Peer Community In Ecology

On the importance of temporal meta-community dynamics for our understanding of assembly processes

Werner Ulrich based on reviews by Joaquín Hortal and 2 anonymous reviewers

A recommendation of:
Franck Jabot, Fabien Laroche, Francois Massol, Florent Arthaud, Julie Crabot, Maxime Dubart, Simon Blanchet, Francois Munoz, Patrice David, Thibault Datry. Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition (2019), bioRxiv, 480335, ver. 3 peer-reviewed and recommended by Peer Community in Ecology. 10.1101/480335

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The processes that trigger community assembly are still in the centre of ecological interest. While prior work mostly focused on spatial patterns of co-occurrence within a meta-community framework [reviewed in 1, 2] recent studies also include temporal patterns of community composition [e.g. 3, 4, 5, 6]. In this preprint [7], Franck Jabot and co-workers extend they prior approaches to quasi neutral community assembly [8, 9, 10] and develop an analytical framework of spatial and temporal diversity turnover. A simple and heuristic path model for beta diversity and an extended ecological drift model serve as starting points. The model can be seen as a counterpart to Ulrich et al. [5]. These authors implemented competitive hierarchies into their neutral meta-community model while the present paper focuses on environmental filtering. Most important, the model and parameterization of four empirical data sets on aquatic plant and animal meta-communities used by Jabot et al. returned a consistent high influence of environmental stochasticity on species turnover. Of course, this major result does not come to a surprise. As typical for this kind of models it depends also to a good deal on the initial model settings. It nevertheless makes a strong conceptual point for the importance of environmental variability over dispersal and richness effects. One interesting side effect regards the impact of richness differences (ΔS). Jabot et al. interpret this as a ‘nuisance variable’ as they do not have a stringent explanation. Of course, it might be a pure statistical bias introduced by the Soerensen metric of turnover that is normalized by richness. However, I suspect that there is more behind the ΔS effect. Richness differences are generally associated with respective differences in total abundances and introduce source – sink dynamics that inevitably shape subsequent colonization – extinction processes. It would be interesting to see whether ΔS alone is able to trigger observed patterns of community assembly and community composition. Such an analysis would require partitioning of species turnover into richness and nestedness effects [11]. I encourage Jabot et al. to undertake such an effort. The present paper is also another call to include temporal population variability into metapopulation models for a better understanding of the dynamics and triggering of community assembly. In a next step, competitive interactions should be included into the model to infer the relative importance of both factors.

References

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Revision round #1

2019-02-21
Dear Dr Jabot

First of al 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 particulalry 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

Best

Werner Ulrich

Preprint DOI: https://www.biorxiv.org/content/early/2018/11/29/480335
Reviewed by Joaquín Hortal, 2019-02-15 11:13

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 thant the -arguably useful but simple- partitioning approaches to metacommunity analyses, as is correctly discussed in the introduction.

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).

- 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).

- 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.

- 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, disucssiong also the kind of data needed, etc..

Other minor issues are: - I think figure 1 may work better as a box, to highlight is importance. - By definition, turnover is the change of composition that does not include nested changes... Please use oher words in the paragraph located just above figure 2. - 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. - Put a running name for each empirical dataset in italics at the beginning of each paragraph describing it, for the ease of reading.

PS. Please accept my apologies for the delay with this review.

Reviewed by anonymous reviewer, 2019-02-20 21:15

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. 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.

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)! 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.

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).

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.

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.

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.

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. 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 is not introduced how alternative models were contrasted. Summing up environmental paths in figure 5 involve an assumption of independence that may be difficult to support. The relationship between difference in environmental conditions and time between observations may be affected by cycle dynamics in real environmental variables. It is assumed a linear relationship between geographic distance—or environmental distance—and communities' turnover, this linear expectation is very difficult to support. Again, it is not evident how the variables for the path analysis were constructed and how the dynamic was included in the model. 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.

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.

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

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.

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. at) 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.

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.

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

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.

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

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 habtitats. Ecology 75:2-16. Vannette, R. L., and T. Fukami. 2017. Dispersal enhances beta diversity in nectar microbes. Ecology Letters 20:901-910.

Reviewed by anonymous reviewer, 2019-01-21 16:26

Review of "Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition"

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.

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 sensus 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).

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.

Author's reply:

Download author's reply (PDF file)