

In this manuscript Tadeu Siqueira and colleagues test the hypothesis that small communities are more dissimilar among each other because of ecological drift than large communities, which are mainly structured by niche selection. They investigate this issue from in situ ecological observations (combining biodiversity and environmental data from boreal and tropical streams). They used linear models to test the effect of community size on beta diversity, incidence- and abundance-based beta deviations (that are metrics comparing observed beta diversity to null expectations). As expected from theory and recent experimental evidence, they demonstrate that small communities are more driven by random processes than large communities. As a consequence, the authors suggest that ecological drift plays an important role in small communities by increasing the chances of species with low competitive ability to occur within the metacommunity. They conclude that environmental pressures will make smaller communities more vulnerable to novel conditions and community dynamics more unpredictable, as random demographic processes should prevail under these conditions.

The article is well written and results are original and of interest for community ecology. However I have two main concerns which can lead to conduct more analysis, clarify or revise some assumptions, interpretations and conclusions. The most important concern is about expectation and interpretations of deterministic drivers underlying beta diversity, but it does not challenge the main result of the study, that is beta diversity in small communities is more driven by random processes than in large communities.

All the best,  
Romain Bertrand

Main concerns:

1) Assumptions and interpretation about deterministic drivers underlying beta diversity:

- Tested expectation/assumption number 2: "Second, we expected that watersheds with larger communities in Brazil would have lower values of beta diversity compared to smaller communities, but high positive values of beta deviation. This would indicate that niche selection and sufficient dispersal rates are the main processes resulting in large communities to be more dissimilar than expected by chance."

I don't have the same interpretation that the authors. When beta deviation is greater than 0, ecological or biological processes lead to higher community dissimilarity than expected by chance only (Chase et al. 2011). The main deterministic drivers that can explain such a pattern are niche selection inside the focal area (the watershed in the present study) and when dispersal among sites is low (leading to dispersal limitation). So why the authors consider that sufficient dispersal rate lead to dissimilar communities? May be it's just an error and authors wanted to say "insufficient"?

- Tested expectation/assumption number 3: "Finally, because the smallest boreal stream communities are as large as the largest tropical communities (Heino et al. 2018), we expected that boreal communities would show a weak or lack of relationship between (positive) values of beta deviation and community size. This would indicate that deterministic niche selection is the main processes determining the structure of boreal communities because boreal stream insect communities are usually large enough and not subject to strong demographic stochastic effects."

I don't really get the justification of this expectation. It's like the authors expect a non linear relationship between beta deviation and community size, with a community size effect decreasing as increase the community size. Authors have to explain a bit more their expectation and used previous works to justify their choice. Furthermore, is species diversity the only factors which could explain such a pattern in the present study? I mean authors compared two different regions with contrasted community size that do not overlap at all. So how to be sure that increase in community size is the only factor which can explain a weak or lack of relationship between beta deviation and community size? It could be the difference in environmental condition between region. To properly tested for that authors should investigate the relationship between beta deviation and community size within a region with large range of community size (from low to very large community).

-In the introduction, authors explained that “we need estimates of beta diversity that account for differences both in species richness and species relative abundance”. So authors presented results for incidence- and abundance-based beta deviation, and demonstrated opposite relationships of these metrics with community size (and contrasting effects of environmental heterogeneity). But they did not discuss these differences. Moreover, the authors described general expectations in the introduction which did not depend to the kind of beta deviation investigated. So it strengthens the intriguing characteristic of the results. Why incidence-based beta deviation is negative and increase (at least in tropical regions) with community size while abundance-based beta deviation shows the opposite? Which results we have to consider in priority or are the most robust to explain beta diversity variation? May be both analysis because they provide complementary information... Moreover, sometimes authors mixed results of incidence- and abundance-based deviation to validate their expectations. The authors expected high beta deviation values in large subtropical communities, and a positive relationship between beta deviation and community size. They verified this expectation for abundance-based beta deviation only. Then, the authors expected a weak or lack of relationship between values of beta deviation and community size in boreal streams. In this case, they verified this expectation for incidence-based beta deviation only (I also noted that in this case, the authors expected such a pattern for positive beta deviation values but here authors reported negative values...). Why considering incidence-based beta deviation to validate some expectation and abundance-based beta deviation in other case?

- What factors drive the increasing or decreasing relationship between beta deviation and community size? In case of abundance-based beta deviation, authors considered that “niche selection was likely sufficient to cause non-random variations in genera relative abundances among large communities” because positive beta deviation values increase with community size. In case of incidence-based beta deviation, authors considered that “large size of boreal communities allowed niche selection to be strong enough to drive spatial variation in genus composition among communities” because negative beta deviation is unrelated to community size. Two different results but same interpretation. Why? In the last case, authors found a positive relationship with spatial heterogeneity which suggests niche selection. But how authors can explain that niche selection occurs while beta deviation values are negative ? It would mean that niche selection structured the difference in species composition among communities but that high dispersal rate has a higher effect leading to more similar community than expected by chance. If authors have this interpretation, please write it clearer. Moreover, “if environmental filtering is strong, sites with similar environmental conditions should be more similar than expected, while sites with dissimilar environmental conditions should be less similar than expected. Likewise, when dispersal limitation is strong, nearby pairs of sites will be more similar than expected, whereas distant pairs of sites will be less similar than expected” as explained by Chase et al (2011). So why environmental heterogeneity has a significant and positive effect on beta deviation in only one case while authors seems to consider that niche selection is a strong driver of community dissimilarity? In the fourth paragraph of their discussion, the author discussed the effect of high dispersal rate as a potential drivers explaining higher similarity in species composition among communities than expected by chance. I fully agree with the discussion but why authors did not find any effect of the “spatial extent” variable (ie the distance average among communities within a watershed)? Finally, in introduction and summary authors talked about interaction among factors (such as ecological drift and niche selection for instance) driving species assemblage. But this interesting idea is quickly abandoned in the rest of the article. While it’s not presented directly like this, my view of the discussion is that interaction between niche selection, dispersal rate and ecological drift determine species assemblage in the study. It is likely that community size modulates the effect of niche selection and dispersal rate on species assemblage (as the authors suggested in some parts, eg “community size ... may mediate the interplay between deterministic niche selection and ecological drift as drivers of beta diversity in tropical and boreal metacommunities”). Authors can and should test for that directly by adding interacting effect between community size and environmental heterogeneity as well as between spatial extent and community size. Considering the current interpretation of the

