

Dear Recommender,

Thank you for your decision letter dated February, 25th 2019, concerning manuscript “Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition”. We thank the reviewers and yourself for your careful work during the review of our manuscript. We are happy to submit a revised version of our manuscript, which has much benefited from the previous reviewing process. Please find below a detailed point-by-point reply to the reviewers and Recommender. We also apologize for the long delay to come up with a revised version of the manuscript. This was necessary to satisfactorily answer to the reviewers’ comments. We submit on the website of PCI Ecology a PDF with tracked changes, while the corresponding clean revised version (without tracked changes) is uploaded on Biorxiv and can be accessed here: <https://www.biorxiv.org/content/10.1101/480335v2>

Sincerely,

Franck Jabot for the authors.

## Response to comments

### Comments from the Recommender:

Dear Dr. Jabot,

First of all I'm sorry that it took so long for this review. I had considerable problems to get the reviews in time. Now, I've got three expert opinions that are very detailed and that contain many valuable advices. In general the referees see much value in your work. I fully agree with them. The path analytical framework is very promising and in line with a recent renewed interest in structural equation modelling. Matias Arim makes particularly valuable propositions of how to improve this paper. I'm sure that you will be able to adjust your contribution accordingly. Waiting for your revision

We thank the Recommender Werner Ulrich and the three reviewers for their constructive comments that greatly improved our manuscript.

The changes we have performed in the manuscript are the following:

- 1) We have removed the mini-review.
- 2) We have included a goodness of fit measure in Figure 4 and Table S4.
- 3) We have included a novel Table 1 that summarizes the simulation scenarios.
- 4) We have modified the text of the manuscript at various instances to answer to the reviewers' comments. Notably, we have included Fig. 1 in a novel Box 1 that provides detailed rationale for this figure and presents some counter-examples that can be thought of; we have moved the presentation of the path model in the introduction section; we have provided more implementation details on the path analyses in the method section; we have expanded the discussion section (last two subsections).

More details are provided in the point-by-point reply to the referees' comments below.

### Comments from Reviewer 1:

This is a nice proposal for a Structural Equation Modelling (SEM)-based approach to metacommunity analysis. It is great because it explicitly incorporates temporal dynamics, and as such is worth presenting to the research community and see whether its utility extends further from the, arguably, four successful examples on freshwater systems that are presented in the text. In any case, its use will provide more deeper insights than the -arguably useful but simple- partitioning approaches to metacommunity analyses, as is correctly discussed in the introduction.

Thank you for this positive assessment of our work.

There are however

- The literature review is not necessary, and it only distracts the reader. In fact, it is not discussed. So I would just delete it, it is not worth including here. There are many journals where you could publish it as separate short Correspondence piece, such as e.g. *Frontiers of*

Biogeography, discussing a bit the current biases and limitations in the knowledge on temporal metacommunity dynamics. Check a longer example of the utility of such kind of review at Noriega et al (2018 Basic Appl Ecol). If you decide to do this short correspondence piece, include also the lines for all metacommunity papers in plate A of current Fig. 3, and convert the yearly data of #papers in columns or vertical lines, leaving the lines only for accumulated numbers of papers (see e.g. Hortal et al Oikos 2008).

We followed this recommendation and deleted this mini-review.

SEMs are explicitly designed for hypothesis testing, and this framework provides a great setup for this. So I'm missing some text (ideally at the beginning of the methods) highlighting and explaining why the choice of a SEM analytical framework is good for tearing apart metacommunity dynamics from empirical spatial and temporal metacommunity data. I'd take a look to Shipley's papers (e.g. 2000 Struct Equ Model Multidiscip J; 2009 Ecology) and Grace's book (2006 Structural Equation Modeling and natural systems, Cambridge University Press).

We added such an explanation (l.158-161).

I wonder whether you could include or at least accommodate the effect of disease outbreaks (i.e. spatially-structured demographic stochasticity, see Ricklefs Ecol Lett 2015) in description of the framework. I know is not easy, but it would be worth at least mentioning it.

We mentioned this in the discussion as a perspective and suggested a way to accommodate this for the special case of travelling waves (l. 498-503).

