Dear Dr. Martins,

Thank you for the opportunity 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 appreciate the constructive comments from you and the reviewers. We have fully revised the manuscript as a regular research article. In particular, we have made the following major revisions:

1. We have added a sensitivity analysis where we matched uninvaded and invaded plots based on spatial distance, resulting in a new table and figure in the Supporting Information (Table S1 and Figure S2) comparing these results to our main approach (plots matched by environmental distance).

2. We have conducted a new set of analyses based on a large subset of plot comparisons (n=29,933) in the North American Desert Ecoregion where we directly tested several hypotheses about factors that might increase the likelihood of disagreement between occurrence- and abundance-based metrics of beta diversity using a novel statistical approach. These analyses have resulted in a new Figure (Figure 3).

3. We have also made considerable revisions to the text. We now provide a more comprehensive theoretical background for both the mathematical and biological reasons that occurrence- and abundance-based metrics of beta diversity might yield contradictory trends in homogenization/differentiation in our Introduction and Discussion sections. We also identify processes that affect beta diversity that are more difficult to capture in the space-for-time method we employed here (i.e., compositional changes in the native community) and suggest future approaches to understand these dynamics in our Discussion.

Please note that this manuscript has also received an additional review by an unaffiliated researcher at the United States Geological Survey, as is required by federal protocols. We have appended this review to the GEB reviewer responses that can be found below.

We hope you will find our revised submission suitable for publication in *Global Ecology and Biogeography* and look forward to hearing from you.

Sincerely,

Dan Buonaiuto on behalf of all coauthors

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

This work aims to explore how two groups of metrics (occurrence-based and abundance-based) behave when measuring patterns of homogenization/differentiation in plants. I commend the authors for their aim and impressive dataset. I find the general topic of the manuscript is both relevant and interesting for GEB, however, there are some major concerns about the framework and strength of the analysis at this stage.

Thank you for taking the time to review and comment on our manuscript. We are pleased you found the topic interesting and relevant, and have strengthened the structure and analyses of our study based on your feedback, and the comments of the two reviewers. We detail these changes below.

The authors presented this as a 'method' type paper, however, I confess that I struggle to see what's new "new analytical techniques, new software, etc., or critical evaluation of methods in macroecology.- GEB Author Guidelines. As of now, I think this fits better as a research article, particularly (one looking at distinct patterns of homogenization/differentiation with plant invasions, or even the role of different invaders), although even under that category, the article needs much improvement to fit within GEB standards (see notes below). If the authors want to make the case for a 'method' paper, they need to make a much stronger case for novelty and clearly justify how their approach/metrics/models are novel or/and how they have critically evaluated established methods (the latter which I assume was the aim of this manuscript). Perhaps expand to compare multiple metrics and unpack from which methodological choices or index assumptions, differences can arise.

Our intention with our original submission was to provide a *critical evaluation* of whether or not occurrence- and abundance-based metrics of beta diversity consistently yielded the same estimates of homogenization/differentiation, but we recognize that our submission did not fully address this issue. Your comments, as well as those from the reviewers, helped us realize that we have the data to explicitly test hypotheses about the biological factors that relate to differences between metrics, and as such we have re-written this manuscript as a research article, and included several new analyses. We are grateful for your guidance in helping to shape this updated submission.

On this note, the authors state in the discussion that "A goal of this study was to compare the empirical differences of abundance- and occurrence-based calculations of biotic homogenization to the theoretical differences reported in Cassey et al. (2008)". If this is true, then it needs to be made more obvious in the introduction (not just have Cassey et al. as an example – Line 92-97). Perhaps lay down the expectations based on such work or potential expected differences. Figure 5 seems to be more of an intro/conceptual figure where the authors lay down their expectations or potential difference scenarios based on the

relationship between metrics. The scenarios here could be used as a base for hypothesis testing, a point also highlighted by the reviewers.

