Cover Letter

Dear Dr. Alonso,

Thank you for the thorough and helpful review by yourself and three reviewers. We did our best to respond to all points raised, and we made changes throughout the manuscript.

We would like to acknowledge that this revision took a very long time to be resubmitted – several external events combined to delay the revision substantially. We believe that the relevance and novelty of the manuscript have not changed, and therefore hope you will find the revision acceptable.

We hope that despite the delay the revision will be accepted.

For clarity, we give below our responses in blue, with the edited/new text in green.

Yuval Zelnik, on behalf of all the authors

Recommender (David Alonso)

This paper studies how spatial patterns of species diversity and ecosystem function are affected by and emerged from the interaction among three different scales: the scale of dispersal, the scale of environmental spatial variability, and the scale of at which species typically interact. The question of scale in Ecology is extremely relevant. It is at the core of the discipline.

I think this ms in the present form has strengths but too many weaknesses. This preprint has been carefully read by three reviewers and myself. The reviewers make interesting and constructive comments from different angles. Please read them carefully and try to address them. They all agree this is not an easy paper to read and review. It took longer than expected to find reviewers. It requires solid expertise in theoretical/mathematical approaches in ecology, and even in this case, the reader needs to go through the material several times in order to get his/her head around. After reading the ms, and from reviewers' overall comments, I also have the impression the manuscript lacks clarity. Certain points need a better justification. Methods need to be better explained. Parts of the discussion need to better emphasize the relevance of the contribution, particularly, in practical settings.

In addition to the specific issues raised by the reviewers, here I will highlight some general points where I find the paper has a lot of room for improvement. As you will see, coincidence with some of the major points raised by the reviewers emerge.

We thank the recommender for summarizing the major comments – we see three themes here, which we describe generally here and in more detail in response to the reviewers. We think these major comments boil down to communication, which we have worked to remedy based on this constructive feedback.

Point 1: Overall readability: We added many explanations for the more technical aspects. We cut out less relevant parts of the discussion and reorganized the appendix and references to it from the main text to make it more useful.

Point 2: Clarity of the manuscript: We clarified in the introduction, methods and discussion the context of our study (e.g. what is meant by metacommunity, what are main assumptions are).

Point 3: Explanation of methods: We added more specific comments in the introduction and methods about what our model does and how it is similar and different from previous studies. We also added figures in the appendix that visualize more technical aspects (e.g. landscape construction) and added accompanying text to make them more useful.

A1. The connection of the main model in Eq (1) to previous literature should be better explained. I agree with one of the reviewers: this does not seem to be a metacommunity model in the typical sense. Eq (1) does not correspond to a set of local populations connected through dispersal and distributed over a discrete number of local sites. Metacommunity models inherit the discrete nature of local populations (or patches), while Eq (1) considers space as a continuous variable. In my opinion, Eq (1) is better regarded as a S species generalization of the Fisher equation with non-local interactions [1]. This comment makes me think that the analysis of the Eq (1) will be more robust if the authors could start by comparing first its dynamics agains a simpler bench mark, for instance, without considering environmental heterogeneity at all. What kind of spatial patterns emerge from the interaction of dispersal (the Laplace operator) and non-local interactions on a uniform environment? This question has been addressed before for a single species [1], and, recently, in the context of predator-prey interactions [2] without non-locality. To make the connections to this literature is fair and necessary. Spatio-temporal chaos and Turing instabilities naturally appear in this type of models in some areas of the parameter space.

We can absolutely see why reviewers have noted that we have not used a traditional metacommunity model, which is an aspect of our approach that we feel is tracking progress in the field - a point we should absolutely make more explicit in our revision. For example, an excerpt from Logue et al (2011) essentially calls for an approach like ours, and in effect make it clear that our type of model is indeed a meta-community one:

"Applying metacommunity paradigms to nature, which is not only patchy and heterogeneous [41] but also stochastic [34], is not straightforward [5]. Different organisms respond differently to processes (e.g. at different scales) and local communities often lack discrete boundaries, rendering a direct implementation of simple theoretical approaches to natural systems difficult. With regard to the latter, most empirical studies addressed permanent habitat patches with discrete boundaries and focused on insular metacommunity types (e.g. lakes, ponds, islands or moss patches). Yet, this preponderance reflects the dominant type of metacommunity paradigms rather than the dominant type of metacommunities observed in nature."

Although metacommunity ecology was formed on a simplified view of discrete local patches, implicitly embedded within an unsuitable matrix, with patches interconnected by regional

dispersal, we are now at a place theoretically and computationally where more realistic applications are possible. We have remedied this in the following ways.

To the Introduction we have added (l. 112-116):

"Although metacommunities tend to be modelled as systems of discrete patches embedded within an inhospitable matrix, Chase and Leibold [31] describe this approach as useful (easing computation and interpretation) but limited -- they foreshadow a "coming transition" in ecology in favour of models that allow "patches" to emerge from the structure of the environment, which our model achieves."

