

Dear Dr. Martins,

Thank you again for the opportunity to continue to revise our manuscript: “Using plant invasions to compare occurrence- and abundance-based calculations of biotic homogenization: are results complementary or contradictory?” for *Global Ecology and Biogeography*. We are pleased that you and both reviewers found our most recent version of the manuscript to be significantly improved, and are grateful that your input has helped shape a higher quality and more impactful presentation of our study.

In the current set of revisions, we have addressed your remaining comments, as well as the minor revisions suggested by the reviewers, which we detail in the following pages. We hope you will find our revised submission suitable for publication in *Global Ecology and Biogeography* and look forward to hearing from you.

All the Best,

Daniel Buonaiuto, on behalf of all Co-authors.

Comments from the reviewers are in italics. Author responses are in plain text

EDITOR'S COMMENTS TO AUTHORS

Editor: Martins, Ines

Comments to the Author:

The authors have submitted a fully revised manuscript, where they have carefully addressed most of the concerns I and the reviewers raised in the previous review. I particularly appreciate the authors' effort to tackle the methodological issues raised and improve the overall structure, presentation, and narrative of the paper.

There are only a few minor comments and one remaining issue that I ask the authors to answer before moving forward. In previous interactions, reviewers have raised some concerns with the way the authors introduce some of the tackled concepts (or lack of). While the authors have made substantial improvements, some points remain on the subject that I ask the authors to consider. Please see the reviewer's comments on the subject for further recommendations.

We are pleased that you found the manuscript to be much improved. In this updated submission, we have addressed your remaining comments and those of the reviewers, which we detail below. Thank you again for your feedback and for the opportunity to continue to revise this manuscript with GEB.

Line 219 – Fixe the jump of line

We have corrected this formatting issue

Figures looks great, but I just have few smaller suggestions:

Figure 1- I'm unsure of the need for the inner outline boxes, right now is just making the figure look more crowded. Font sides within panels are still somewhat different (for instance text in 1b 1. still as a different font size then 1b 2.). I don't think you need the header in Fig 1c as it's clear in the figure caption that's a roadmap for interpretation.

Thanks for this attention to detail. We have adjusted the figure and standardized the font sizes.

Figure 2 – make axis numbers bigger (or at least the same size of figure 3).

We have increased the size of axis labels and text for this figure.

Figure S1 - Please revise y axis labels. Can you make it more informative? right now it shows the file? name. Please do revised size of axis in all figures to guarantee readership.

Apologies for forgetting to replace this draft version of the figure in our previous submission. We've now updated this figure with the proper plot labels. We also increased the sizing on the axis labels for Figure S2 to match Figure 2 in the main text.

Thank you.

Dr. Ines Martins, Editor

REVIEWER COMMENTS TO AUTHORS

Referee: 1

Comments to the Author

I would like to thank the authors for fully considering my previous suggestions and revisions. I believe that the new analyses add to the novelty of this paper. I only have minor suggestions for clarification. Thank you for your time spent with our manuscript and constructive feedback. We are pleased you found the updated version more novel.

Minor comments:

L. 213–215: Why did the authors have to generate randomly generated absence records? Was it unfeasible to construct binomial GLMs for the presence/absence data that the authors already had? If they can do, I recommend not to use randomized absence data and use the original presence-absence data. Or more clarification would be helpful.

Thanks for raising this point. We now see that this sentence was poorly phrased and corrected it in the updated manuscript. We did indeed use real presence/absence data (i.e., absences were surveyed points where the focal species wasn't recorded). Because there were many more absences than presences (as is typical of biological survey data) we randomly selected a subset of the true absences points equal to the number of presences points (i.e., so that $n_{\text{absence}} = n_{\text{presence}}$) to compare results for many species against each other and minimize detection bias. We have clarified this in the text at line 220 -221.

L. 280: Figure 2b -> Figure 1b?

Thanks for catching this. We have corrected this typo.

