Dear Dr. Eric Harvey,

Thank you very much for handling the revised version of our manuscript. We are glad to see that you and the reviewers saw great improvements on the previous version. We are also glad to say that we have implemented almost all suggestions you all made. Please find bellow a response to every comment and suggestion made by you and the reviewers.

Hope you find that this new version is appropriate for recommendation. But in case you think more revisions are need, we will be happy to work on another version of the manuscript.

All the best,

Tadeu Siqueira, on the behalf of all authors.

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Round #2

Decision

by Eric Harvey, 2019-05-14 16:38
Manuscript: https://doi.org/10.1101/515098 version 1.2

Decision on prepint 515098 for PCI Ecology recommendation

Dear Dr. Siqueira,

I am happy to announce that your article entitled "Community size affects the signals of ecological drift and selection on biodiversity" is accepted for recommendation at PCI Ecology pending minor revisions. We therefore invite you to revise and resubmit your final manuscript version. The manuscript will not be sent for further peer review.

Both reviewers and myself were satisfied with the way each earlier concern was addressed. There are still some minor concerns from one reviewer and myself about clarity, especially related to the justification behind using both incidence-based and abundance-based metrics, expectations and interpretation of the results. There is also a point raised by myself and one of the reviewer about the habitat heterogeneity co-variant and the way it is interpreted (or should be) in the light of the negative relationship between beta-deviation and community size that needs further clarifications. I would invite you to consider especially those points, but also others raised by the two reviewers and myself, which I think could improve the manuscript.

The two reviewers comments are attached to this email and my own comments are copied below,

Best wishes, Eric Harvey, Recommender at PCI Ecology,

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Minor comments on "Community size affects the signals of ecological drift and selection on biodiversity"

Introduction

[from line : to line]

[92:96] This would effectively mean that small communities could maintain high diversity via neutral co-existence (on the long term leading to one dominant species, of course). Diversity in smaller communities could even be higher than in larger communities where convergence to dominance by a few strong competitors might occur faster without disturbance. (just a general point to consider - no need to modify anything here).

R. Thank you for the comment.

[180:241] This new addition is great! I think the writing is a bit unclear and should be clarified. For instance for E1 and E2 it would be clearer, I think, to refer to predictions for 'beta-diversity' and 'beta-deviation' rather than 'beta-diversity' and 'null expectations' - to be coherent with the text above in terms of wording.

R. Done.

[184:189] Would not it be as likely that largest communities would have lower beta-deviation than expected by chance? The authors reject that possibility right away, but in both case (lower or higher than expected by chance) niche selection and dispersal rates could be the main processes. There are two things to consider I think: (i) the scale of habitat heterogeneity (HET): if within sampling site HET is very high vs. among sites (in one watershed) - then niche based processes should lead to lower dissimilarity than expected by chance, while if HET is low within site, but high among sites - then niche based processes should lead to more dissimilarity than expected by chance. (ii) dispersal: sufficient dispersal will work along with the species sorting scenarios mentioned at point (i) but very high will lead to mass effect (and thus lower dissimilarity than expected by chance) while limiting dispersal will lead to higher dissimilarity than expected by chance. Because you are testing for HET with the PERMDISP, then it can give an idea whether results are influenced by HET or dispersal. For instance, negative beta-deviation with community size, with no HET effect could only be explained by high dispersal limitation, right?

R. We agree with everything you said in (i) and (ii). But we think differently about the last sentence. Negative beta deviation – i.e., communities are less dissimilar than expected (i.e., they are more similar) with no effect of HET would be the result of excessive dispersal. As you said, high dispersal would lead to mass effects, and thus to lower dissimilarity than expected by chance.

[240:241] "are also expected to increase b-diversity" - remove "be"

R. Done.

Figure 1 nice figure! I guess the red and blue points represent subtropical vs. boreal locations but this should be stated in the legend. Also for E1 to E3 on the second panel of figure 1 - should it be 'beta-deviation' instead of 'beta-diversity'?

R. We included the colors in the legend. Regarding beta-diversity vs beta-deviation, we are not sure. Beta deviation is the departure of beta diversity from null expectations. So, we think it would not make sense to say that beta deviation is close to or far from null expectations. So, we kept that text unaltered.

Methods

I am very satisfied with the changes. The two beta-deviation procedures are very well explained and Figure S1 help to clarify.