To the Discussion we have added (l. 500-520):

"Our metacommunity model differs from traditional metacommunity models in several important ways. Traditional metacommunity models tend to include discrete local patches embedded within an implicit inhospitable matrix, interconnected by rates of dispersal, often from a spatially-implicit regional pool of dispersers. By contrast, "patches" in our model emerge from the environmental template (Fig. 3),the structure of which may be viewed differently by different species according to their fundamental niche. Further, these patches may have fuzzy boundaries, within-patch heterogeneity, as well as different shapes and sizes. Individuals may be lost to the matrix (i.e., habitat falling outside of the fundamental niche) if they disperse there or may form stepping stone populations to reach new patches. In doing so, dispersal limitation is more likely to emerge as the spatial grain of the environment exceeds the scales at which species disperse, a major result of our study. These features align with the recent calls [48,31] to develop more realistic metacommunity models applicable to a wider range of systems, beyond discrete, patchy, island-like systems. Given these strengths, the next step is to extend a model like ours to multi-trophic systems, beyond "horizontal" (sensu Vellend [49]) competitive communities. Our model is naturally amenable to multi-trophic systems, as predators often perceive the landscape at a different scale than their prey (i.e., a different interaction scale) and would perceive the scale of the environment via spatial distributions of their prey--additionally, there is an opportunity to move beyond Lotka-Volterra dynamics for modelling species interactions, towards more mechanistic consumer-resource approaches [50]. Most metacommunity models have been applied to competing species [17], with multi-trophic extensions becoming more common in recent years [51]."

A2. I think the analysis of Eq (1) would also benefit from a dimensionless approach. What if in Eq (1) we expressed length in units of the typical scale of environmental heterogeneity? This dimensionless length would reduce the complexity of the problem to only two typical scales, the relative scale of dispersal and the relative scale of ecological interactions (both with respect to the environmental scale). The authors implicitly take this approach when fixing the environmental scale to what it seems to be a magic number, and then present their results across different values of the other two scales, but a more explicit approach would be better and more elegant.

Dimensionless analysis could indeed be useful, as it would reduce the complexity of the problem. However, we did not do this for two reasons. 1) From a readability perspective, we believe that doing so would make it less relatable for empiricists. 2) From a technical perspective, it is difficult to use a dimensionless approach for this type of model. While we can measure the env. scale (E) in practice, we don't really know how to set it, so we cannot define an explicit relation between I, D and E (which would allow us to use a dimensionless approach to explore the 3 scales while only technically changing 2 of them). Beyond that, since we are

using numerics, we are bound by some practical consideration – we need the 3 scales to be larger than the grain size (i.e. a cell) and smaller than the system size (which is bounded by simulation time consideration), so that we would need to make sure the rescaling of eq. 1 is consistent every time we use it (i.e. for every different value of E). Overall it did not seem very practical for our purposes.

A3. Although Eq (1) is deterministic, species parameter sets are drawn from certain probability distributions (see Table 1), which amounts to different stochastic realizations of the same model. This is the approach initiated by May, further elaborated by Allesina, Grilli, and others, and recently extended to include dispersal by Baron and Gala [2]. This approach focuses on the distribution of eigenvalues over the ensemble of species configurations defined through random realizations of the community matrix. In the case of this model, species are defined in a more complex way by drawing their defining parameters from certain distributions (Table 1). In this case, not only a competitive community matrix is chosen at random, but also the species optima, local carrying capacities, and niche widths. Although in this context analytic results might be impossible, stability analysis and some numerics can be used to better link probability of stability to the underlying parameter distributions.

Classic papers in the random matrix approach differ from our work in three ways:
1) Most importantly, as you note, they focus on stability properties rather than any of the macroecological patterns that we study.
2) Secondarily, they are usually concerned with a well-mixed community rather than a spatially-extended system, though Gravel et al. (2016) have generalized May's result to a metacommunity context, and Baron & Gala (2020) provide a complementary take.
3) Finally, these studies usually ignore the process of assembly through which some species may go extinct, causing the parameters of surviving species to not be fully random (though this has become a focus of study in recent years, see Barbier et al. (2018) or Baron et al. (2022))

Here we take as a starting point the study of macroecological patterns in an assembled metacommunity. All the parameter regimes that are displayed are ones where we do in fact reach a stable equilibrium. Classic random matrix approaches could potentially inform us on the limits of validity of this setting, but would not help us deduce abundance distributions and other features such as SAR or BEF relationships (more involved techniques are required, see Bunin (2017)).

We now clarify this point, e.g. stating in the abstract and appendix (section A1) that we assume an equilibrium setting, and in the methods we note the distinction from other studies that focus on stability questions.

In the abstract we added (l.27-28): "and stable equilibrium setting"

In the methods we added (l.151-156): "We note that our communities, in the chosen parameter regime of moderate competition, contain many species in a stable equilibrium (i.e., due to the assembly process). Our methodology thus differs from the extensive literature that has considered models with random interactions in order to study stability-complexity relationships [34], including more recent works in a spatial context [35,36], as we rather focus on the abundance and diversity patterns arising from community assembly."

REFS:

Gravel, Dominique, François Massol, and Mathew A. Leibold. "Stability and complexity in model meta-ecosystems." *Nature communications* 7.1 (2016): 1-8.

Baron, Joseph W., and Tobias Galla. "Dispersal-induced instability in complex ecosystems." *Nature communications* 11.1 (2020): 6032.

Barbier, Matthieu, et al. "Generic assembly patterns in complex ecological communities." *Proceedings of the National Academy of Sciences* 115.9 (2018): 2156-2161.

Baron, Joseph W., et al. "Non-Gaussian random matrices determine the stability of Lotka-Volterra communities." *arXiv preprint arXiv:2202.09140* (2022).

Bunin, Guy. "Ecological communities with Lotka-Volterra dynamics." *Physical Review E* 95.4 (2017): 042414.