In the updated version of the manuscript, we are more explicit about our goal of testing the theoretical predictions of Cassey et al 2008 with empirical data in the introduction (lines 183-188, 216-220). In place of Figure 5, we have added a subsection to the introduction called "What factors might increase the likelihood of disagreements?" where we lay out predictions about how characteristics of the native and non-native species pools, and distance could affect the likelihood of discrepancies between occurrence- and abundance-based metrics and test these predictions with our data. We feel this approach has led to a more comprehensive and impactful study and appreciate you and the reviewers urging us in this direction.

Please see my further notes/suggestions below:

Methods:
I appreciate the effort the authors when into tackling some of the common biases with this type of analysis. These measures of similarity or dissimilarity are useful if both sites have identical environmental conditions, the same turnover rate of individuals and species, etc. While the authors have tackled issues related to environmental distance, other problems remain, such as spatial distance, which cannot be tackled by simply controlling for environment.

Thanks for this comment. In our preliminary analyses of these data we had also tried matching invaded and uninvaded plots based on minimum distance between them. Because this approach yielded similar results, we did not include them in our original submission but now see the paper would benefit from this kind sensitivity analysis. In this updated re-submission we include a version of our main analyses based on these spatial match plots (lines 333-341), with a new figure and table in the Supporting Information (Table S1, Figure S2) to emphasize our results are robust to this methodological decision.

The authors used a space-for-time approach, and while space is used as an analog of time, I don't understand the choice to include only the more recent survey (line 165). What years were those? If multiple years are available for some plots, shouldn't one select the surveys sampled in the year that more closely matches the year (or average year) where the others surveys were sampled? –Unless this scenario is really a minority of the cases, then perhaps I will suggest running a sensitivity analysis on what will happen if alternative year*surveys were picked.

Thanks for raising this point—we realize now that we may have overstated the importance of these plots, as they only make up 2% of the full dataset. Only half of the

revisited plots had been sampled more than twice. We have clarified this point in the Methods section.

Because the number of plots that were resampled were so small, choosing different time periods did not change the sample year distribution substantially if we use alternative sampling metrics for repeated plots (see below).
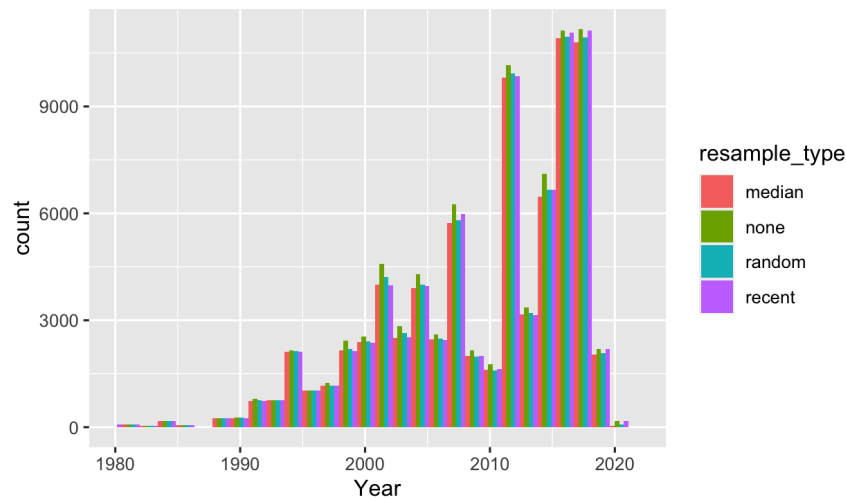
Because these repeated samples make up such a small proportion of the data, we feel it would be very unlikely that including different time points would change the relationships we observe.

In line 172 the authors mention that "We matched plots based on five environmental variables that a preliminary analysis found to be important predictors of native species cover", but nowhere is this analysis described. Please expand on what was done here (in the main or supplementary).

We apologize for this omission in our original submission. We have added more details about how we selected these variables at lines 300-323.