The two closure paragraphs are a bit thin. I'd rather construct a longer and more robust section on applications of your framework, where you discuss the link to process-based models, but also how and when it could be useful to assess the metacommunity dynamics of natural systems, discussing also the kind of data needed, etc..

We followed this recommendation and splitted this part of the discussion into two sections « applying the proposed framework to metacommunity data » and « linking the proposed framework to process-based dynamical models » (l 480-535).

Other minor issues are: - I think figure 1 may work better as a box, to highlight its importance.

We followed this recommendation.

- By definition, turnover is the change of composition that does not include nested changes... Please use other words in the paragraph located just above figure 2.

We replaced « turnover » by « community dissimilarity » (l. 150-158).

- The description of the characteristics of the simulated scenarios (second paragraph of the section) may work well as a table. I'd check if it provides a more clear way of passing the message.

We followed this recommendation and added a new table 1 (l. 289-291).

- Put a running name for each empirical dataset in italics at the beginning of each paragraph describing it, for the ease of reading.

We followed this recommendation.

#### Comments from Reviewer 2:

The ms submitted by Jabot and coauthors propose a conceptual framework to assess metacommunity processes based on biodiversity dynamics. Specifically, determinant of temporal turnover on diversity are deconstructed with a structural equation model. Metacommunities have mostly been analyzed on single date implicitly assuming dynamical clos to equilibrium. On the base of simulation and analysis of four exceptional databases, it is shown that the proposed approach may outperforms analysis not considering temporal dynamics. The combined evidence from simulations and real metacommunities support the action of multiple ecological processes and the existence of spatial and temporal structure on the environmental determinants of community dynamics.

This is a potentially interesting article in a theory that is moving it focus to metacommunity dynamics and demanding improvement in their conceptual frameworks.

Thank you for this positive assessment of our work.

However, I have some concerns.

1) As a general comment, the better performance of any analysis considering temporal dynamics may be related to the additional information about the study system, not necessarily to a better conceptual or methodological approach.

Yes, we agree with this. The point of our framework is not about statistical power. It is about developing a consistent conceptual framework for analysing the temporal dynamics of metacommunities. We argue that this framework is more pertinent biologically in that it relaxes the assumption of dynamical equilibrium that is implied when performing analyses of spatial metacommunity patterns, as done in the vast majority of empirical metacommunity studies. We further evidence with simulated metacommunities that the inferences made within this framework are consistent with what has been simulated.

To avoid any misunderstanding of our message, we removed the end of the section « analysis of simulated data » comparing the results based on spatiotemporal data with those based on solely spatial or temporal data.

2) In my opinion, the conceptual model of figure 1 has to be better introduced and supported. I find the introduction a bit large and also a bit out of focus. Actual content may be significantly reduced without loss of information. I think that more attention has to be devoted to support of the conceptual model of figure 1, both from previous studies and/or conceptual deduction. I can think in counter example for some assertions. For example, if dispersal is relatively strong, the increase in populations persistence because incoming dispersal will reduce temporal beta diversity—species with a better performance at the metacommunity level dominate and persist among local communities. If local filters are relatively strong the increase in dispersal may enhance spatial beta diversity. The increase in dispersal may enhance priority effect and spatial beta diversity (Vannette

and Fukami 2017). The increase in community size may stabilize populations reducing species turnover (MacArthur and Wilson 1967)!

We see here that clarifications are needed indeed! This comment is dense. We below first reply to the counter examples developed by the referee to explain why we partly disagree with these interpretations. Second, we explain how we clarified these points in the manuscript. Our main message here is the following: the general scheme of Figure 1 represents a simple verbal reasoning. One may find counter-examples in particular systems. In such cases, the heuristic path model that should be used to analyse metacommunity data may be different from the one that we propose in Figure 2, but even in this case, this does not discard the general rationale of our approach.