A4. Non-local interactions are somehow magical. I mean, in reality, information never travels at infinite speed. A focal individual at local position x never feels instantaneously the competition of a second individual located further away from the focal one. It remains to be proved that non-local interactions are the best way to represent a spatial scale not related to species dispersal, but to the shorter time scales associated to individual foraging behavior, and short-time scale movements underlying competitive interactions. In the case of trees, competition can be well represented by a spatial kernel taking into account the typical size of the tree crowns, while dispersal occurs at longer spatio-temporal scales. For animals, the interpretation of the a competition spatial kernel is less obvious. This comment is related to the one by one of the reviewers when saying that the results probably apply to horizontal competitive communities (sensu Vellend) in a straightforward way, but it remains to be seen if they apply rightaway to all kind of communities, or further work will be needed to carefully extend these results to other types of community structures.

Indeed non-local interactions are "magical", but in a sense, so is dispersal and in fact each and every modeling choice. While there is a potential issue of non-local interactions being instantaneous in the model but not in reality, two things should kept in mind: 1) this issue exists is most spatial models in some form, for instance species dispersal via diffusion leads to small but instantaneous movement across large distances. 2) we focus here on dynamics around equilibrium, so that such issues with temporal scales are not of high relevance. Following your comment and that of one of the reviewers, we made some additions to the introduction to clarify better what we mean by these interactions, and to the methods to make clear that the instantaneous assumption is not obvious yet a reasonable modeling choice.

In the Introduction (l.60-62, 65-68) : "A simple distinction is that dispersing species establish new 'home' ranges when they move across the environment, while mobile species always return to their 'home' range."

"Additionally, species interact indirectly across long distances via intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and many such intermediary interactions are not explicitly studied, thus being best represented by long range interactions."

In the Methods (l.215-218): "We note that while this modeling strategy is not physical as it implies that interactions occur instantaneously across distances, this is not expected to bias our

results since we are focusing on the equilibrium state of the system, where hypothetical lag effects should be minimal."

We are indeed more focused on "horizontal interactions", and this means that some of our specific conclusions may indeed depend on this context. We now added text to the discussion to highlight this issue. It is worth mentioning that our main goal and topic is to consider the ramifications of scale interaction, which is not, on its own, particular to horizontal interactions. This is conceptually similar to other topics in community ecology (e.g. the complexity-stability debate) where the baseline is often to focus on "horizontal interactions" – Vellend's work is by itself such a case, as are the studies using random matrix approaches that you mentioned earlier. In that regard we believe that our results can be seen as the baseline expectations of having interactions of process scales (i.e. dispersal, interactions, environment), and we now propose in the discussion that extending beyond "horizontal interactions" is a natural next step.

In the Discussion (l.491-494, 512-520):

"We note that this second issue may only be relevant when interactions are largely competitive, since our modeling, and thus results, did not consider mutualistic interactions which would likely change the observed trade-off between biodiversity and biomass."

"Given these strengths, the next step is to extend a model like ours to multi-trophic systems, beyond "horizontal" (sensu Vellend [49]) competitive communities. Our model is naturally amenable to multi-trophic systems, as predators often perceive the landscape at a different scale than their prey (i.e., a different interaction scale) and would perceive the scale of the environment via spatial distributions of their prey--additionally, there is an opportunity to move beyond Lotka-Volterra dynamics for modelling species interactions, towards more mechanistic consumer-resource approaches [50]. Most metacommunity models have been applied to competing species [17], with multi-trophic extensions becoming more common in recent years [51]."

In sum, I believe this ms is potentially a great contribution. By addressing the points reviewers and I have raised I believe the paper will be more readable and understandable for wider audiences.

We thank the Recommender for the positive outlook and have substantially revised our manuscript based on this constructive feedback.

References

[1] M. A. Fuentes, M. N. Kuperman, and V. M. Kenkre (2004). Analytical Considerations in the Study of Spatial Patterns Arising from Nonlocal Interaction Effects. J. Phys. Chem. B 108 (29): 10505–10508

[2] Baron, J. W., & Galla, T. (2020). Dispersal-induced instability in complex ecosystems. Nature Communications, 11, 6032.

Reviewer 1 (Shai Pilosof)

In this paper the authors link between the scales in which processes occur and the scales of the patterns they form, while interacting with scales of environmental effects. They use a LV-like metacommunity model that explicitly includes these scales. A major finding is that while increasing the scale of dispersal homogenizes biodiversity in space, increasing that of interactions creates heterogeneity, emphasizing local patterns. Another key finding is that the aggregated patterns of SAR and BEF cannot capture these differences.

Overall I found the manuscript intriguing. Although I enjoyed reading it, this is not an easy paper to read. It is not necessarily a bad thing, but the authors should be aware that ecologists who are not fluent in theory may not get the message, which is an important one. This can be solved by adding an accessible summary. That said, the problem is clearly presented and well defined. The model fits the questions, and its assumptions are specified. The results are generally well presented. I have a few comments to help improve but nothing too major. I certainly recommend this for PCI ecology.

We thank the reviewer for putting the time into evaluating our manuscript, and for these positive comments about the strengths of the paper. As we detail to the Recommender above, we have greatly streamlined the presentation of our approach for a more general audience. For example, we now provide a more accessible summary in the Discussion.