By looking at Figure 3 (and Line 219-223) it's clear (and if I'm understanding it right) that most four plot combinations (matched uninvaded and invaded plot pairs) came from the same original data, so why not make that a rule to start with? That is, matches can only occur between plots from the same study. This way, one can be sure the different sampling methods don't play a significant role in influencing the results.

We appreciate this suggestion, and have now implemented a matching protocol and calculations of beta-diversity so that only plots within the same original Dataset and Level IV ecoregion are compared (updated in Methods at lines 293-295).

Results:

I also feel that much more could have been done to interrogate the results and increase this manuscript's interest level, the reviewers do provide several suggestions on that front. In addition to the results in Figure 3, I found it particularly interesting the potential role of single invaders vs multiple invaders, something that the authors fail to unpack (lines 256-258) or even mention in the discussion. Although I understand it may not be the focus of this particular work, it will be interesting to have a closer look at these trends, even look at the traits of these invaders and if, even when different in identity, they may or may not share common traits when causing homogenization and differentiation.

Thank you for bringing this to our attention. We have restructured our results to now include two subsections, the first addressing the frequency over which we found occurrence and abundance metrics to contradict and the second testing some predicted mechanisms (i.e. single vs multiple invaders and other properties) that may contribute to the patterns. The results of these analyses are now described in the Results section and have resulted in a new Figure 4.

Figures:
The main figures also need to be reconsidered and improved. In my opinion, they are too numbered and could be merged or transformed to be more informative. For instance, Figures 1 and 2 could be merged (have a panel for each). Please carefully re-think what the key results are, what you what to convey, and how each figure helps illustrate them. Moreover, please check that you are using a colorblind-friendly Palette across all your figures and please be consistent with the type of letter, size of the legends, and axis text.

In our updated version of the manuscript we have worked to improve our figures considerably. As you suggested, we have merged figures 1 and 2 (now Figure 1) and fixed their fonts and text to be more consistent.

We have also replaced Figures 4 & 5 (which each reviewer had issues with) with a new Results figure (Figure 4).

Small notes:
Line 197 – Fix the formula

We have addressed this issue

Figure 2: Use Habn vs. Hocc in the axis as well.

We have made this change to the figure (now 1c)

I do hope these suggestions are useful. I think the comments from the reviewers are also straightforward and provide several potentially useful suggestions and recommendations going forward that can help you improve your manuscript, please consider them carefully.

Thank you for submitting your manuscript to GEB.

Dr. Ines Martins, Editor

We appreciate the guidance you provided and feel that it has substantially improved our revised manuscript. Thanks again.

REVIEWER COMMENTS TO AUTHOR

Referee: 1

Comments to the Author
Dear Authors,

An interesting study exploring beta diversity patterns using pure occurrence based methods vs abundance based methods. But its complex as you point out too but also very promising given the potential of the data set and the methods used. I think my concerns are mainly due to the presentation and potentially the lack of looking at (as far as I see it) the differences in native species, which can also drive patterns. Mabye I'm wrong, its really complex and has potentially a lot of different scenarios how 4 communities can be different.

Thank you for spending time with our manuscript and providing such constructive and detailed feedback. We are happy you see potential in our dataset and methods, and have worked to improve the presentation of the materials and scope of the analyses as you have recommended. We detail the changes below.

My first two main comments are related to the imo the imperfect introduction to the topic itself. Is it a rather mathematical oriented study to see the differences of metric behaviour or grounded in ecology to understand the processes better? For both imo the introduction lacks the theoretical basics and introduction. What potentially can lead to what and why. Just mentioning empirical studies doesn't help at all, because the reader doesn't learn about the reasons for the different patterns.

Thank you for this comment—in reviewing our previous submission we can see we did not provide the strongest theoretical grounding for our study, and have worked to improve it.

Specifically, we have added two new subsections to the Introduction (*How frequently do abundance and occurrence metrics disagree?* and *What factors might increase the likelihood of disagreements?*to better address the ecological theory about what can lead to contradictions between the metrics. We then test some of the predictions of these theories in a new analysis reflected in a new Figure 3, and respond to these issues more thoroughly in the Discussion (lines 493-504). We hope these changes provide more concrete grounding for the topic of this paper.

