Dear editor and reviewers,

We thank you for your time and effort reading and commenting our manuscript. We have fully revised it in the light of your remarks, with a particular effort on refocusing the manuscript on our main question and streamlining the whole text accordingly. Due to the deep rewriting of our manuscript, we did not provide a version in tracked change mode, which was too difficult to read and use.

We have extensively explained our revision below, intertwining our answers (in bold, blue font) with your questions, comments and remarks. We hope that you will find this new version easier to follow, with clear hypotheses and predictions matching each of our results.

We are very much looking forward to reading your opinion about this new version,

Yours sincerely,

On behalf of all the authors,

Fabien Laroche

Decision by Damaris Zurell, 2019-07-19 15:53

The preprint "Simulated neutral metacommunities support the habitat amount hypothesis" uses a neutral metacommunity model to simulate communities in fragmented landscapes, and based on these simulated data the authors test the relatedness of different connectivity indices and their value in explaining species richness. Two independent reviewers have assessed the preprint and both acknowledged the ambition and effort taken in the preprint. Specifically, both reviewers found that a comparison of existing connectivity indices is valuable to guide future analyses. However, the reviewers also raised some criticism, mainly regarding the presentation and structure of the preprint as well as the discussion of results. Overall, I find the reviewers comments very thoughtful and constructive and hope they will help further improving the preprint. I add some own thoughts below. I hope reviewers' and my comments will help improving the preprint and I would welcome a revision.

My main concern is the streamlining of the preprint. The simulations and analyses are quite complex and require very clear sign posts for guiding the reader. This was also echoed by one of the reviewers.

We have created sign posts in the manuscript, namely “patch delineation”, “index scaling”, “global performance of indices” and “landscape features”, which are explicitly introduced as separate sets of questions and prediction in introduction, developed into separate sets of analyses and results in Methods and Result section respectively and discussed in turn in Discussion.

The authors suggest that studying the question how structural connectivity affects species presence and species richness would be facilitated by three methodological advances: optimizing indices, combining indices and changing the grain of habitat description (L 82-86 / L 463-465).

“Optimizing indices” has now been split into the “index scaling” section and “the global performance of indices”, the “grain of habitat” is now “Patch delineation”. “Combining indices” has been dropped in the present revision, as we will explain below.

However, I find this point not developed well enough in the text. First, in the introduction, it should be explained a bit more whether this proposition stems form existing literature (reference) or is an original proposition by the authors.

The introduction now has one paragraph per sign post with bibliographical references to existing literature where we extensively develop our working questions.

In any case, this point needs elaboration and clear explanation as it is central to the preprint. For example, what exactly do the authors mean by "optimizing"?

We hope that splitting “Optimizing indices” in two independent subquestions has made our point clearer.

Then, one way forward for streamlining could be to make it explicit throughout the text, which analyses step corresponds to which of these three suggestions - that's one example of guiding the readers with sign posts.

We followed this advice and used the same sign posts through introduction, methods, results and discussion. We hope it contributes to readability and clarity.

The study is very complex and very technical, so sign posts are vital for not losing the reader in to many technical details and jargon. I would also consider changing the title of the preprint as it does not reflect the goal of testing the different indices or even improving them. My intuitive expectation when reading the title "Simulated neutral metacommunities support the habitat amount hypothesis" would be that the preprint concentrates on exploring the habitat amount hypothesis (or more generally, the SLOSS debate) in different fragmentation scenarios, which is not exactly what the study is doing.

We agreed. The present title “When should patch connectivity affect local species richness? Pinpointing adequate methods in adequate landscapes using simulations” is now closer to the questions and the results of the preprint.

Abstract: some phrasing in the abstract is a little vague. Again, I suggest placing clear sign posts. For examples, in phrases such as L 11-12 "the effect of connectivity on species presence and community richness in empirical studies is often quite limited" or L 27 "leading to very strong effect sizes upon community richness", the context is not entire clear. I suggest clarifying up front what the background is to this study, which is the question in how far connectivity between patches contributes to explaining species richness. It is all there in the abstract (e.g. L21-22 "the most fruitful methodological choice to improve the explanation of species richness"), but a little rephrasing, restructuring and signposting will help the reader to identify the red line.