Specifically, we now say (l. 412-419):

"In doing so, below, we highlight the following three take-home messages of our results:

- the scale of one process (here, environment) can cause the emergence of characteristic scales of other processes (dispersal, interactions)
- two interlinked ecological patterns (biodiversity and ecosystem function) and their relationship to each other are oppositely affected by two forms of organismal movement
- averaging ecological patterns at any one scale misses a rich patterning of spatial variance that is closely tied to process scales"

In general, the Discussion has been revised to remove any text that created unnecessary complication (e.g., how dispersal scales were set, Turing patterns, now relegated to the Supplement).

Comments

Introduction

B1. The statement that it is generally assumed that interactions are local is not completely true. Studies like that of Poisot 2012 in Ecology Lett (and those that have followed), which look at gamma and beta diversity of interactions across patches already treat this problem specifically. Multilayer networks are a next step to this because they explicitly connect (via interlayer edges) the processes that operate between layers of interaction (e.g., interlayer links connecting patches). I do agree though that the issue of interaction scale explicitly and how it interacts with scales of dispersal and environment has not been studied systematically (as far as I know).

We have added the following qualifier to this statement (l. 57-58), citing Poisot et al. (2012) and Pilosof et al. (2017). Multilayer networks are certainly a step in the right direction, being able to link interaction networks at local scales to a global realization of their interactions at the landscape scale. However, like metapopulation or metacommunity dispersal networks, the modelization of these interactions across space is implicit. Our work takes this a step further to explicitly model them across space.

"(Although exceptions exist, e.g., studies using multi-layer networks to link interaction networks at local scales to their realization at the global scale [13,14])."

B2. Fig. 1: The illustration of the spatial scales in panel A is not clear. Why do arrows range outside the distributions? Maybe a clearer illustration would be to show two species interacting in two patches and other two species interactions in one but not the other? The dispersal is also not clear. Panel C: Not clear what are the yellow and white circles

We have revised this figure in the following ways. In Panel A, we now include a spatial x axis (with the wording distance) to clarify that the kernels relate to the distance from a specific location. We corrected the oversight where some kernels were not wide enough, making for a confusing representation. In Panel C, this was an oversight on our part: green is one species, yellow is another species, and white = the absence of a species. We now show the environmental condition of the patch by coloring the border of the circle green (an environment that favours the green species) or yellow (an environment that favours the yellow species). Thus, mass effects or ranged interactions have caused the exclusion of a yellow species in its preferred habitat by the green species. We added the following text to the caption (and made a few other changes in it):

"Comparison of ecological scenarios along scales of I, D and E. Yellow and green represent two different species, with circle and its rim representing the resident species and the favoured species, respectively"

Model

B3. Environment definition: not clear how V varies in space. What is an environmental scale? Some tangible examples would also help here. Also, per L 213: What does a value of E=32 mean? How did you obtain it and what is the range? What is an environment of 320x320? Does that mean that x and y have coordinates 1..320? It would be nice to see a map (landscape) of environmental heterogeneity.

The environmental variable V, much like species optimum H_i, takes a value between 0 and 1, with a degree of autocorrelation governed by a spectral color and cutoff (see Appendix). The environmental scale is the degree of spatial autocorrelation, that is, the typical length scale of environmental heterogeneity in the landscape. The value E=32 is chosen out of five scale lengths that we focus on (see, e.g., Fig.2): 1, 3.2, 10, 32, and 100. These five values are equally distanced along a log scale, and essentially allow us to have a clear separation between the scales I, D and E, while also being substantially smaller than the system size (320) and larger than the smallest scale in the system (1, i.e. one cell). We chose the value of E=32 specifically as it was easier to use it to demonstrate the results, but we also compare it to E=10 in the Appendix. An environment of 320x320 is a landscape with 320x320 cells, and yes, each cell has a specific (x,y) coordinate ranging between 1 and 320.

Following the questions and suggestions, we have made some additions and changes, mainly to the Appendix but also in the main text. We have now: i) added a more thorough explanation to Appendix section A2 (generating the landscape), with a new figure (S2) for a clearer representation, and we also changed the main text description accordingly. ii) We added a clarification about the choice of scales in the methods. iii) We changed the Appendix section A (measurement of scales) so as to make it more clear how we measure E and what this means.

In the methods (l.257-263): "Our distribution of I and D are equally spaced along a log scale and allow us to have a clear separation between the scales of each ecological process, while also being substantially smaller than the system size (320 cells) and larger than the smallest scale in the system (1 cell). Details on the construction of the environment are given in the Appendix section A2. We choose a value of E=32 specifically as it is the most straightforward to demonstrate our results (see Appendix section A3 for other values)."

B4. Interactions definitions: How does β affect the results? It seems to be a really important variable in defining interaction scale, but there is not sensitivity analysis.

This is indeed a good point. We have done such a sensitivity analysis while building the model, but not in an organized fashion. We now do this, and we added a new figure to the Appendix. In it you can see that for low values of beta (from 0 up to 0.5 or so) the effect of I, the spatial scale of interactions, is minimal. Once beta gets closer to 1 (e.g. 0.9, like the value we use in the main text) then the effect of spatial scale of interactions becomes evident. However, when beta gets very high (close or equal to 1) then we get an issue with normalization, which leads to extremely high and unrealistic densities of species. We therefore choose the value of 0.9 so that we can potentially see a clear effect of the interaction scale I (i.e. if I is large enough), without getting extremely high and unrealistic densities. To be clear, when we say unrealistic, it is because we do not expect that changing the interaction scale will change densities by orders of magnitude, which can occur if beta=1. We include a short discussion on this issue in the Methods section (l. 225-227) along with the figure in the Appendix (S12).