My 2nd main comments becomes specifically clear in the "space-for-time-approach" intro. You compare different plots without a justification why you are doing it? If you would be interested in ecology you should here justify the comparison of different habitat types, which you potentially have in your data set. You say something about environmental similarity of the plots, but the details are not enough imo to understand e.g. the level of mixing different habitat types. Environmental conditions driving community compositions at the plot level (which is the best scale to analyse BH, don't get me wrong) can be very specific and I'm not convinced yet that the few variables are enough. I suggest to show somehow which habitat types you compare with each other in the pairwise matches. As an ecologist who is working a lot with plot level analyses and compositional changes that would be for me a minimum, even if you present propensity score matching (I'm not so familiar with it, thus not able to judge it).

We apologize for the confusion in our matching approach and have added more details about why we engaged in this process in the Methods. Because we are trying to approximate biotic homogenization (a temporal process) from a spatial dataset, we are matching plots in order to minimize the amount of mixing different habitat types, so that the differences we see in plot compositions are most likely to be from biotic interactions rather than environmental differences, which we emphasize now in our Methods section.

Our methods control this in two ways. First, by only matching plots within level 4 ecoregions which are delineated based on the similarity of the "type, quality, and quantity of environmental resources" in each area, we control for macro-scale variation in climate, productivity and space. Then, by using the propensity score matching for additional climate variables (the selection of which we now provide more details about in lines) we further control for microsite variation in the environment.

We hope the additional details we have added here and in the main text (especially the sensitivity analysis where we match plots based on distance rather than environment) clarifies the utility of this method.

Minor comments (p = page/l = line – 2nd line numbering, the original one I guess, the more right line numbering)

Citation style
Not sure what the GEB rule is but I prefer to insert always an "e.g." when I'm citing single refs just as one example of many existing studies.

Thanks for this point. We have added e.g. in areas where our citation is an example of many, for example: lines 204, 206.

P2/l 47
But there is also plenty of evidence evidence for differentiation, also depending on the spatial scale of the used data (e.g.
https://nam10.safelinks.protection.outlook.com/?url=https%3A%2F%2Fwww.science.org%2Fdoi%2F10.1126%2Fsciadv.adj9395&data=05%7C02%7Cdbuonaiuto%40umass.edu%7C3c835fbe949f4a6c99e808dc96e17db2%7C7bd08b0b33954dc194bbd0b2e56a497f%7C0%7C0%7C638551142424817661%7CUnknown%7CTWFpbGZsb3d8eyJWIjoiMC4wLjAwMDAiLCJQIjoiV2luMzIiLCJBTiI6Ik1haWwiLCJXVCI6Mn0%3D%7C0%7C%7C%7C&sdata=jsIgR%2Fgve0lvn97ORzKhVHiWajuVGd6CPmUpVCC5%2Bh8%3D&reserved=0 *) and I dunno what the reference of the Olden Rooney paper is pointing too (generally or as an example for patterns). If the latter it needs some more or another ref which is not 20 yrs old. Back then the line of evidences was very thin, which has changed a lot.*

Thanks for making this point. We do not mean to imply that evidence of homogenization in some studies precludes the fact that differentiation occurs as well. We have now expanded our introduction of differentiation in the second paragraph of our introduction and have added the citation you provided (thanks for it) and emphasize that differentiation is not only possible but common. We have also added additional citations at line 142 providing evidence of homogenization and its effects on ecosystem function.

P2/l 51
I suggest rather to explain BH (biotic homogenization) with the commonly used terms of similarity across communities. A distinct community per se doesn't say anything about a similarity with another community.

We appreciate this suggestion and have made this change (line 144).