*L. 303–304: Isn't it possible that in some plot pairs *Bromus tectorum* was absent in neither of them? How did you treat these cases?*

These cases were not part of our analyses. We added text explaining this at line 318-319.

L. 304: “this” before “haversine distance” may be misleading and could be erased.

We have corrected this typo to “the”.

L. 318: How did the authors decide “whether or not B. tectorum was the dominant invader”? Were there any thresholds? I am curious why the authors did not use the coverage value of the invader. Maybe converting this originally continuous value into discrete (i.e., whether-or-not data) could lose some information. It is ideal if the authors try to re-analyze the data using continuous value (% cover?), but if this was unfeasible the authors should specify thresholds (% cover > XX) to decide the dominance of the invader and why that value.

We apologize for this confusion and can see how the choice of the word “dominant” was misleading in this case. Since we only analyzed plots with one invasive species present in them for this analysis, the word dominant is superfluous here and we have removed it from this version of the manuscript.

We agree that in general continuous variables provide more information than discrete ones. In preparing this analysis, we experimented with multiple ways to use continuous values to quantify invasion levels. Because of the pairwise nature of beta diversity estimates, a more quantitative metric would have to capture both the relative cover of the invasive species at each plot, as well as the difference in cover between them. We found this kind of high dimensional value not only difficult to analyze but also difficult to meaningfully interpret. We therefore elected to use discrete values to keep our analyses and their inference as clear and straightforward as possible.

L. 324–325: Can you specify more the distributions for the weakly informative prior?

We have added more information about our prior specification at lines 340-343.

L. 397–398: I could not read from figure 2 that the disagreement is more likely when the effects are small (which means the absolute H indices were small?). Can you elaborate on this more?

Thanks for raising this issue. We have added text to explain this statement at lines 416-418.

Fig. S1: Can you increase the size of the label texts on the y-axes?

We have updated this figure to be more clear and readable.

Referee: 2

Comments to the Author

Dear Authors,

I have to say that the story became much clearer since the 1st round. Several of my former comments were incorporated but not all in depth as I hoped for but that's also a matter of taste and in my opinion an editorial decision, to what extent, e.g. BH has to be fully introduced at the theoretical level (which still isn't). All of my points are minor and can be improved by some text. Generally, I think the story is now much clearer though still complex. The discussion is well written and I did not had comments.

Thank you for all of your constructive feedback on our manuscript—we are pleased you found our revised version to be much improved. We appreciate your point that this is a complex topic that blurs ecological complexity and mathematical properties, and have done our best to achieve further clarity following your comments below.

Minor comments (l/L = continuous line numbers)

L49

“decline or shift” I would say. Or you refer to “per site”.

We have made this change in the manuscript.

l50

I personally would like to see/read here few words which biodiversity level you are addressing here? Taxonomic, functional etc? BH is quite vague as term. Be more specific already in the introduction.

We agree that it is well established that biotic homogenization can occur at multiple different levels of biodiversity, and that additional clarity would be helpful for the reader. To solve this, we now clarify that we analyze taxonomic homogenization in the abstract (line 22). As we further elaborate in the Introduction (now lines 175-179) the general principle of abundance-weighted and occurrence-based metrics of beta diversity we discuss can apply to multiple dimensions of biodiversity, so we have elected to keep this phrasing broad.

l80

I think generally you should mention that you can only compare mathematically very similar metrics. And not e.g. turnover vs nestedness metrics, irrespective if they offer an abundance or just occurrence version of it.

This is a good point, and we acknowledge that there are many ways to estimate beta diversity that range in complexity. We have incorporated this suggestion into our Methods at line 267-268 where we now highlight that the metrics we evaluate are mathematically related.

l142

This is not a comprehensive description to make this argument. Do the few new arriving species, occur at all compared plots? If so, say it. And are the lost species, lost at all compared sites? Say it. Only with those additional information I, the reader and you could hypothesize of we would find differentiation or homogenization. Moreover it also depends on the amount of species already occurring and the metric. If these are just few out of hundreds, it might not be enough to change a pattern due to many more shared or not shared. Be more specific here or any statement coming from those few words is not necessarily true and thus wrong, I fear.