"We choose β to ensure that the effect of interactions changes with their spatial scale (see scales subsection below), but local competition is never negligible (see more details in the Appendix, Fig. S12)."

B5. L 188: I is not defined (only later)

We now refrain from using "I" before defining it, and instead use "spatial scale", while also referring to the next subsection about scales.

B6. For which real-world cases this model is relevant?

In a new paragraph of the Discussion, we discuss the strengths of our approach as broadening the range of systems it can be applied to as well as where the model would need to go next (i.e., multi-trophic metacommunities). The relevant text reads (l. 510-520):

"These features align with the recent calls [48,31] to develop more realistic metacommunity models applicable to a wider range of systems, beyond discrete, patchy, island-like systems. Given these strengths, the next step is to extend a model like ours to multi-trophic systems, beyond "horizontal" (sensu Vellend [49]) competitive communities. Our model is naturally amenable to multi-trophic systems, as predators often perceive the landscape at a different scale than their prey (i.e., a different interaction scale) and would perceive the scale of the

environment via spatial distributions of their prey--additionally, there is an opportunity to move beyond Lotka-Volterra dynamics for modelling species interactions, towards more mechanistic consumer-resource approaches [50]. Most metacommunity models have been applied to competing species [17], with multi-trophic extensions becoming more common in recent years [51]."

Results

B7. Fig 4 and related results: I do not see evidence for the claim that "a large interaction scale I leads to a stronger SAR." The plots on the local and regional BEF look qualitatively (and almost quantitatively) similar to me. If they are not, this should be shown statistically. The individual runs make the plots messy and do not add meaning. I would leave the mean curves, and maybe, if it is not too hard on the eyes, add shades for CI.

In the SAR, I do not see how "a large interaction scale I leads to a stronger SIR" (Line 339). (what does "stronger" mean?) I do see, however, that when the area is small, the effects of dispersal and interaction scale determine the order of the curves: from the intercept to the inflection point around E, their order corresponds first to the dispersal and then, when dispersal is equal to interaction scale. Therefore, SAR is able to capture scale when I,D<E. What are the "replicates"? This is a deterministic model. So what is the difference between them?

Thank you for pointing out confusion in the description of our SAR results. This statement is only true when dispersal is low. We have revised this text to now read (l. 395-397):

"The main impact of process scale is that, by amplifying landscape heterogeneity, a large interaction scale I leads to a stronger SAR when large interaction scales are coupled with short dispersal scales."

To address the comment about replicates, we have added following sentence to the figure caption of Fig.4:

"Although our model is deterministic (i.e., each replicate has only one possible outcome, given a specific set of parameter values and initial conditions), differences among replicates reflect differences in parameter values caused by sampling those values from distributions (Table 1)."

For the BEF results, it looks like the text in our original submission was not updated to reflect the most up-to-date version of this figure, we apologize for the confusion. The reviewer is correct that these two plots are nearly identical. We have revised the text to read (l.378-388):

"Next, we turn to two types of cross-scale outcomes (Fig. 4). First, we consider the relationship in BEF curves (i.e., total biomass vs. species diversity) at neighborhood (i.e., single cell) scales. In doing so, we find that BEF curves (Fig. 4, left panel) reflect underlying process scales. In particular, they exhibit a hump-shaped relationship for large interaction scales, suggesting that patches with the largest total biomass are not the most diverse, but rather have a few high-performing species. This result ties into our previous observation that the interaction scale tends to amplify environmental heterogeneity, and may thus put more weight on selection effects, where abiotic conditions select the best-performing species at the exclusion of others. We also examined BEF curves measured at larger scales, i.e., when spatially aggregating 100-cell neighborhoods, and found qualitatively identical patterns (Fig. 4, middle panel)."

For both BEF and SAR plots, we agree that the plots are messy, but it seems necessary to show the variability in these, and not just the averages. And using other forms (e.g. shaded confidence intervals) will not work well given the 5 different colored lines. We changed the plotting a bit, with thicker lines for the averages, and a different plotting of individual replicates, in hopes that the plots are more clear now.

Discussion

B8. The discussion is very long. I think it can be more concise to highlight the main findings are their implications. For example, I would definitely remove the paragraph between lines 412-427.

We appreciate this comment and have revised to shorten and hone in on our message. The paragraph about Turing patterns has been removed, as well as another paragraph about placing dispersal on comparable scales to other processes.

Reviewer 2 (anonymous)

The authors have performed a great job trying to link the scales of process and pattern in ecology using a Lotka-Volterra metacommunity model. They point to the importance of the spatial scale of species interactions, previously neglected. Although this may be considered as a simplification of more complex mechanisms, it is a valuable approach as an effective way of taking those into account. Their main finding, that the scale of environmental heterogeneity influences the patterns produced by dispersal and interactions, is relevant nowadays.

This being said, some aspects of the manuscript can be improved. I have the general impression that the manuscript is lengthy and might be more clear, so some editing might help. Also, I have two major comments, both in the discussion, and several minor ones.

Major comments:

C1. l.356-359 This conclusion seems unsupported. You only show results for a single environmental scale (E=32), therefore saying that environmental scale sets the characteristic scale of biodiversity and functioning seems an overstatement. You should show that the SAR does the same for at least one or two more values of E (even though I am sure it would be the case), maybe in the supplementary. Also, I am not sure that functioning, measured with BEF, is set with the environmental heterogeneity alone, as I fail to see from where do you derive this claim.