P2/l65
How can occurrence based methods be effectively show the importance of rare species? Maybe I misunderstand what you mean. You said occurrence vs/or abundance, so I see occurrence based methods

as a method, that doesn't take into account the abundance of species. How can you know then that a species is rare? Rephrase or add a sentence to explain.

This is a good point, and we have removed this statement, focusing rather on the addition and removal of species rather than their rarity.

P 4/l 103
Not only natives or non-natives can change their abundance. Clarify and be more specific. Moreover why do you say "invasive" species, when comparing to natives. Say non-native or be more specific why all in a sudden you refer to invasive species. These are two different species groups!
More generally I have the feeling that the theory behind beta diversity wasn't properly introduced or your viewpoint not made clear enough. Changes in community similarity are driven first of all by species gains and losses, irrespective of the origin of those species. Anything else is an add-on those processes. If you are interested in the effect of non-natives on beta div patterns then you should say it and not mixing different levels. But then you also have to consider what happens if natives change their abundance in the one or other way. So line 105 is first of all wrong. Its not only driven by those two processes and "mainly" I wouldn't subscribe to neither from what I read here.

Thanks for highlighting the difficulty of this statement. In our updated version of the manuscript, we have shifted this discussion to talk about the occupancy-abundance relationships more generally, and how several kinds of disturbances, including invasion, can disrupt this equilibrium assumption (lines 222-228).

P 4/l 108
I'm sorry to be picky with language but I guess that's my jobe here too 😉 *You assess BH but beta div or similarity patterns. BH is one possible result of such an analysis.*
More generally, I feel there is a theory founded intro into the differences among abundance and pure occurrence patterns missing. What can lead to differences between those two measures? It could be few sentences looking at the math of those measures and the most simple example of two sites. Rare species becoming more abundant or a new species coming in which is not gained among the samples etc etc. You focus a lot on empirical examples but I think it rather needs a a more foundational intro into the processes potentially behind such differences. In the end its first of math and coming from there ecology. Both I feel is missing.

Thanks for this point. We now refer to "homogenization/differentiation" when discussing changes in beta diversity (throughout the manuscript). We now include an additional introductory subsection (line 222) to discuss the theory about why these metrics can produce different results and use Figure 1a to conceptually demonstrate how the mathematical weighting of species abundances result in different estimates of beta diversity, and therefore, homogenization/differentiation.

P5/l 136

Invaded by what? You really need to explain your system first 😊

We now clarify this at line 215-216.

P6/l 172
What prelim analysis? By whom? Where? How? Please specify and give more details here and/or in an appendix. What is the human medication index? Maybe I miss something (then sorry and link the info here again) but I'm surprised how less information you're giving in a time, where reproducibility should be common. I couldn't do nor judging anything just with the info here.

We apologize for this omission in our initial submission and have provided more details about our variable selection process at lines 300-323 as well as included a citation explaining the HMI at line 300.

Fig S1
Spelling mistake.
Matching of what? I personally don't understand the caption here and suggest to explain it a bit more. Generally I thought you match only environmental similar plots and not "all". But e.g. in Fig 2 caption you say beta div was calculated between all pairs ? Maybe I'm just to stupid (which totally can be 😊 *) but then you still need to clarify it a bit better please.*

Thanks for raising this, we have expanded this caption to indicate that the environmental matching was done to establish invaded and uninvaded analogues, and beta diversity was calculated among all plots in each category.

P6/l 186
I don't fully understand from the sentence. Did you calculate beta div among and all invaded plots within invaded plots only and the same for uninvaded plots? Please clarify.

We have restructured this sentence to more clearly reflect that we calculated beta diversity between all invaded plots, and all uninvaded plots separately (line 344-346).

P6/l 189
I know the Morisita Horn index, I guess it's the one. Please stick with the common term here. I haven't head of a "Classic Horn" index so far.

We used the Classic Horn (which is related to but different from the Morisita Horn), and now include a citation for it.