Counter-example 1: « if dispersal is relatively strong, the increase in populations persistence because incoming dispersal will reduce temporal beta diversity ». We argue that this is possible, but highly unlikely. Indeed, the reasoning here is focused on the most abundant species that may be indeed locally stabilized due to dispersal. But many less abundant species at the regional scale are likely to appear transiently in local communities due to increased dispersal thereby producing an opposite pattern. Communities generally harbour a larger number of rare species than abundant ones, so that the second pattern is likely to outweigh the first one.

Counter-example 2: « the increase in dispersal may enhance priority effect and spatial beta diversity ». This reasoning is peculiar to transient systems that establish in an empty habitat. We added some material on this in Box 1 (l.128-131).

Counter-example 3: « the increase in community size may stabilize populations reducing species turnover ». As for counter-example 1, this reasoning applies to the most abundant species of the community. On the opposite, larger community size also implies a larger number of rare species that are only transiently present in the community thereby increasing the temporal turnover of the community.

We clarified in the manuscript that Figure 1 is a verbal reasoning, that counter-examples may appear in particular systems and that this would require to develop ad hoc heuristic path models for analysing such systems. Still, we argue that our verbal reasoning is likely to apply to many ecological systems (l. 128-135 and 161-163).

In addition, the analysis of spatiotemporal turnover has to be supported on the introduction. The actual presentation in methods not provides a novel approach or conception. However, a well-supported presentation of the expected insight from the simultaneous analysis of all the turnover components may involve a truly novel perspective to the analysis of community dynamics. The third paragraph of method may be in the introduction. In addition, I may appreciate a more extensive review of the literature supporting each prediction, as well as, potential condition in which predictions may revert. Some prediction requires more attention to its support and alternatives. In addition, the evident expectations about the increase in communities' turnover with the spatial, temporal and environmental distance among communities—which increase with the spatial and/or temporal distance—is not summing up a novel perspective. The use of path models to explore these connections neither is a contribution novel enough to be consider a novel perspective.

Thanks for these suggestions. We moved and modified the previous method section « Analysing metacommunity dynamics with statistics of spatiotemporal turnover and path analyses » in the introduction to provide a better justification of the path model proposed (l. 137-163) As already explained above, we also clarified the fact that alternative path models may be fruitfully considered in particular systems in which alternative relationships may be more pertinent (l. 161-163). Additional material to justify the analysis of the spatiotemporal turnover of communities can be found in l. 84-100. Finally, we amended the last paragraph of the introduction to tone down the aim of this contribution (l.173-178).

3) I have similar concerns to figure 2. The approach to relate different spatiotemporal turnover to environmental variables has a clear value. However, I am not convinced that there is necessarily a truly novel perspective, or synthesis supported by a deep review of the literature, and deductive advances that support for links among dynamic variables (or the lack of them).

The novelty here is to propose an operational analytical framework to assess the influence of ecological processes on metacommunity dynamics with temporal metacommunity data. This framework is further tested with simulated data and applied on four real datasets.

4) In addition, the authors performed a vote counting metanalysis for the 147 studied available in the ISI Web of Science about metacommunity dynamics from a total of 1679 mention “metacommunity” between 1975-2018. Studies were biased toward freshwater and terrestrial—grasslands and forest—environments, covering a wide range of taxa. This result represents a contribution by itself but is a bit disconnected from the rest of the ms.

We removed this part of the manuscript, as also recommended by Reviewer 1.

5) Parameters for simulation were estimated by trial and error. Understanding the limitation of simulation times, the reported existence of strong nonlinearities on the effect of parameters on community structure and dynamics, call attention about the robustness of reported results.

The aim of the simulation study was to asses on clear-cut ecological scenarios whether the proposed analytical framework is able to detect meaningful signatures in the spatiotemporal metacommunity patterns. An in-depth sensitivity analysis of the effect of the various model parameters on metacommunity patterns would be highly valuable but is clearly out of the scope of the present contribution.

6) I seriously miss a thoughtful consideration of the expected relationship among turnover components and its determinants. It is a central issue in the present study that have to be deeply considered.

We added novel material in Box 1 that justifies the expected relationships between turnover components and ecological processes (l.119-127).

7) More information has to be provide to properly understand the path analysis herein performed. Temporal dynamics can be included by different approaches on path analysis, consequently the selected options have to be presented.