The only thing I would add is a justification of using the two different beta-deviation methods (as mentionned by one of the reviewer that part of the study still remain unclear and poorly justified). The text describes well how they are technically different, but what were the authors trying to compare or to gain from using both methods? That would help to build up expectations for each approach in terms of processes and mechanisms and to interpret the results.

R. We think this justification is stated in the third paragraph of the introduction, where we described the differences between incidence- vs abundance-based dissimilarity coefficients and stated how they can complement each other (L 87 - 110). Do you think it is necessary to reinforce some of those ideas in the method also? In general, we decided to use both methods because of the reasons explained in the Introduction section (e.g., variation due to changes in relative abundance can be captured with the use of abundance-based indices only) and we think it would be inadvisable to set new expectations after knowing the results.
We included the following sentence in the paragraph describing abundance-based beta-deviation.

"*As selection and drift act on individuals, but not adding or removing entire populations, the use of abundance-based metrics should provide complementary information about assembly mechanisms. Thus, to estimate abundance-based β-deviations, we followed the procedure described by Kraft et al. (2011):...*"

Results

line 489 and 491-492 are stating the same information, I think.

R. We removed this sentence: *Raup-Crick (incidence-based) β-deviation was negatively related to community size in Brazil (Table 1)*.

[494:495] That's interesting - I would have expected environment heterogeneity to explain the beta-deviation results - otherwise what sort of niche-based processes can explain the results? (dispersal as mentionned above or is it that the heterogeneity variable used is simply missing the important piece of the environment that might drive the pattern? As mentionned by one of the reviewer - this should be clarified)

R. We are not completely sure about the reasons behind this lack of relationship. The whole beta deviation approach indicates that ecological drift plays a major role in smaller communities, whereas in larger communities, niche selection should play a more important role. However, environmental heterogeneity within watersheds (sets of five streams) was not related to beta-deviation. We think this is because we might have failed to measure key abiotic and biotic variables (e.g., biological interactions) underlying community variation. Alternatively, despite including key correlates of beta diversity, our snapshot analysis might not have been enough to represent the complexity of all mechanisms involved in niche selection within watersheds. We included this last sentence in the introduction.

[524:525] "species abundances AND genus composition" Since Raup-crick is negative with community size I would expect that the positive relationship with Bray-Curtis beta-deviation could only be explained by the abundance turnover part of Bray-curtis, right? (i.e., Raup-crick covers the composition only turnover part and it goes in the opposite direction)

R. Done. Yes, we agree that the positive relationship with Bray-Curtis b-deviations is due to variation in relative abundance distributions.

[603:605] Beta-diversity would give that information but, here, should not that be rephrased as something like: "This suggests that departure from null expectations related to compositional change is similar in..." ?

R. Done. Thanks.

Discussion

[704:741] Statements in this paragraph are correct. But since environmental heterogeneity did not correlate with bray-cutis beta-deviation, I am wondering what the authors think could be the main driver of selection in those system that could explain higher dissimilarity than expected by chance in the largest communities (if not dispersal limitation nor among-sites habitat heterogeneity)?

R. We do not know. Again, we might have failed to measure key abiotic and biotic variables (e.g., biological interactions) underlying community variation. Alternatively, despite including key correlates of beta diversity, our snapshot analysis was might not be enough to represent the complexity of all mechanisms involved in niche selection at this watershed scale. We think anything beyond that would be very speculative.

[763:765] That means that within watershed environmental heterogeneity does not explain the negative relationship between beta-deviation and community size.

R. Indeed.

[784:824] Very good paragraph with nice additions.

R. Thanks.

[854] stochastic processes: I would add between parenthesis that the study refers to stochastic processes related to changes in richness and abundances.

R. Sorry, we could not find the part of the text you referred to. Maybe line numbering did not match.

[863:864] given no effects of environmental heterogeneity in the results - I am not sure what are the evidence for local environmental filtering in the results?

R. The evidence we have to support the role of local environmental filtering is that abundance-based beta deviations were positive and high. This alone suggests that communities are more dissimilar than expected by chance in terms of variations in species relative abundances, which could be a consequence of two processes: niche selection (e.g., via environmental filtering) and/or dispersal limitation. We exclude the possibility of dispersal limitation playing a major role because incidence-based beta deviation was negative, meaning that communities were less dissimilar than expected by chance in terms of variations in species composition. The absence of a relationship between beta deviation and environmental heterogeneity cannot be used alone to disregard the role of niche selection completely.