We deeply rephrased the abstract to improve clarity.

Minor comments: L 32-51. Also in niche theory it is generally acknowledged that dispersal or colonization ability are important determinants of species' distributions. See for example the

BAM diagram introduced in Soberon (2007; Ecol Letters, doi: 10.1111/j.1461-0248.2007.01107.x) and cited often. I feel this would be worth acknowledging here.

We made a sharper introduction starting directly from TIB, there is no reference to Niche Theory anymore.

L 41. "TIB" - abbreviation not defined yet.

It is now, at the first line of main text in our revision.

L 46-51: As the study seems to hinge heavily on these statements or references, these should be discussed in more detail.

We have considerably develop and detailed this paragraph (ll. 49-78)

L 82-86: is there any reference that supports these suggestions?

The new Introduction now allocates one paragraph per suggestion, clearly showing where it comes from and giving associated references.

L 141. Maybe spell out again briefly which factors were varied to make up 2700 simulations.

Done (ll. 225-227).

L 159-160: either spell out the names of the indices instead of just providing the abbreviation, or at least reference Table 1 here.

Table 1 is now referenced just before the first introduction of indices names (l. 240).

L 187-189. The rationale for scaling "the 63 vectors to mean 0 and variance 1" should be explained here. Also, in L 192-193 - Does averaging over the 90 landscapes not result in discarding valuable information about the variance, e.g. variance introduced through different spatial clustering (Hurst factors)? I would consider standardising the distance matrices by the variance over all matrices of the 90 landscapes, and use these standardised values for clustering instead of the simple mean.

First, note that indices classification is not central anymore in our study since we reduced the number of indices involved. It has been moved to appendices.

Scaling vectors of connectivity values within landscapes ensures that Euclidean distance between vectors becomes a function of the Pearson correlation between vectors only. We mentioned this point in the caption of Fig S4.

Introducing the variance of the correlation among indices across the 90 landscapes tested is an interesting suggestion. However given that (i) we reduced the number of indices, (ii) average correlation among indices generate clear patterns among the remaining ones and (iii) this analysis is not central anymore, we did not feel that it was necessary to introduce further refinements.

Fig.1/Fig.2 - referring to the Appendix to understand the indices names is maybe not the best. Consider including simplified names in the figures.

We do not refer to appendices anymore for indices names and always use simplified names in main text.

Additional requirements of the managing board:

As indicated in the 'How does it work?' section and in the code of conduct, please make sure that:

-Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.

-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.

We have not completely finished to compile all the fragments of the code (community simulator, landscape generation, virtual datasets and result analyses) in a single annotated script. We commit ourselves to uploading it on a Zenodo repository before final decision is made about our work.

-Details on experimental procedures are available to readers in the text or as appendices.

-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

We added this section.

Review by anonymous reviewer, 2019-07-08 11:22

GENERAL COMMENTS

I have read with interest this preprint submitted by Laroche et al. This study aims to clarify which connectivity indices (CI) are relevant to quantify the effects of structural connectivity on community structures, particularly species richness. This question is particularly relevant as there are currently many CI used in the landscape ecology literature. The originality of this study is the use of metacommunity models and simulations in virtual landscapes, in order to avoid any observation bias that might appear in an empirical study. This approach seems relevant, even it forces the authors to formulate strong ecological hypothesis to properly guide their study and free themselves from excessive computation time. In particular, all the species used have similar characteristics in terms of dispersal capacity and habitat preferences. One of the conclusions of the study is that it supports Fahrig's Habitat amount hypothesis (HAH,

Fahrig, 2013). I would be interested in authors' opinion on Hanski's response to it, particularly his sentence 'Analysing multispecies communities is problematic, because different species typically have somewhat different habitat requirements' and the following part (Hanski, 2015).