We completed the corresponding section (l. 292-306).

The length of time series used in the path model of simulations are not mentioned. This length determines the statistical power and also inform about the coherence between real datasets, typically with few years of dynamic, and model results.

It was precised (now in l. 259-261).

It is not introduced how alternative models were contrasted.

Alternative models were not contrasted. We instead assessed the significance of each path in the full model depicted in Fig. 2.

Summing up environmental paths in figure 5 involve an assumption of independence that may be difficult to support.

We performed this summation to ease the readability of the figure, but we report individual values of the paths associated to each environmental variable in Table S11-14.

The relationship between difference in environmental conditions and time between observations may be affected by cycle dynamics in real environmental variables.

Yes, we can think of many, more complex, relationships. As explained above, we argue that alternative path models should be built for particular case studies if needed. We develop this idea in the discussion section « applying the proposed framework to metacommunity data» and mention this particular case of cyclic environmental variation (l. 496-498).

It is assumed a linear relationship between geographic distance—or environmental distance—and communities' turnover, this linear expectation is very difficult to support.

In theory, we agree with this statement, but:

1- Actually, this is what we observe in the simulated datasets: when there is a relationship, it is linear (Fig. S5-10).

2- If some relationships are not linear in particular case studies, variable transformation procedures can be applied.

3- most importantly, we are not aiming at building a path model for prediction but rather at assessing the presence of correlations between spatiotemporal community dissimilarity and some putative drivers. In this context, linear models are parsimonious.

We precise these points in the discussion section « applying the proposed framework to metacommunity data » (l. 507-515).

Again, it is not evident how the variables for the path analysis were constructed and how the dynamic was included in the model.

See our answer above (l. 292-306).

Finally, most of the concerns presented elsewhere to partition of variance as a method for the analysis of metacommunity mechanisms (cited in the ms) are equally or more important in the proposed path analysis.

Yes, we agree with this point. We argue that we propose an operational way forward to analyse temporal metacommunity data in a consistent framework. By « consistent », we mean that we demonstrated with simulated datasets that the path model was able to correctly infer the processes involved in the simulations. This being said, we agree that more powerful analyses of temporal metacommunity data may be developed in the future. This is the spirit of our last discussion section « Linking the proposed framework to process-based dynamical models » (l. 517-535).

#### Specific comments

The last sentence in abstract focus in a generalization about four empirical result. However, the focus of the article is the conceptual framework and associated methodology. I think that the abstract could be improved with a final sentence more connected with ms objective.

We added a novel final sentence in the abstract (l. 30-32).

Introduction, 1st paragraph, line 11. Patch-dynamic may be enhanced (or attenuated if frequent enough) by perturbation but only require patch release because mortality (Tilman 1994) or population extinction (Roughgarden 1974), whatever the underline determinant—stochastic demographic events, senescence, succession, predation, etc.

We amended this sentence accordingly (l. 45-47).

Introduction, 1st paragraph, line 22. Neutral “paradigm” not preclude environmental heterogeneity. Indeed, from Hubbell 2001 neutral theory predicted changes in richness and species abundance in gradients of community size and isolation. So, patches may differ in area, isolation, productivity, disturbances, etc. Indeed, any heterogeneity among patches may be consider ensuring that there are no differences in species response to heterogeneity related to species traits.

We amended this sentence accordingly (l. 56-59).

Methods. The lattice IBM is appealing and well connected with the questions in hand. I wonder is the model presentation may not be simplified, not presenting here parameters that are not used (e.g.  $a_t$ ) or avoiding mention to other potential analysis based on the model as temporal structure on environmental dynamic. It is not clear if all cells are simultaneously or sequentially updated.

Actually,  $a_t$  is used (we vary parameter  $e_2$  that determines the range of  $a_t$ , see l. 209-210). Cells are simultaneously updated. We now precise this in line 225.

Discussion. The second paragraph for first time connect the path model with mechanisms. I think that this have to be done since introduction or methods. The third, fourth and fifth paragraph recapitulate results with weak advance on discussion. The independent consideration of each database fail to provide a thoughtful discussion about the contribution of all the results combines to the aim of the ms.