Finally and this is just for the sake of the discussion, I will quote here a comment I made in the previous round of revision and the authors reply. After I will respond to that reply (nothing needs to be changed here):

< Comments. The results suggest that smaller communities should have higher beta-diversity but also higher < local richness compared to larger communities dominated by a few species. I apologize for the self-advertisement < (I generally avoid to do this), but in that case I feel like this recent study would be very relevant to cite: < “Harvey Eric, Gounand Isabelle, Fronhofer

Emanuel A., and Altermatt Florian. 2018. Disturbance reverses classic < biodiversity predictions in river-like landscapes. Proceedings of the Royal Society B: Biological Sciences < 285:20182441." - but I will leave this at the authors discretion (this is only a suggestion). < Response. That was not the case. Smaller communities should have lower species richness and higher beta < diversity if there are mainly driven by drift. The point here is that each locality has a different set of < (reduced) species composition, making beta diversity higher. Also, with low richness, even one local extinction < of species affects pairwise dissimilarities strongly while does not so in high richness. In larger communities, < local species richness is higher, but a set of species with high fitness occur in most of the >localities, < making beta diversity lower.

In a sufficiently large regional pool, I could easily imagine smaller communities having higher species richness than larger communities but still having higher beta-diversity. Imagine that smaller communities experience higher drift because of constant disturbance reducing community size, leading to neutral co-existence (as mentioned in your manuscript), while larger communities experience no disturbance and higher dominance. This could effectively lead to higher richness in smaller communities. You could still have higher beta-diversity among the smaller communities however because of random extinctions and turnover (i.e., replacement from the regional pool). The same would be true, however, just with random demographic variations without actual extinctions (if you use a beta-diversity indice influenced by relative abundances). I am happy to continue that discussion.

R. This is indeed a good discussion. Theory suggests that if ecological drift is the main process structuring a local community (no matter it is small or large), one species would eventually dominate in the long term. In nature this does not happen very often as there is dispersal from other communities and also disturbance. Besides that, larger communities can be defined as those having more individuals per area, as we did, or simply by measuring total area (as other authors have also done). The larger the number of individuals (or area) the higher species richness. Maybe we could join our efforts to think about experiments and/or simulations to test these ideas. Thanks again for your comments.

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Reviews

Reviewed by Kevin Cazelles, 2019-04-28 23:09

I have enjoyed reading the new version of this manuscript. I think that Dr. Siqueira and colleagues have carefully addressed the large set of comments we collectively (the recommender and the two reviewers) made. I am overall satisfied with the response to my own set of comments and many additions done by the authors are very helpful. The current manuscript reads well, and in my humble opinion, this version of the manuscript is very close to be a publishable manuscript (and so, close to be recommended by PCI). For this round of review, I have very few suggestions to further improve the manuscript.

R. Thanks. We are very glad to hear that you enjoyed this new version.

- l.114-115, I would add "two": "[...] in two climatically highly different regions [...]".

R. Done.

- l. 117-119: I suggest to slightly reword the two sentences.
  - The first sentence should mention the existence of the community size gradient and describe it. It would make a lot of sense to include the following part: "the smallest boreal stream communities are as large as the largest tropical communities" that is currently mentioned l. 140-141. This is important because the reader need to be aware of this early in the manuscript to understand the expectations after.
  - The second sentence should only describe the first expectation (E1).

R. Done. The sentences read like this now: "*This allowed us to make specific predictions considering a community size gradient. Our previous study showed that local community size is, on average, five-fold larger in boreal than in tropical streams, with the smallest boreal stream communities being as large as the largest tropical communities (Heino et al. 2018). Thus, we expected that β-diversity would be high (E1) and close (E2) to null expectations (random assembly from the regional pool) in watersheds with the smallest communities (some watersheds in Brazil only; Fig. 1).*"

- I would slightly reword the expectations:
  1. E1 should state that departure from null expectation is high for large community and small for small communities (because of the choice of the null model);
  2. E2 should be about the sign of that departure for large community (positive or negative deviation);
  3. E3 will be clear enough once the part about the community size gradient between the two regions is made clear at that point of the manuscript.