authors, we can expect that the effect of spatial heterogeneity and spatial extent increase with community size. It will demonstrate that large community size are more determined by deterministic processes. Be aware that environmental heterogeneity captured the abiotic dimension of the niche selection but not species interaction, as well as that distance used to compute the spatial extent should consider the kind of dispersal of the genera studied (fly, stream vector, ...).

## 2) Controlling or correcting for sampling bias in beta diversity metrics:

The authors compared species assemblages among different streams, watersheds and regions which are characterized by different habitat characteristics. As a consequence, depth, width and velocity of streams are likely different. The authors have corrected one of their community metrics by the stream width to account for habitat size. It's a good point to do that because larger is the sampled habitat size higher is the probability to catch individuals and new species (or genera in their case). But stream width is only one dimension of the habitat size. May be it is more important to account for both stream velocity, depth, and width in order to correct metrics by the volume of water filtered during sampling (more they filter water higher is the probability to observe individuals and species; except if high stream velocity is considered has an environmental pressure which constrain species diversity and abundance). Difference in water volume filtered among streams could artificially increase the beta diversity of watershed as well as the difference of beta diversity among watersheds, and as a consequence bias the results. One solution could be to correct metrics but in this case why authors have corrected the size community metric only while beta diversity is likely impacted by this potential bias too? Another solution could be to not correct metrics. For example, they could use linear mixed effect model with a qualitative variable in random effect controlling for habitat size.

Minor comments:

### INTRODUCTION:

-“A solution is to use a null model to produce expected values, contrast observed and expected values and use the difference between them as estimates of beta diversity; called beta deviations hereafter (Kraft et al. 2011, Myers et al. 2013, 2015, Catano et al. 2017). In this case, positive and negative values of beta deviation indicate that communities are more dissimilar and less dissimilar than expected by chance, respectively. Beta deviation values close to zero indicate communities are as dissimilar as expected by chance (Kraft et al. 2011, Chase et al. 2011, Catano et al. 2017, Petsch et al. 2017).”

Here, authors provide only a solution for the first issue described (sampling bias) but not the second one (beta diversity index accounting for both compositional and abundance changes).

- may be at the end of the introduction authors could briefly tell that they study the issue through a modeling approach testing for community size, environmental heterogeneity and spatial extent. I mean we know that authors consider these two last variables since methods only while it's an important good point for the present study. Added that in the summary could be good too.

### METHODS

-authors should provide maps in SI in case of readers have no access to Heino et al. 2018 (like me).

-Regions have the same areas? And watersheds? I mean if there are high differences in areas it could impact beta diversity among watersheds as well as the species pool, and as a consequence the results.

-“Also, we estimated the median population size per stream, average it within watersheds, and defined it as another measure of community size.” What is population here? The number of individuals belonging to a genus?

-“Fitted models provided similar results with all measures of community size and, thus, we show here results based on the former measure.” So authors presented results based on the community size corrected by habitat size?

-incidence-based beta deviations: "beta-deviations were calculated as an index rescaled to range between -1 and 1". OK but how did authors compute the beta deviation concretely?

-abundance-based beta deviations: "the (local) total abundance": is it the community size, ie the total number of individuals?

-why accounting for species frequency occupancy in incidence-based beta deviations but not for abundance-based beta deviations when computing null model?

-"Results were similar with both definitions of species pools, and thus we only show results based on the former definition." So authors presented results based on region?

#### -DISCUSSION:

-"probably together with deterministic assembly processes, as beta deviation values were different from zero"

Difficult to really judge because authors did not test for that. May be they could look at the significance of the intercept. If it is different to 0, it likely means that community diversity differences are more determined by non-random processes even in case of smallest communities. If it is not the case, so random processes drive differences between genus diversity among communities.

-"Also, in general, these results are in line with our predictions,"

expectations/assumptions sound better than predictions.

-"dissimilarity should be low when niche selection is spatially constant (e.g., harsh conditions within the metacommunity, Chase 2010)".

Authors refereed to a specific example with low environmental heterogeneity (as they wrote) but with extreme conditions which can strengthen low beta diversity. In this case it's more the high environmental pressure which explain low beta diversity than spatially homogeneous environmental conditions.

-"Flenner and Sahl (2008) estimated annual range expansions of up to 88 km" => range

-"If these inferior competitors have high dispersal rates, a trade-off suggested by theoretical models (Cadotte et al. 2006), then they would have a higher chance to occur in some small communities within the metacommunity." In this case authors refer to small communities where stochastic processes are predominant. So why talking about "high dispersal rates" while dispersal rate is by definition non constraining for species assemblage in case of stochasticity?