We have previously only used two values of E (32 in the main text, and 10 in the Appendix). We realize now that this was not sufficient, and we therefore ran many simulations so as to test 10 different values of E, ranging from 3 to 56. We note that it is difficult to change E to very small or very large values due to the grain size of the system (i.e. 1 cell) and system size, respectively. Using these new simulations we now show in the Appendix section A3 how the inflection point of the SAR curve changes (Fig. S6) and also how the overall distributions of species abundances changes under different values of E (Fig. S5).

C2. l.462-465 This is the main weakness of the experiment, using only Lotka-Volterra competitive interactions to extract conclusions applicable to general ecosystems. Other mechanisms may not be well described under L-V dynamics, such as consumer-resource interactions or parasites (see Lafferty et al. 2015 Science), so this weakness should be addressed in the manuscript, maybe in the line of considering L-V dynamics as an effective way of describing this more complex processes.

In a new paragraph of the Discussion, we discuss the strengths of our approach as broadening the range of systems it can be applied to as well as where the model would need to go next (i.e., multi-trophic metacommunities). The relevant text reads (l. 514-519):

"Our model is naturally amenable to multi-trophic systems, as predators often perceive the landscape at a different scale than their prey (i.e., a different interaction scale) and would perceive the scale of the environment via spatial distributions of their prey--additionally, there is an opportunity to move beyond Lotka-Volterra dynamics for modeling species interactions, towards more mechanistic consumer-resource approaches [50]. "

Minor comments:

Abstract

C3. l. 24 The scaling of species interactions, which may be non-local through mobility, is a relatively new concept that deserves a better explanation. Also, the mention of vectors is not straightforward. Do you mean a vector of environmental states? Or maybe vector species transmitting a disease? Both? The clarity of the phrase in this line should be improved.

We realize now that the context of long-range species interactions (and thus its scaling), as well as the specific terminology of "vectors", was not very clear (see also our response to next comment). We have rephrased the sentence in the abstract, removing the mention of vectors to avoid any confusion. See also response to next comment for further changes made in introduction and methods.

In the abstract (l.23-25): "Furthermore, many studies leave out the scaling of a critical process: species interactions, which may be non-local through movement or foraging and must be distinguished from dispersal scales."

C4. l. 28-30 I have trouble dissociating mobility into an interaction component and a dispersal component. Maybe an intuition related to this may be inserted in l.25, consequently improving the interpretation of this result.

We better explain the distinction between species interactions and dispersal in the Introduction and methods. For example, mobile species always return to their 'home' patch; dispersing species establish new home patches when they move across the environment.

In the Introduction (l.60-62, 65-68):

"A simple distinction is that dispersing species establish new 'home' ranges when they move across the environment, while mobile species always return to their 'home' range."

"Additionally, species interact indirectly across long distances via intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and many such intermediary interactions are not explicitly studied, thus being best represented by long range interactions."

In the Methods (l.209-212):

"This scale may represent the distance an animal forages from its nest (without establishing a new nest), the scale at which trees gather resources with their roots, or the effective distance an immobile species interacts with its neighbors via an intermediary species (where the intermediary is not explicitly modeled)."

C5. l.35-36 Here, I would say that, the scale of environmental heterogeneity influences the scale of the patterns produced by the other processes.

We rephrased and reorganized this part of the abstract. We hope it is now more clear (l. 30-35).

"Interestingly, the specific scale at which dispersal and interaction scales begin to influence landscape patterns depends on the scale of environmental heterogeneity – in other words, the scale of one process allows important scales to emerge in other processes. This interplay between process scales, i.e., a situation where no single process dominates, can only occur when the environment is heterogeneous and the scale of dispersal small."

C6. - The abstract ends without much discussion of the results. You don't address why are these results important.

We added a conclusion sentence to the abstract (l.38-42).

"Overall we conclude that long-range interactions often act differently and even in opposite ways to dispersal, and that the landscape patterns that emerge from the interplay of long-ranged interactions, dispersal and environmental heterogeneity are not well captured by often-used metrics like the Species-Area Relationship."

Intro

C7. l.48-50 I would prefer a more deductive reformulation of the critical question. Given the scale of specific processes, which patterns are possible at different scales? Note that currently the question follows a more abductive reasoning linking the observed pattern to the scale of the processes.

We have rephrased this question (l. 51-53) to sound more causative as opposed to correlative. Specifically, we have revised from:

"A critical question remains: how is the scaling of ecological patterns, such as patterns of biodiversity and ecosystem functioning, **related to** scales of specific processes, and why?"

To:

"A critical question remains: how is the scaling of ecological patterns, such as patterns of biodiversity and ecosystem functioning, **generated by** scales of specific processes, and why?"

C8. l.54-55 However, at each point in time, interactions are usually local. The concept of interactions at distance is useful as a simplification of complex dynamics implying different processes, in other words, a mean-field approximation to more basic underlying processes.

We agree this is indeed the case. We added two sentences on this to the paragraph, to clarify and highlight this issue. Please note that in the methods we also note the topic of long-range interactions being often from intermediaries.

Text added to the Introduction (l.60-62, 65-68): "A simple distinction is that dispersing species establish new `home' ranges when they move across the environment, while mobile species always return to their `home' range."