To be clear about the changes for E1 and E2, below are the changes I would make to lines l.119-124:

[...] we expected that (E1) β-diversity would be high and close to null expectations KC: I would remind the reader of the nature of the null model in watersheds with the smallest communities (some watersheds in Brazil only; Fig. 1). This would indicate that ecological drift plays a major role in structuring these small subtropical communities. Second, all else being equal, we expected that (E2) β-diversity in watersheds with the largest communities in Brazil and Finland would be far from null expectations KC: this first part of E2 should actually be part of E1 , but lower than in the smallest watersheds (Fig. 1).

R. Done. Now the text reads like this: "*Thus, we expected that β-diversity would be high (E1) and close (E2) to null expectations (random assembly from the regional pool) in watersheds with the smallest communities (some watersheds in Brazil only; Fig. 1). This would indicate that ecological drift plays a major role in structuring these small subtropical communities.*"

***Second, all else being equal, we expected that (E2a) β-deviation would be positive in all watersheds, but higher in the largest communities (Fig. 1)*".**

- l. 323-334, I would again recall what are the null expectations here (what is the null model used to generate them).

R. We think the previous ("*Based on null models, our estimates of β-diversity accounted for both differences in species richness and species relative abundance that deviate from random assembly (i.e., β-deviations).*") and following ("*This means that the high β-diversity we observed among smaller communities was, to some extent, indistinguishable from patterns generated by random changes in local genus richness and community size.*") sentences explain the nature of the null model.

- Figure 1: I would add the meaning of the colors in the caption.

R. Done.

- I think the authors should combine Figure 1 and S1 (and maybe S2), this would be a great summary of the methods and expectations.

R. We tried that. The figure was huge as a whole, but some of its parts, including text, were very small. So, we decided to keep the current format. Thanks again for your comments on both rounds of reviews.

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Reviewed by Romain Bertrand, 2019-05-09 17:06

I found significant improvements in this new version of the manuscript. It is well written (the introduction is really informative and the method is clearer for me). The results are still original, and I see great potential for this work. Moreover the replies of the authors to my previous commentaries are well argued. However, I still believe that discussion could be improved. I give some ways to do that below.

All the best, Romain Bertrand

R. Thanks. We are glad to hear that you found this version was improved.

NB: line numbers used below do not consider correction in the manuscript.

Main concern:

The discussion is quiet confusing for me sometimes. I think the authors can improve it notably by:

- explaining the reason which could lead to different effects of community size on incidence- and abundance-based beta deviation. In the current version of the manuscript the authors detailed potential causes of the negative and positive effect of community size on incidence- and abundance-based beta deviation independently. So the authors did not really confront these opposite results. Why niche selection increased difference in species abundance composition but not in species occurrence? May be it's a matter of environmental sensitivity... Observing changes in species composition (occurrence) among communities required likely more environmental heterogeneity than changes in species abundance. The authors could discuss this point, notably by shorting lines 385-417 to save some space.

R. We think we have explained the reasons for the differences we observed when using abundance- vs incidence-based beta diversity. For example, here:

"*Thus, in terms of which genera were more abundant or less abundant, and more aggregated or less aggregated, communities within the same watershed differed from each other more than expected by chance, especially in mid to large communities. As dispersal within watersheds was likely not limited, this positive relationship indicates that niche selection was sufficient to cause non-random variations in genera relative abundance and aggregation patterns among large communities. We suggest that as community size increases, demographic stochasticity becomes less important and selection determines which species are more abundant locally and widely distributed within the metacommunity. In this case, small random variations in the number of individuals of relatively abundant genera occurring in larger communities, which can only be detected with abundance-based β-diversity metrics, do not result in major changes in genus occurrence*."

And in the following paragraph:

"*Indeed, although small communities had (Raup-Crick) β-deviations values close to random assembly expectations, as we expected, the relationship between incidence-based β-deviation and community size was negative in Brazil. This result contradicts our expectations and indicates that the genus composition of streams harboring mid to large communities in tropical watersheds is less dissimilar (negative values of β-deviation) than patterns predicted by random assembly – i.e., these communities share more genera than expected… First, dissimilarity should be low when niche selection is spatially constant, as the environment maximizes the fitness of a few species (Vellend 2016)… Thus, it is likely that even the large size of boreal communities was not sufficient to allow niche selection to be the main driver of spatial variation in genus composition among those communities*."