P7/l 202
Again, that might be due to a missing proper theoretical foundation of that rather unusual pairing in combination with space for time or me being too slow here. The invasion is just one process here. How

can you exclude that any pattern you find (homogenization or differentiation) isn't due to the loss or gain of distinct natives in one sample (also leading to homogenization) or differentiation due to the gain of shared and/or shared native species? I guess you don't have to because you are saying e.g. "differentiation with invasion" and not "because of". If this is the reasoning I would clearly say it somewhere here. If not clarify it too 😊 *But generally I think you would have a much stronger story if you would also look into the native species changes or at least into the effect of losses. On the other hand its already a complex story. If you don't see a chance to include some analyses around the losses, at least discuss their potential effect on your patterns. Though I like the scenario based flowchart in Olden AmNat 2003a bit more but yours is also helpful. Move it up and spend some time to explain it in the methods or so. This is important to make readers understand what potentially is going on.*

In this study, because we have spatial data rather than temporal data, we are not actually measuring the process of homogenization (gain and loss) but rather differences in beta diversity between measuring between invaded and uninvaded plots. We have added a paragraph (lines 528-534) to this discussion discussing this limitation and calling for more studies that compare homogenization/differentiation estimates with these two metrics in time series.

P9/l 267
You calculate beta div, not BH. BH is one possible outcome as you show.

We've clarified this state as homogenization/differentiation.

P10/l 300
I also would include here, that usually studies looking at larger spatial scales use occurrence data, such as gridded atlas data or regional species lists. Spatial scale matters especially for beta div.

This is a great point and we have added text about scale at lines 506.

P10/l 305
Honestly I totally disagree if you say "see here, please use both metrics to learn more". I'm more puzzled than before 😊 *I agree it has potential but you don't give any indication what I would learn from seeing differences in occurrence vs abundance based measure or maybe there are not most prominent here.*

We now more fully address how comparing both metrics for the same data can improve inference about the processes contributing to change in beta diversity, highlighting this with our case study. We also now focus on the fact that another benefit of using both metrics is to better understand whether the patterns we found are consistent across different study designs and identify how changes in the native community affect the agreement between abundance- and occurrence-based metrics (lines 531-543).

P10/l 319
"rapidly" in which direction and manner? Turn over towards new species, gains of new natives, losses etc? Be more specific.

This statement no longer appears in our updated Discussion.

Figure 5
I have the feeling that this figure is too simplified given all potential scenarios. Maybe I'm wrong. But comparing it a bit to Olden AmNat 2003 it looks like 4 quadrants are not depicting all possible changes (gains/losses of different natives and/or non-natives).

We agree this figure was an over-simplification. Because many opposing patterns can drive the same changes in beta diversity that are beyond the scope of our inquiry, we have elected to not include it in our updated resubmission, and instead focused on testing the specific predictions of our case study.

REFs
Some journal are written w capitalized letters (e.g. Pecl et al, Winter et al), but most aren't.

Thanks for catching this. We've standardized our references formats for resubmission.

Referee: 2

Comments to the Author
I carefully read the paper "Using plant invasions to compare occurrence- and abundance-based calculations of biotic homogenization: are results complementary or contradictory?". The authors have analyzed a large vegetation dataset to investigate the consistency of the biotic homogenization/differentiation patterns informed by occurrence- and abundance-based beta-diversity. They found that both metrics generally agree in the direction of homogenization/differentiation, suggesting that they can be used interchangeably to this end. This paper also summarizes the scenarios when this would be not the case, providing a guideline for using the two metrics complementarily to understand the ongoing anthropogenic impacts on ecosystems, more specifically on beta diversity. The research question is relevant the analyses are sound, and the writing is good.

Thank you for your time and effort on this manuscript. We are pleased you found our study to be well-written and relevant, and our analyses to be sound.