Thank you for raising this point. Our prediction here is based on a mathematical argument that the gain of a species at high abundance has a greater impact on abundance-based metrics than

occurrence-based metrics and the loss of species already at low relative abundance has a greater effect on occurrence-based metrics than abundance-based ones. We have added text in this section (lines 147-150) to detail this logic which we believe will make these predictions more intuitive to readers.

l 148/149

You need to be more specific in your language. Maybe its just me. Distance decay is first of all a pattern and not a state. If you refer to it, then also mention at which end of the gradient you are referring to. Plots far away from each other or what? I guess you refer to plots far away.

Moreover why do you refer to invasive species (especially when you use non-native later on)? Does the impact of the species matter? I guess not. I would use non-native or alien or whatever but there is no need to call them invasive. And why non-native at all? Why is the origin of the species compared to a larger area important here? It could be “just” a new arriving species from the species pool but so far not in the plot. The same mathematical feature for your BH pattern.

Thanks for raising these points. We have adjusted these lines to stress that distance decay is a pattern and that similarity is expected to decrease with increasing distance between plots (line 152-154).

Additionally, we agree the the defining species as an invasive can be highly context specific, and have adopted the descriptor “non-native” throughout the manuscript when describing these the species in our dataset. Thanks for raising this issue.

l174

I don't understand how you focus on only one driver and not e.g. climate and land use? You use vegetation plots. Climate and land use act there as well 😊 How to you account for it? I think you need to use few more words to explain your reasoning. Just because you have non-native species in your plots doesn't mean that e.g. species losses aren't driven by other global change drivers. Quite the opposite. They are very rarely driven by invasions, especially in plants. So far the introduction reads like you wanted to use as fewest words as possible but in my opinion you lost clarity and rigorousness in your statements and argumentation lines. I guess you know all of it but as said, I can only guess, and that's not how research papers should work.

We agree that many drivers of global change can lead to biotic homogenization and have made sure to state this in several places in our manuscript (e.g., lines 57-60, 178-180) and, as we have detailed on our Methods, we have done our best to account for environmental & land use patterns (i.e., with the inclusion of the Human Modification Index) that may also drive composition differences between our invaded and uninvaded plots. We agree that it is possible to interrogate discrepancies between abundance- and occurrences-based calculations of biotic homogenization as a function of climate or land-use change, but the comprehensive dataset we use here is most intuitively linked to invasion status. Only ~2% of the plots in the dataset were sampled multiple times providing very little power for addressing the impacts of climate change,

and land use metrics were coarse at the scales considered in this study. In contrast, the dataset includes non-native species information at the plot scale, providing a unique opportunity to assess patterns of occurrence- and abundance-based beta diversity associated with non-native species. We appreciate your point that our associative analysis cannot mechanistically link invasions to changes in beta diversity, and we make sure to address this limitation in our Discussion (lines 457-463).

l194

Is the tool only for invasive species? I guess not. Please be consistent with terminology.

In this case, we use existing terminology; “Invasive Species Habitat Tool” is the published name of the tool.

l207 /l 212

“additional” to which? You haven’t mentioned which others you already use. You just said you obtained environmental data. Not which. Please mention all data you use from which data source specifically. Which INHABIT variables have you used? Mention them and add few words on the details here.

Thanks for this point. We have removed the term additional for clarity, and list the variables we selected based on our preliminary analyses in lines 213-241.

l 208

“Preliminary” done by you? I’m not 100% but is the paragraph here the description of this preliminary variable analysis? Not 100% clear.

We have clarified this statement. It now reads:

“...five environmental variables that we found to be important predictors of species cover in a preliminary analysis”

l214

What is L4? Explain more please.

Thanks for catching this. We now refer here to “Level IV” to be consistent with our descriptions of the ecoregion proved in lines 206-207.

l224

Selected soil N as what? Additional to other variables? As only environmental variable? Its not 100% clear to me.