And finally, here:

"*The magnitude of β-diversity deviation from the null models (negative and positive values) and how it related with community size (negative and positive slopes) indicate that stochastic and deterministic processes affect species occurrences and their abundances differently. While incidence-based β-deviation was negative and decreased with community size in Brazil, abundance-based β-deviation was positive and increased with community size in both regions. These results indicate that: (1) as communities get larger, demographic stochasticity plays a less important role and excessive dispersal combined with niche selection tend to homogenize the genus composition of larger communities; and (2) variations in genera relative abundances are the result of local environmental filtering*."

We slightly modified this last sentence to accommodate your suggestion:

"…(*2) niche selection was strong enough to produce variations in genera relative abundances, but not to determine compositional changes among communities within the same watershed*."

- by discussing expectation 3. What about the non-linearity vs the linearity relationship between beta- deviation and community size? If it's not important, the authors could remove this expectation.

R. As text was already long, and this was not a central part of the manuscript, we decided to remove it.

-the authors could be more direct in some parts.

R. We reviewed the text again and fixed some sentences following suggestions of the reviewers.

Minor comments:

lines 100-101: "...as estimates of β-diversity; these are called beta deviations hereafter."

For me the index comparing beta diversity to null expectation is not beta diversity. I think it's better to use directly beta deviation.

R. Done. Now the text reads like this: "*A solution to the first issue is to use a null model to produce expected values under random assembly from a large species pool, contrast observed and expected values and use the difference between them as estimates of β-deviation; i.e., the extent to which β-diversity departures from null expectations (Kraft et al. 2011, Myers et al. 2013, 2015, Catano et al. 2017).*"

Line 148: "...to be increase..." => to increase Line 149: Refer to Fig S1.

R. Done.

Lines 157-158: "watersheds dominated by agriculture (mainly pastures, and Eucalyptus and Pinus plantations)" => I propose to change 'by agriculture and forestry".

R. Done.

Fig. 1:

-Is color necessary? If yes please give color meaning in legend.

R. Done.

-E3 => the authors talked about beta diversity in fig 1 while they talked about beta deviation at lines 142-145.

R. We excluded E3 from the manuscript, following your suggestion (bellow).

- this figure is good and informative to add. But I was quiet confused when I saw the results because in Fig 1 the authors presented relationships grouping both region in a same fitted model while it's not the case in the results. By doing this it's like some expectations consider that Brasil and Finland inform two successive parts of the relationships. But the authors did not test for that in their analysis. May be the authors can verify such expectation of continuous pattern from Brasil to finland observations. But it means that the averages of beta deviation and diversity values at similar community size are closed or equal, and I am not sure it's the case when I look to the results. The authors have two options: 1) test for that expectation or 2) modify Fig1 and/or provide more explanations.

R. We modified the figure, also considering your suggestion about removing E3.

Line 219: "...β-deviation per region, with one value per watershed". I propose to add "incidence-based β-deviation".

R. Done.

Lines 243-246: What is the satellite? The image resolution? Give these information or at least a reference if the method has been already described.

R. Done. "*We mapped land use and land cover of Brazilian and Finnish watersheds using 5-m resolution RapidEye multispectral imagery and the CORINE database (https://land.copernicus.eu/pan-european/corine-land-cover), respectively*."

Lines 249-250: The authors should provide correlation among covariables in order to evidence no multicollinearity in data.

R. We included this sentence to accommodate this comment: "*In tropical data, the strongest correlation between explanatory variables was between environmental heterogeneity and spatial extent (r = 0.47), whereas in the boreal data, it was between community size and spatial extent (r = 0.36). All other correlations were lower than 0.07.*"

Results: For some results authors concluded if results supported or not the expectations presented in Fig. 1., but not for every analysis while it could improve the understanding of the results and give to the reader better chances to follow how the authors conducted the work.

R. We now indicate support or lack of support for our predictions following the description of our results.

Lines 277-278: "Beta diversity of tropical smaller communities were closer to null expectations than those of larger communities (Fig. 3)".

I propose to add: "Incidence-based beta..."

R. But here we are referring to both coefficients of beta diversity, not only incidence-based. In both cases, beta diversity of tropical smaller communities was closer to null expectations than those of larger communities.