"Additionally, species interact indirectly across long distances via intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and many such intermediary interactions are not explicitly studied, thus being best represented by long range interactions."

C9. l.55 Is reference [13] here correct? [13] is a simulation study on heteromyopia… Also I have doubts on l.58

We took out the reference, and changed the example (l.59-64).

"Yet many species move, forage, or otherwise interact with each other at a range of spatial scales [15,16], even in the absence of dispersal. A simple distinction is that dispersing species establish new 'home' ranges when they move across the environment, while mobile species always return to their 'home' range. Many move daily across multiple habitat types, such as seabirds connecting marine and terrestrial ecosystems [15], or predatory insects moving between different habitats in the landscape [16]."

C10. l.58 Salmon returning to their natal streams does not seem an intuitive image for the spatial scale of species interactions (I would frame it in dispersal with some caveats).

See comment above, we changed the text and this example is no longer used.

C11. l.95-96 This statement is a bit vague. Maybe an example of the kind of biodiversity problems that the study might help solve would convince the reader of the importance of this work.

We see that this statement was perhaps too general to be useful. We now give a concrete example (l.104-107).

"Resolving these issues will be useful for both basic and applied biodiversity problems, for instance allowing us to scale up to landscape scales our predictions of biodiversity loss and its effect of ecosystem productivity, that are often based on local scales [30]."

Methods

C12. l.143-145 I feel that the explanation of species interactions beyond local scales should be introduced before, probably in line 58.

We now added to the introduction a more clear explanation on this issue in l.60-62 and l. 65-68 (also noted in our response above to C8) .

 "A simple distinction is that dispersing species establish new `home' ranges when they move across the environment, while mobile species always return to their `home' range."

"Additionally, species interact indirectly across long distances via intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and many such intermediary interactions are not explicitly studied, thus being best represented by long range interactions."

C13. l.210-215 More information is needed here on spectral color and cutoff. Ecologist may not be familiar with these metrics (I am not) and some explanation and references (if available) would be useful, apart from mentioning [33] in the appendix.

We now give more details for this here (l. 249-254), and also we expanded the appendix section "generating the landscape", for instance adding a figure that demonstrates different values of color and cutoff and their effect on the landscape.

"The scale of the environment combines two features often used in the literature to generate realistic, spatially-autocorrelated landscapes [41]: spectral color ρ, which indicates the relative importance of long-range and short-range variations in the environment, and spectral cutoff k_c, which indicates the finest grain of variation (Appendix section A2). The effective environmental scale E is controlled by these two parameters."

C14. l.230-236 Experimental design does not seem clear enough. There are 20 different D&I settings for a given landscape (E=32 for example), called replicates in the methods. However, in figure 4 it seems that each individual D&I settings has more than one replicate (20 in fact). Please clarify how many experiments are performed for each E or D&I setting.

We are not sure what exactly was the cause of the confusion in the previous phrasing, but we now rephrase the paragraph and added more details, to clarify the simulation design. We had 20 landscape replicates, and for each one we ran simulations for different combinations of I and D, 25 combinations in all (see Fig.2), giving us a total of 500 simulations (for the main text. In the Appendix we have more simulations for various uses, for example 500 more simulations for E=10). The new text now reads (l.280-287):

"We use 20 replicate landscapes, allowing environmental structure to vary among replicates while keeping the environmental scale constant. Replicates with other values of environmental scale are presented in the Appendix. Each landscape replicate uses a different set of species and their interactions, chosen at random. Each replicate landscape was used to systematically vary the spatial scale of interactions I and dispersal coefficient D, with 25 different combinations (5 values of D and 5 values of I, as given in Fig. 2, giving a total of 500 simulations. We ascertain the generality of our findings by comparing across replicates."

C15. l.259-260 For measuring BEF, why do you choose locations at random when you could sample each location once? Also, do your results change if the regional scale is set differently?

We use random locations so as to be able to measure BEF in a simple yet general way, for any given region size and without introducing bias. There is no effect on the results for small regions (e.g. region size 1, which we use), but when using larger regions (e.g. for region size 100) other methods may introduce bias, and we avoid this potential issue by using random sampling. The results are not very sensitive, e.g. there is no discernible difference for size 100 or 150, and overall they show the same qualitative features we describe in the main text.

In the methods (l.309-310): "In this way the BEF measurement is done consistently for different region sizes."

C16. l.267-277 This part would be more accessible including some schematics of what you did in the Appendix.

As recommended, we now add a figure to the Appendix (Fig. S2) where we demonstrate the different steps, via 4 panels: 1) the species biomass spatial distribution. 2) The convolution resulting in a correlation map. 3) Transects through this correlation map. 4) Sum of transects resulting in the correlation function.

Results

C17. l.282-297 Little is said about the pattern in Fig. S3, that is contrasting to the one in Fig. 2, and therefore interesting. There, the effect of dispersal is clear at all scales.

We are not sure what is meant by saying that the effect of dispersal is more clear, as in both figures each of the five columns looks quite different. We mainly did not put as much emphasis on this figure since similar effects overall can be seen in the biomass plots (Fig.2), which is less sensitive to choice of metrics and threshold effects – there are many ways to measure

biodiversity, and the plots will look different depending on this, but not necessarily in meaningful ways.

C18. l.321 The mention of figure S4a is probably wrong (S5a instead?).

Indeed this was a typo, which we now corrected.