Nonetheless, I feel that the paper does not provide a deep understanding of the biological mechanisms behind homogenization after invasion and thus remains confirmative and descriptive. I think the authors can directly test the scenarios of homogenization that are nicely summarized in Fig. 5. For instance, the authors demonstrated that pairs of plots that share the same invading species tend to show more inconsistency between the metrics (Fig. 4, which by the way was difficult to interpret and I recommend revision. See my minor comment). This is a good start, and it seems to me that the authors can do similar

analyses to biologically explain the homogenization/differentiation patterns and when/why the abundance- and occurrence-based metrics do not agree (that is, the authors can do hypothesis-testing for the patterns summarized in Fig. 5). The authors noted in the discussion that the scenarios in Fig. 5 are not the only ones that cause homogenization/differentiation, but it seems that they can directly test these kinds of hypothesized patterns. This is just a suggestion, so I would leave its necessity to the judgment of the authors and the handling editor.

We are grateful you brought this up and your critique was shared by the editor Dr. Martins. In the updated manuscript, we now make specific predictions in the introduction about characteristics of the non-native and native species' pools that could generate discrepancies in homogenization/differentiation (lines 223-247, replacing figure 5) and test this with our data, resulting a new Figure 4 and expanded Results and Discussion sections.

Another major concern about the analyses is whether the authors considered the spatial proximity of paired plots. They nicely ensured that the pairs shared similar environmental conditions, but I could not read from the text how they treated the spatial distance, which is another major driver of beta diversity. Homogenization (lower beta diversity in invaded plots) would be concluded more if the invaded plots are more spatially concentrated than non-invaded plots are, simply because of dispersal limitation. The authors should guarantee that the paired plots are nearby enough (analogous to the similar environmental conditions) or the distance between plots is not much different between the invaded and non-invaded plots. Mapping the sampling locations would be also helpful.

Thank you for this point. In the updated version of our manuscript, we present a sensitivity analysis in which we matched invaded and uninvaded plots based on minimum spatial distance, which yielded very similar results to our environmentally-matched analysis, and we have included these analyses in Supporting Information Table S1 and Figure S2. We experimented with ways to map the plot matches, but given the large size and geographic scope of this analysisL, we felt the map did not provide tremendously useful information about the spatial distribution of the plots.

Minor comments:
L. 175: Related to my second major comment, what are the size of the ecoregions, and how many were there in the dataset? This kind of information would help readers to grasp the spatial scale of this study.

We have added this information at line 293.

L. 219: Was the vegetation data collected in the same spatial scale (plot size)? If so, how large were the plots? If not, the difference in the plot size could be very problematic for calculating beta diversity—In such cases, I think the authors should calculate beta diversity among paired plots with the same size.

We appreciate this concern and agree that different sampling protocols could strongly affect inference on beta diversity. In our updated analyses, we only match and compare plots within the same original dataset to control for size and sampling differences among plots.

L. 222: I could not see why the authors focused on the "absolute" difference. Please specify the motivation for doing that.

We originally included absolute difference as a metric in our analyses because it was one that Cassey et al (2008) reported in their theoretical analyses of the issues we discuss in this paper. In the updated version of the manuscript, we have separated our analyses comparing empirical data to their theoretical results from our analyses that seek out mechanistic explanations for why abundance and occurrence metrics contradict, and only include absolute difference as a metric for the former.

L. 247: "y=0 line" might be more appropriate than "x-axis". (also the "y-axis" in L. 250)

Thanks for this suggestion. We have made these changes.

L. 289: I was confused here. In the proceeding sentence, the authors concluded from the result that the abundance- and occurrence-based metrics generally agree. Why "consequently" do we have to consider the scale and application when deciding which metric to use?

The results of our case study, which shows that the metrics are more likely to disagree with increasing distance between plots (Figure 3c), now better illuminate the issue of scale, which we now say more explicitly before making this statement in lines (493-504)

L. 304: I think the line break is unnecessary.

We have reformatted our Discussion section and this line break no longer appears.

L. 317: (e.g., Figure 5; quadrants A, C) -> (e.g., Figure 5; quadrants A, B)?.

We no longer include Figure 5 in our analyses, and have replaced it with an introductory section: *What factors increase the likelihood of disagreements?*.