We define community as a set of species that share similar habitat requirement. We believe that it is possible to find such communities, e.g. saproxylic beetle communities living in tree hollows. However, we perfectly agree with the reviewer that the neutrality assumption is a strong assumption because species usually differ in the way they use habitat and the way they disperse. Differences in the use of habitat is not really our topic and we consider it as one of the processes unrelated to TIB, which can lead to weaker explanatory power of connectivity on species richness in real systems. We extensively explained the position of our study with respect to these processes at ll. 176-188 and ll. 528-538

The difference in dispersal abilities is more related to our topic since several of our results are based on species dispersal, including patch delineation and index scaling. We extensively discussed how heterogeneity of dispersal affect our conclusions at ll. 462-479 for patch delineation and ll. 515-527 for index scaling.

The use of binary landscape with a homogeneous matrix resistance also constitutes a simplification that has probably consequences on the results found (we could have imagined more heterogeneous virtual landscapes with additional modelling of resistance surfaces and species movement using circuit theory).

We fully agree that the addition of heterogeneous resistance cost between habitat and matrix is an important next step, as we mentioned at ll. 566-583. In particular, we expect that it will rehabilitate indices based on topological distance in graphs.

Although the limitations of the study (mainly due to these initial hypothesis) are well identified and described by the authors (L425 sqq), these assumptions are the main weakness of the analysis. This preprint is nevertheless a valuable advance in the analysis of connectivity indices and fills a gap in structural connectivity studies. This study should be of great help in the future for those seeking to quantify the impact of connectivity on community structure or the presence/absence of particular species, including in empirical studies. The clearing of the jungle made by all the CI in the literature is more than welcome.

MORE DETAILED COMMENTS

In terms of concepts used, the latest work by Fahrig (Fahrig 2017a, Fahrig 2017b) and some of the responses to it (e.g. Fletcher et al., 2018) that questioned the concept of habitat fragmentation and its effects on ecological indices such as species richness could be a valuable addition to your introduction.

The revision of our manuscript departed from L. Fahrig's habitat amount hypothesis and is more clearly focused on the assessment of patch structural connectivity explanatory power on species richness, in line with the Theory of Island Biogeography. We therefore did not feel the need of strengthening the reference to L. Fahrig work about fragmentation.

Once having generated virtual landscapes and metacommunities, the statistical analysis is performed in three steps: (i) classification of CI by analysing the correlation among them, (ii) analysis of the correlation between the different CI and species richness, (iii) combination of CI to better predict species richness. The classification of CI is performed using a non-supervised clustering method implemented in R. This method seems relevant and the results showed tend to validate this approach, as it clearly distinguishes patch-based indices on the one hand and cell-based indices on the other hand, and flux and connector indices within the latter.

We removed what we formerly called patch based indices (now indices with coarse patch delineation) from the classification, because we realized during our revision that they should not be used alone but in combination with patch area to ensure fair comparison with what we called cell-based indices (now indices with fine patch delineation). The way we used the classification to compare these two groups of indices hence became useless for our results.

Functionally similar CI like buffers and dF seem very correlated and this result is used later in the paper.

The correlation between CI and species richness is calculated using a linear model. The use of a linear model is not justified by the authors. We could however imagine other types of relation between different CI and species richness.

This was a very good comment. We checked the shapes of the relations and the relationship is not linear at all, which somehow invalidated our use of Pearson correlation as a measure of indices performance. Consequently, we repeated all our analysis using a quadratic model, which seemed more appropriate (see our new Figure 1).

The different CI are then sorted by ascending average Pearson correlation coefficient r (figure 2). The authors may have privileged the use of a likelihood-based method (LL, AIC, BIC) as indicator of the quality of the predictors, see Burnham & Anderson, 2004.

We switched to coefficient of determination, which is a classic metric of explanatory power.

They also could have selected the median instead of the mean, but the narrow distribution (cf. error bars) suggests that this choice has no incident. Finally, the authors tested the combination of the CI dF computed at cell grain (which performed the best in the previous analysis) to a dllCconnector index to improve the prediction of species richness. This step is interesting and showed that the adding of a connector index to a flux index generally leads to an improvement of the prediction.