We have adjusted this statement to indicate that we selected soil N from among the collinear variables mentioned in line 230 to use in our analyses.

Moreover I can understand that you have to find a way of comparing plots along an environmental similarity gradient. But what would be interesting is to what extent is habitat type considered. You can have completely different habitat types with different plants on soil wise or ph wise quite similar plots. Can you explain few words on habitat diversity per ecoregion or so. Yes its macroecology, and that's totally fine but for botanical studies it needs few more descriptions to judge its meaningfulness, when comparing so many plots. And seeing your feedback from my last comments I think you should tell the readers why you can't go into habitat types. Just say that this is the best you can do at this scale etc.

Thank you for recognizing the effort we have made to define habitat types based both on environmental factors as well as EPA Ecoregions. We do recognize that there are many other vegetation classifications at even finer scales that could be used to delimit particular plant community types (e.g. midwestern oak-hickory forest). At the scale we are working at, these have drawbacks in terms of consistency and meaning at a continental scale. Moreover, because vegetation classifications are defined by the plant communities themselves, we do worry that this would introduce circularity into our arguments that revolve around differences in plant communities as a response. Because of this, we have taken a primarily abiotic approach to defining habitat. While this includes a great many predictors of plant habitat, it is also inevitable that we miss some or represent others (e.g. soils) imperfectly due to limitations in those data.

We now explain this in our manuscript at lines 247-250.

1227

I don't understand what you mean with "did not consider L4..." . Explain better please.

We ran this model across all Level IV ecoregions, and make this statement here to contrast with the occurrence based models from line 219 where we fit a model within each ecoregion. We now clarify this difference in line 233-234.

1245

This is in my opinion sill not convincing, though better than in the 1st version. If I understand it correctly (still not properly spelled out), you work in similar large scale habitat of a desert? If so, you can say, that even in 45km distance the habitat is very similar. Something like this helps the reader to understand that you don't compare apples and peaches. Still with similar PH and/or soil N, habitats and thus plant communities can be very different. But that doesn't seem to be the case here, or? Be clearer here.

Thanks for raising this issue. In our updated submission, we have worked to clarify our spatial matching procedure. Noting the standard deviation in line 258, you can see that some matched plots were very close together while others farther away. The purpose of this sensitivity analyses is to show that the coherence of abundance- and occurrence-based metrics of BH are robust to whether plots were matched based on environmental or spatial distance, not to make any inference about the spatial scale of habitat properties, which we clarify in lines 254-256.

1257

Is there a reason why you don't use the Horn index with same abundance of each species in each community (which should be equal to occurrence 1) as the non-abundance measure? In this way you compare mathematically the same indices? Or vice versa, how similar are mathematically the Sorensen and the Horn index? We know that they are but I think you need to show it in the paper.

This is an important point. In this study we calculated beta diversity using Hill Numbers which correspond mathematically to the Horn and Sorensen indices. In the updated manuscript we have clarified this at line 267-272, which includes the citation that derives these metrics mathematically.

1 265 & generally

I still feel that the introduction needs a sentence where you make clear that bc of space for time you focus on species gains. However, the differences in plots can also be driven by "losses" of natives. I made this comment before and still feel its somehow missing to understand that you don't consider this aspect of BH. Maybe its just me. And I made this comment here and then went back what I wrote the 1st time and saw I mentioned it clearly and asked for clarification.

We agree this is an important limitation of our approach. We have added text into the introductory paragraph of our methods (line 187-188) to address this more explicitly.

We also emphasize this limitation in our Discussion and make suggestions for future research directions at lines 457-463:

[Our approach] "...limited our ability to identify how changes in the native community affected the likelihood these metrics disagree. This suggests that the study of biotic homogenization would continue to benefit from more work comparing occurrence- and abundance-based calculations of beta diversity particularly with alternative study designs and especially with repeated sampling that measure change in these metrics over time."

1 301

Level I – It's the first time you mention this level. I have zero clues what it means.

Thanks for catching this. We now define the scale of these ecoregions at line 314-316