

Review PCI

Linking intrinsic scales of ecological processes to  
characteristic scales of biodiversity and  
functioning patterns.

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## 1 Comments to the Authors

The manuscript describes the effects of the scales of different ecological processes on biodiversity patterns. I read the paper in depth and it took me a good amount of time to go into the details of this work, which is novel and well written.

The authors presents the results of large scale simulations for a spatially explicit Lotka-Volterra (LV) community model where they study, via different parameterizations of the LV equations, three ecological processes and their effects on spatial patterns of biodiversity and ecosystem functioning. More specifically, the authors manage to investigate the effect the environmental scale (E) via parameterization of species growth rates, of interaction scale (I) via parameterization of the interaction matrix, and of dispersal scale (D) via the diffusion coefficient. For different scenarios, obtained changing the scale of such processes, they measure regional patterns such as the species area relationship (SAR) and biodiversity and regional ecosystem functioning relationship (BEF) and local patterns such as local BEF and spatial correlation of species biomass distribution.

The main results of the paper is the assessment of the effects of species interactions at broader scales than they are usually considered as well as the joint investigation of classical scaling patterns, i.e. SAR and BEF. The authors find that the scale of interactions tends to increase species heterogeneity in contrast to dispersal that tends to blur species distributions across the landscape, such effects are, however, strongly dependent on the (spatial) scale of the environment. The advantage of using a simulation study is the possibility to manipulate separately the scales of different processes and thus asses effects that would not be easy to distinguish from real systems. The disadvantage of using only simulations is that some of the results might be unrealistic, especially if there is no clear road map for calibration and/or potential application of the models.

I enjoyed reading the manuscript and checking all the details until the last appendix. I haven't found any major problem with the methodology or the results, and believe the study is robust and original. This work tackles important questions related to scaling in ecology and could also have useful application for ecosystem management. I have several suggestions and questions whose answers could improve even more the readability of the paper in relation to both conceptual/theoretical and practical/applied aspects of the study. I will base my review on a few main points, articulating into more detail parts of the manuscript where, in my opinion, there could be room for edits and/or changes.

1. **Metacommunity framework** The authors claim to use a metacommunity model. To my knowledge, classical metapopulation (Hanski et al., 1999) and metacommunity (Leibold and Chase, 2017) models are based on patch dynamics, i.e. they describe the dynamics of occupied patches for different species. In lines 97-108 and lines 222-224, it is stated that "patches" emerge from the environmental structure of the landscape (line 100), while equation 1 describes biomass dynamics in space and time, and the lattice used to measure regional patterns is of  $320 \times 320$  pixels (parameter  $L$  table 1). I assume also that solving the LV equations on the landscape requires a spatial (and temporal) discretization of the variables. Are those 102400 pixels the actual patches of the metacommunity model? and is the resolution of the lattice the same used for the spatial discretization of the LV equations? In other words, it is not so clear how the patches emerge from equation 1 in relation to how equation 1 is practically solved. Is this a metacommunity model on a square lattice where dispersal can occur only to neighbouring sites and interactions can be non local? It would help if the authors could clarify such differences in relation to how the equations have been solved, for example giving more details of the methods used to solve equation 1 in lines 237-245 or in the appendix. Moreover, still in relation to the nature of space (i.e. discrete vs continuous spatial variables), if this is a metacommunity model, would it be also useful to consider other measures of species diversity such as  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity? How these measures would relate the measures of diversity introduced by the authors?
2. **Interactions scale** The main novelty of the paper is the introduction of interactions acting at different scales, that is, if I understood correctly, non local interactions. I believe that this is an important part of the work and that it should be addressed with care. In particular, it is not still completely clear to me how the non local nature of species interactions across the landscape relates to dispersal. It would help to give more detailed (and more quantitative) examples of such non local interactions e.g. in the introduction (lines 51-61) and in the discussion. Here the temporal scale of the dynamics plays also an important role. the role of time scales is briefly mentioned in the discussion (lines 457-460), and could be strengthened throughout the whole manuscript, especially in the way equations

are written down. Wouldn't it be useful to clearly state that the considered interactions are non-local and also instantaneous? And if there are interactions that are non-local but not instantaneous (as it seems the case for the example given in line 57-58), wouldn't it be necessary to introduce a time dependence and/or a delay in the interaction matrix? What would be the effect of introducing such time dependence in the results?

Finally, the interaction matrix is a random uniform matrix with identical local and non-local components (equation 4) where inter-specific competition is always smaller than intra-specific competition. I wonder how realistic this choice is, and what could be the effect of considering different interaction structures and/or to use different interaction structures for local and non local components of the interaction matrix. Besides coexistence, could this choice also affect the stability of the community and the way equilibrium is reached?

- 3. Calibration and potential inference** This is a theoretical study mainly based on simulations. No data is used, but the potential use of data and the challenges of inference are discussed. While it is very necessary to carry out these studies, it is also important to properly relate them to the real world. This part could be improved in the manuscript, in my opinion, in two ways: First by a more quantitative description of the different scales at play, and second by a clearer road-map to potential calibration of the model to real data. The authors could provide more numbers of the spatial scales and the specific systems they have in mind. Are those mostly plants? Are we talking about meters, kilometers, hectares? How many? Also, which temporal scale would relate to the spatial scales presented? The author could give examples of specific systems and/or experiments where their results could be tested. On the practical side, the model has many parameters and it is stated in the discussion (lines 385-395) that is not clear whether inference to disentangle the different process from data is possible. Would it be possible to further extend the simulation study to test inference frameworks? What would be needed, in terms of computational power and experimental data, in order to check potential applicability? How many and which parameters would be inferred from real data? For example, not all the parameters of table 1 are clearly mapped into the model equations (1-5). The parameters  $\rho$  and  $k_c$  are described in the appendix and it took me a while to understand how they relate to the species growth rates. It could be useful to describe more explicitly the transformation from the space of frequencies where environmental color is defined to the spatial landscape e.g. by adding more details of the FFT in the main text and/or the appendix. This would then allow to better understand how such parameters could be inferred. Besides inference, I also believe is a part of the methods where further details could be provided. Finally, at the end of the discussion landscape management is also discussed. Do you have specific management application in mind? e.g. would this model be helpful to manage agro-ecosystems?

In general, I found this a good paper to read; the introduction clearly explains the motivation of the study and builds on relevant recent and past research, and the conclusions are adequately supported by the results. The results are robust and the interpretations of the analysis is not overstated, but could be further improved by taking into account some of my comments. The above points provide all the questions that came to my mind while reading this paper, they are intended to be constructive and I hope you will answer to the ones that more useful to improve the manuscript, which is already in a good state and, as I already said, is also very well written (I only found two typos: *interring* in line 394 and *inasmuch* in line 410).

## References

- Hanski, I. et al. (1999). *Metapopulation ecology*. Oxford University Press.
- Leibold, M. A. and Chase, J. M. (2017). *Metacommunity ecology, volume 59*. Princeton University Press.