We removed this part, for no combination proved statistically robust after accounting for the quadratic effect of patch connectivity indices. We replaced it by a test of whether observing a fluctuation of connector indices independent from target flux index (flux indices being what we now call patch connectivity indices) tend to swamp the effect of target flux index on local species richness.

This conclusion could have been discussed in a more detailed way in the discussion (L410 sqq), particularly discussing the concepts underlying the indicators that were combined. Note that

different combinations of CI (not necessarily including dF) could also have been tested and could have theoretically showed better results. I guess that the authors could not test all the possible pairwise combinations due computation time and therefore chose this method.

CONCLUSION

This preprint is an ambitious analysis of a large quantity of structural connectivity indices found in the literature.

We have reduced the number of indices considered to focus on flux indices only. When building a stronger organization of ideas and predictions in introduction, it appeared to us that connector and flux indices do not play the same role in the analysis of patch connectivity. While flux indices are what people usually think about when thinking about patch connectivity (i.e. a habitat amount around the focal patch), connector indices rather deal with habitat configuration among the focal patch. TIB focuses on how flux indices modulate local species richness. Therefore, we reckoned that it was more natural to consider the connector status of patches as a "nuisance" parameter that can modulate the effect of flux indices on species richness rather than dealing with all kind of indices without any hierarchy. As a result, we used the expression "patch connectivity index" for what were flux indices in the previous version of the manuscript and introduced the concept of connector noise.

The use of simulated metacommunities in virtual landscapes allows getting conclusions that avoid observation bias that could appear in empirical studies, even if it comes with the formulation of strong ecological hypothesis that require tempering a possible generalization of the conclusions. The conclusions are nevertheless very interesting and constitute a valuable contribution on the analysis of CI and their power as predictors of species richness. The paper is clear and well written. We can only regret an angle that is sometimes too technical and not detailed enough on the conceptual aspects, especially those underlying the indicators used or the relation between CI and species richness (assumed to be linear in this study).

We hope that the streamlining and simplifications that we operated on the manuscript have contributed to make it less technical and more conceptually grounded than the previous version.

OTHER DETAILED COMMENTS

L271: "The effects of buffers and dF at cell grain on species richness […] increased with the habitat proportion in the landscape". This does not seem perfectly clear (figure 3), especially between a habitat proportion of 0.2 and 0.4 (buffer and dF) or 0.1 and 0.2 (dF). The error bars seem to overlap, which would tend to temper this statement.

After we accounted for non-linearity in patch connectivity, it became clear that intermediate proportion of habitat maximizes the effect of dF and Buffers (Figure 3; discussed at ll. 584-602).

L366: "A decreasing exponential kernel" L392 sqq: I would have expected a more functional/ecological explanation to this question of the optimal buffer radius in relation to the community dispersal.

We now have a whole section that comments the relationship between scale of effect and dispersal, and its practical implications.

REFERENCES CITED
Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research, 33(2), 261–304. https://doi.org/10.1177/0049124104268644
Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography, 40(9), 1649–1663. https://doi.org/10.1111/jbi.12130
Fahrig, L. (2017a). Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics, 48(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612
Fahrig, L. (2017b). Forty years of bias in habitat fragmentation research (Vol. 1). https://doi.org/10.1093/oso/9780198808978.003.0005
Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., … Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? Biological Conservation, 226, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022
Hanski, I. (2015). Habitat fragmentation and species richness. Journal of Biogeography, 42(5), 989–993. https://doi.org/10.1111/jbi.12478

Review by anonymous reviewer, 2019-07-06 17:41

The manuscript entitled "Simulated neutral metacommunities support the habitat amount hypothesis" utilizes simulations to examine the effect of connectivity indices on species presences and community richness. The authors found that buffer indices (or flux indices – i.e., patch structural connectivity indices based on the distance between the focal patch and the surrounding habitat - generated from habitat cells instead of habitat patches) improves explained species richness within landscapes.

1) General comments Novelty

The authors analyze the role of metrics of connectivity indices in virtual metacommunity models to predict species richness. The literature on the subject is somehow expressive. The authors evaluate current connectivity methods, combined methods and changes in the grain size from habitat patch to habitat cell to improve model performance.