We have modified the introduction section (see above answers). We have also modified the discussion section, notably the two last subsections (l. 480-535).

The paragraph that follow figure 4 legend is a mixture of discussion and novel methods.

This paragraph has been removed.

Figure 5. I recommend the addition of parameters and significance on the figure. In addition, a test of global performance of the model and sound alternatives may be consider.

We added the SRMR statistic. All path coefficients are included in Table S4 (so as to keep the figure readable).

Baselga 2010; Fortune et al. 2018, are no cited.

Corrected.

Figure 2. Community size and change in species richness may be related by the effect of J on richness. Larger richness will involve larger absolute change in richness and

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey. Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. *Theoretical Population Biology* 5:163-186. Tilman, D. 1994. Competition and biodiveristy in spatially structured habitats. *Ecology* 75:2-16. Vannette, R. L., and T. Fukami. 2017. Dispersal enhances beta diversity in nectar microbes. *Ecology Letters* 20:901-910.

This is not so clear: if the relationship between species richness and community size is concave (in general it is), a same change in absolute number of individuals in the community will lead to a larger increase in species richness in smaller communities. We checked if such an additional path was supported and found that it was not (data not shown). We prefer not to mention this in the paper to ease its understandability.

### Comments from Reviewer 3:

The manuscript by Jabot and colleagues describes ambitious research that aims to model both temporal and spatial turnover in metacommunities to elucidate the underlying drivers of community composition. The authors use a mix of simulation modeling and structural equation modeling, to validate their approach, and empirical datasets coupled with the same statistical approach to test drivers in sampled metacommunities. I have some concerns with the approach taken, which I will detail below, but I want to start my review by acknowledging the overall vision of this research and the approach the authors have taken. As the authors state in their manuscript, metacommunity research often relies on using snapshots of spatial patterns to infer underlying mechanisms of community assembly, mechanisms that should be apparent if we were to observe community dynamics unfold through time. Temporal data should provide a lens to capture these dynamics more directly, especially when combined with spatial data that allows us to observe dynamics like dispersal. This manuscript could provide an important step towards harnessing the insights from temporal and spatial data.

Thank you for this positive assessment of our work.

My main concern with the manuscript lies in the path analysis that was performed. In particular, it was not clear to me how temporal trends were captured, and why even simulated data did such a poor job of detecting temporal trends. In the metacommunity models described, some fraction (1-m) of individuals stay in their parent cell. This fraction should lead to a high level of temporal autocorrelation, even if the environment is changing through time. One of the challenges of detecting this autocorrelation lies in the way time is modeled statistically, 'time' can be thought of in two ways: 1) a variable that changes with census period and represents some deterministic change that is (or is not) captured with environmental sampling, and 2) a 'variable' that captures inertia or lags in a system, meaning that it measures the degree of community similarity to previous time period(s) that are not due to environmental conditions. In a neutral model, for example, we expect the second measure of time (autocorrelation) to be very important, with only drift, speciation and migration causing composition to change through time. Statistically, #1 is often represented for an entire landscape, and is valid when things like climate fluctuations influence all communities measured. It can also be modeled on a community level, such as when successional trajectories are common among communities but each community is initiated at a different time. The second case (#2) can only be measured within local communities, and is often measured with an autocorrelation structure. This is important, because simply including 'time' or 'date' in a statistical model without specifying that it is measured within communities may well show no effect, even if temporal autocorrelation is high. From my read of the manuscript, it seems that the authors have ignored #2, yet this effect of time is central to understanding species turnover (or lack thereof).

No, we have considered #2 since we look at « Delta\_t » and not to « t », ie. we assess whether the temporal distance between two censuses (Delta\_t) explains community dissimilarity.

The second concern that I have is that it is unclear how their approach differs from (or is superior to) a recent approach proposed by Ovaskainen and colleagues (Ovaskainen et al, 2017. Ecology Letters 20: 561-576). I would appreciate a more detailed discussion that compares approaches.

We added such a discussion in lines 524-528.