L. 345-37: I could not imagine the other causes of the difference in the abundance- and occurrence-based metrics in predicting homogenization/differentiation. Please exemplify some?

We agree that this statement was unclear and, with the shift in focus to additional analyses, we no longer include this paragraph in our Discussion

Fig. 4 c, d: I had difficulty interpreting the result. How about making the x-axis the category (multiple vs. same datasets or different vs. same invaders) and the bar proportions the matching pattern?

We have re-made Figure 4 (now figure 3) to reflect our new analyses and think the result is now much more clear.

USGS Interval Review:

Thank you for allowing me to review this manuscript comparing beta-diversity indices computed using occurrence- and abundance-based approaches. The issues and aims are clearly presented, the text and layout are well written and logical, the analyses are appropriate for the data, the interpretations are within the scope of what the data supports, and I found the conclusions compelling.

Thank you for reviewing our manuscript—we appreciate your time and effort. We are pleased you found the issues to be presented well, and the analyses and conclusions compelling.

Major comments:
Scale of previous studies is a large component of the Introduction. In the last sentence of the second to last paragraph in the Introduction I suggest including that your guidelines apply to scales of both small, localized systems and large, cross-system studies. In the Discussion I recommend including your perspectives on scale you gained from your extensive empirical comparison of the beta-diversity metrics.

Thanks for these suggestions. We have added text stating that inferences we make here are relevant across multiple scales (line 259) and added a paragraph discussing scale to the Discussion (lines 486-488)

I checked that the citations were included in the references and vice versa - all match. I noted where formatting changed in the references, which should be standardized to journal guidelines.

Thanks for checking on this. We have made these changes.

I included several minor comments throughout the manuscript, mostly identifying discrepancies in format and order.

L28: Suggest replacing with 'plots'.

We have made this change.

L61: Order here is alphabetical but chronological elsewhere.

We have updated our citations following the journal specifications.

L89: Reference format varies throughout the manuscript and needs to be standardized to journal format.

In our resubmission, we have cleaned up our reference formatting.

L104: This could apply across multiple plots or at a single plot sampled over time.

We agree with this point and have reframed this sentence to discuss occupancy-abundance relationships more broadly.

L105: Order switched.

We have now standardized the order of these statements throughout the manuscript.

L134: Should this include a hyphen?

We have added hyphens throughout the updated manuscript.

L136: Should this be hyphenated?

We have added hyphens throughout the updated manuscript.

L138: Check that these guidelines include issues of scale -- small, localized systems vs large-scale, cross-system studies. Suggest including mentioning scale here as it was a large part of the Introduction.

We have added this point at line 259.

L152: Not sure how space fits in with the paired plots. I suggest including space in a separate sentence that will help set up the space-for-time approach you use.

We removed this phrase (now line 264) and elaborate further at lines 268-271.

L154: Interesting choice of words. I think 'yielding' would be better.

We now say "yielding" here (line 267).

L161 & L163: Depending on journal requirements you may need to provide the full database name.

We now provide the full database name at the first mention on lines 214 and 276

L178: The other variables are obvious, but suggest you include a sentence describing the human modification index.

We have added a citation describing this index at line 293.

L258: Throughout the Introduction, Methods and most of the Results the calculations are listed in occurrence- and abundance-based order. I suggest standardizing the order.

We have standardized the occurrence-abundance order throughout

L265: Should this include a hyphen?

We have added this hyphen.

L270: Order switched

We have standardized the order with the rest of the manuscript.

L395, 438, 440, 476, 481: Check this format--all caps

We have cleaned up our reference list.

L502: Throughout the Introduction, Methods and most of the Results the calculations are listed in occurrence- and abundance-based order. I suggest standardizing the order.

We have standardized the occurrence-abundance order throughout.

L510: Should this include a hyphen?

We have added this hyphen.

L522: Consider replacing with 'occurrence'.

We now say occurrence here (line 753)

L530: Should this include a hyphen?

We have added this hyphen.