and “continental analyses”).

The Authors explicitly test for idiosyncrasy, following Junior and Nobrega 2018, but they do not answer the concern I raised about the variables not being equally representative in all regions considered.

**Response: We appreciate the reviewer's praise about the thoroughness with which we have followed up on his/her suggestions. Regarding the last sentence, however, we note that we did not explicitly test for idiosyncrasy. This is something that was performed admirably by Júnior and Nobrega (2018) but is not in the purview of our study and would go beyond its set goals.**

In order to answer to my concern it could have been sufficient for example to show (if so) that the variables estimated for each continental group were in most cases included in the variables estimated based on the full dataset.

**Response: We have added a sentence to the corresponding results section outlining the degree of overlap in bioclimatic variable selection for the three different species classification schemes (line numbers: 253–255). We hope this additional information adds the context the reviewer is looking for.**

Moreover, when looking at idiosyncrasy, I do not agree with the choice of the Authors to compare the different analyses looking at how much the extent estimated with the species and continental analyses is in accord with trends estimated with the full dataset. In my view this procedure would be correct if the estimates based on the full dataset were clearly unbiased (as the simulated data in the Junior and Nobrega 2018 reference, that use the same procedure to test for idiosyncrasy), but, as I previously explained, so far I am still not convinced that considering different continental subgroups could not be a better choice.

In my opinion this issue could be solved easily if the Author would accept to compare the three datasets (“Full”, “continental groups” and “species”) with a different method able to identify idiosyncrasy (e.g. comparing the variance of TSSs as detailed by Junior and Nobrega

2018). If following this, both the “species” and “continental” datasets show convincing signals of idiosyncrasy all Authors’ choices will be shown to be fully justified (and the results based on such datasets can then be removed from the paper because shown to be biased).

**Response: We appreciate the reviewer’s emphasis on what is clearly an underappreciated confounding factor in habitat modelling. However, we are afraid we do not concur with his/her suggested approach to address this problem for a variety of reasons:**

- (1) Firstly, much of what the reviewer suggests would take our manuscript into new directions and lead our discussion beyond its intended scope. We did not set out to replicate Júnior and Nobrega’s (2018) admirable study on the role of idiosyncrasy in bioclimatic variable selection based on different species classification schemes. Instead, we reference the latter authors’ important result showing that idiosyncrasy indeed affects such analyses as a confounding factor when explaining the patterns of overlap among these different approaches.**
- (2) The reviewer suggests “this issue could be solved easily” if we use an approach comparing variance of TSSs. While concurring that TSS is undoubtedly an excellent evaluation method for niche models, its application is justified for the generation of presence –absence distribution models i.e. threshold dependent output. In our study, the main objective was past habitat reconstruction, for which ordinal score models with different presence probabilities are more suitable than dichotomous presence-absence based approaches. Our threshold independent ROC curve approach (i.e. Area Under the Curve) is an effective measure for that. Hence, we do not believe that TSS analysis is appropriate in our context (see also Allouche et al. 2006).**

I also found a couple of typos that you could correct: “Ne” should be written with the “N” in italic and in line 237 you find “earth” instead of “Earth”.

**Response: We have carried out the wording changes as suggested by the reviewer in the revised version of the manuscript.**

## REFERENCES

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