Writing style and paper message.

The manuscript is not easy to follow, and the main message of the paper is hard to grasp. Part of the reason is because the manuscript lacks a set of hypothesis/ predictions to be tested.

We paid particular attention to make our questions and predictions explicit, making use of the signpost strategy suggested by the Editor. In Introduction we formulated general predictions and in Methods we precisely explained how these general predictions are tested.

Take for example the last paragraph of the introduction (L. 100-107): what do the authors mean by "refine previous results about how optimizing flux connectivity indices modulate the effect size of connectivity on local species richness by considering a broad set of indices with

contrasted scaling and heterogeneous theoretical backgrounds in a single study"? The MS requires a complete revision to clarify the research hypotheses and predictions.

A second part of the problem is that the flow of the ideas in the MS is truncated due to long sentences. I recommend a complete revision of the paper to address the messages clearer.

The manuscript has been deeply revised with these two comments in mind.

2) Specific comments for revision

a) Major issues

Community composition vs. species richness

The authors use "species richness" and "community composition" as interchangeable terms, which I find confusing. Species composition refers to species "a", "b", "c"…and "n" within a given unit. Species richness refers to a simply number of species within the unit. The main conclusion of the manuscript it that buffer connectivity indices improve models' ability to evaluate species richness at the landscape level. Thus, I suggest re-framing the MS accordingly.

Yes, we agreed. We used species richness in a systematic manner.

Habitat amount hypothesis

The link between connectivity indices and the habitat amount hypothesis proposed by Fahrig (2013) became clear to me only in the discussion section (L. 387-389). Thus, I believe that this link needs to be better explained right at the beginning of the MS. Perhaps the authors could use that hypothesis to derive their predictions to be tested in the MS.

We preferred to stick with the initial angle of the preprint and streamline and explicit our prediction. We admit that the link with the habitat amount hypothesis was less obvious that it appeared to us at first writing and we chose to drop it to gain a better focus on the core questions of the article.

1) Spatial autocorrelation The authors considered habitat cells away from each other's for a minimal distance of 12 cells to reduce spatial autocorrelation. Is there a way of defining this minimal distance empirically? How do they know that 12 cells is the minimal distance to reduce spatial correlation? I suggest addressing the spatial autocorrelation empirically at different distances (# cells), i.e. a sort of sensitive analysis before defining the minimal distance.

The choice of 12 cells is the highest distance that we could set without seriously falling below c.a. 30 sampled cells in the landscape. It is therefore not calibrated based on a spatial autocorrelation analysis, but it aims at limiting it as much as possible.

The risk associated to spatial autocorrelation is to generate bias on the estimates of patch connectivity effects on species richness and generate false positive discovery rate. However we do not work directly on the effects of patch connectivity indices, but we compare the average of a large number (always >=100) of coefficients of determination across models in distinct landscapes or for distinct indices. At last most of the effects

presented are very significant, with strong effects. Therefore, so we do not believe that spatial autocorrelation is a central issue in our approach.

b) Minor issues

L. 32-33. I see no reasonability to talk about niche theory or species composition if the study address problematics related to species richness.

We streamlined and clarified the introduction, which led us to remove this section.

L. 36-38. This phrase is too long and confusing.

We simplified (now lines 10-11).

L. 38 "…thanks to large population sizes" replace by "from reduced population sizes".

This sentence does not exist anymore.

L. 53-57. This phrase is too long and confusing.

This sentence does not exist anymore.

L. 101-104. This phrase is too long and confusing.

This sentence does not exist anymore.

L. 100-107. The manuscript lacks clear hypothesis and predictions to be teste.

We deeply rewrote introduction to clarify our hypotheses and predictions.

L. 223. The paragraph lacks a top sentence. What is the meaning of a high correlation between the Cis? Why

We removed this part of results, for it did not fit with our core questions in the streamlining process.

L. 418-420. This phrase is not clear. Please add further explanation of the example provided.

This point is now explained as one of our hypotheses in introduction (section about Connector noise).