Line 278: Fig. 3 => Fig. 3A

R. Done.

Table 1:

-use the same abbreviation in FigS1 and table 1.

R. Done.

- "b = standardized partial regression coefficient." => What does "partial" mean? I think it's a standardized regression coefficient.

R. Yes, we changed to standardized regression coefficient.

Line 283: Fig. 3 => Fig. 3A Line 292: Fig. 3 => Fig. 3B Line 313: Fig. 3 => Fig. 3A

R. Done.

Lines 329-330: " We showed that β-diversity of smaller communities deviates less from null expectations than larger communities".

I agree with the authors for abundance based beta deviation. But for incidence based beta deviation I have a doubt because the range of beta deviation values between Brasil (smaller community size) and Finland (larger community size) are quiet close. Could the authors explicitly test for this difference or use a less general sentence? This comment need to be consider in the abstract too (line 34).

R. We now use a less general sentence, although the only case where we did not find this was for incidence-based beta deviation in Finland. The text now reads as this (abstract): "*Beta diversity of tropical small communities was consistently higher but closer to null expectations than β-diversity of large communities*."; and like this (main text): "*We showed that β-diversity*

***of tropical smaller communities deviates less from null expectations than larger communities*.”**

Lines 342-344: “...and because dispersal ability is highly variable among species in riverine systems (Heino et al. 2015b, Tonkin et al. 2018a),...”

But it’s not the case here as the authors argued that dispersal is not limited in your system (see lines 359 and 385-417).

R. Yes, but even considering high dispersal rates, some species will disperse more than others.

Lines 345-356: may be it will be easier and more informative to test if species abundance varies with community size.

R. We do not think this is the case, as species abundance was used to define community size. Thus, such a test would be circular.

Lines 364-366: “As dispersal within watersheds was likely not limited, this positive relationship indicates that niche selection was sufficient to cause non-random variations in genera relative abundance and aggregation patterns among large communities.”

So if it’s the case why the authors didn’t observe any effect of environmental heterogeneity in the model?

R. We are not sure. One possibility is that we might have failed to measure key abiotic and biotic variables (e.g., biological interactions) underlying community variation, or despite including key correlates of beta diversity, our snapshot analysis might not have been enough to represent the complexity of all mechanisms involved in niche selection in watersheds. We included these possibilities in the discussion.

Line 367: “... selection...” => niche selection?

R. Done.

Line 372: please add “incidence based” for a better understanding.

R. Done.

Lines 379-382: “The streams sampled in Brazil and Finland ... structure of stream communities (Hynes 1975, Allan 2004, Roque et al. 2010, Siqueira et al. 2015)”

May be not necessary. I didn’t understand why the authors referred to environmental difference among watersheds while the results should be more discussed considering environmental heterogeneity within watersheds to explain the low species composition dissimilarity within metacommunity.

R. We agreed and deleted these sentences.

Lines 385-389: "This suggests a tendency towards environmental determinism; ... to be the main driver of spatial variation in genus composition among those communities"

Ok but incidence-based beta deviation is still negative. So it's like despite the authors observed an effect of environmental heterogeneity, it is not able to strongly differentiate community composition within metacommunity.

R. We agree and think the following sentence reflects this idea: "*Thus, it is likely that even the large size of boreal communities was not sufficient to allow niche selection to be the main driver of spatial variation in genus composition among those communities*."

Lines 418-419: "If our watersheds were larger (in extent), dispersal limitation would likely have played a role and niche selection could have been the major driver of community structure."

But watersheds of 500 by 300km in Finland are quiet large enough and should evidence dispersal limitation, isn't it?

R. This (500 by 300 km) is the extent of the whole study area in Finland, not of one watershed. As stated in the methods section: *"In Brazil, maximum distances between pairs of streams within watersheds varied from 2.48 to 8.86 Km, whereas in Finland it varied from 12.77 to 109.5 Km.*"

Lines 456-457: "variations in genera relative abundances are the result of local environmental filtering" => "variations in genera relative abundances are LIKELY the result of local environmental filtering"

R. We modified this sentence to: *"…(2) niche selection was likely strong enough to produce variations in genera relative abundances, but not to determine compositional changes among communities within the same watershed."*

Thanks again for your detailed comments and suggestions.