C19. l.324-327 To me, both local and regional BEF look quite similar, just increasing the axis of species richness, so I would modulate these lines.

Thank you for pointing this out. It seems like the text in our original submission was not updated to reflect the most up-to-date version of this figure, we apologize for the confusion. We have revised the text to read (l.378-386):

"Next, we turn to two types of cross-scale outcomes (Fig. 4). First, we consider the relationship in BEF curves (i.e., total biomass vs. species diversity) at neighborhood (i.e., single cell) scales. In doing so, we find that BEF curves (Fig. 4, left panel) reflect underlying process scales. In particular, they exhibit a hump-shaped relationship for large interaction scales, suggesting that patches with the largest total biomass are not the most diverse, but rather have a few high-performing species. This result ties into our previous observation that the interaction scale tends to amplify environmental heterogeneity, and may thus put more weight on selection effects, where abiotic conditions select the best-performing species at the exclusion of others. We also examined BEF curves measured at larger scales, i.e., when spatially aggregating 100-cell neighborhoods, and found qualitatively identical patterns (Fig. 4, middle panel)."

Discussion

C20. l.413-426 I find that this passage is not very relevant, unless you are able to produce Turing patterns in your setting. I would skip it.

Thank you for this suggestion, we have deleted this text entirely.

C21. l.427-444 This is an interesting but rather technical discussion that may deserve a place in the Appendix, for the sake of brevity and clarity in the main text.

Thank you for this suggestion, which also helped us shorten the Discussion. This text has been moved to the Appendix where we describe how scales were imposed on each ecological process.

Reviewer 3 (Gian Marco Palamara)

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.

D1. 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 × 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 α, β, and γ diversity? How these measures would relate the measures of diversity introduced by the authors?

We appreciate the confusion with our version of a metacommunity model and how it compares to earlier models. In the interest of brevity, please see our response to comment A1 of the recommender, where we describe our revisions to address this comment.

Additionally, in our Methods, we now provide a description of how cells in our model align with patches in traditional metacommunity models. Specifically, on l. 176-184:

"Although at face value cells in our model resemble patches in traditional metacommunity models, given that discrete populations are necessary to simulate Lotka-Volterra dynamics, here it is best to interpret cells as neighborhoods on a landscape. Each neighborhood may take on a unique environmental value and hold unique densities of individuals of different species. Viewed in this way, landscape dynamics can be simulated more continuously, with the numerical limitation of needing to discretize dynamics at their finest resolution. While "patches" can emerge in autocorrelated environments (i.e., a spatial clustering of cells that are suitable to a given species), our model is also generalizable to landscapes with a diversity of environmental structures."

Lastly, although we do not focus on alpha, beta, and gamma diversity in those exact terms, we now point the readers to where they could extract this information for themselves if desired. We have added the text (l. 372-376):

"For those who may be interested in comparing our findings to those typically reported in traditional metacommunity models more explicitly (e.g., [43]), we note that the left and right plots in Fig. S11 essentially show local (i.e., alpha) and regional (i.e., gamma) diversity, respectively, whereas compositional turnover among localities (i.e., beta diversity) is essentially differences between them."

It only makes sense to measure cells as the local scale given that actual patches only emerge in simulations with specific process scales.

D2. 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 intraspecific 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?

We agree that the topic of non-local interactions is both central to the manuscript and can be misunderstood. Following the recommendation, we have added text to the intro and methods to help clarify what we mean by long-ranged interactions and what are the modeling limitations for this. We also note that while there is a potential issue of non-local interactions being instantaneous in the model but not in reality, two things should kept in mind: 1) This issue exists is most spatial models in some form, for instance species dispersal via diffusion leads to small but instantaneous movement across large distances. 2) We focus here on dynamics around equilibrium, so that such issues with temporal scales are not of high relevance.

Regarding the issue of non instantaneous interactions, modeling this explicitly will complicate the model and running simulations substantially, and given the difficulty of modeling even instantaneous spatial interactions over large scales, we do think that our modeling choice is reasonable. As noted, we now clarify in the methods that we use this modeling choice.

In the Methods (l. 209-212, 215-218): "This scale may represent the distance an animal forages from its nest (without establishing a new nest), the scale at which trees gather resources with their roots, or the effective distance an immobile species interacts with its neighbors via an intermediary species (where the intermediary is not explicitly modeled)."

"We note that while this modeling strategy is not physical as it implies that interactions occur instantaneously across distances, this is not expected to bias our results since we are focusing on the equilibrium state of the system, where hypothetical lag effects should be minimal."

In the Introduction (l. 60-62, 65-68): "A simple distinction is that dispersing species establish new 'home' ranges when they move across the environment, while mobile species always return to their 'home' range."

"Additionally, species interact indirectly across long distances via intermediary species, (e.g., plants interacting indirectly via pollinators or herbivores), and many such intermediary interactions are not explicitly studied, thus being best represented by long range interactions."

Finally, in this study we focused on the interplay of scales in a community and the patterns related to it, and not on the assembly and stability of the community in itself. The latter has been the focus of many studies – some of which we previously cited (e.g. Barbier & Loreau 2018), and some we added citations to (e.g. Gravel et al. 2016). We therefore intentionally choose communities with inter-specific competition that is not too strong, as we know such communities will retain many interacting species – which is our main study focus (e.g. we want many species so that we can test the SAR pattern). We now note this focus on stable communities in the introduction and methods.

In the methods (l.151-156): "We note that our communities, in the chosen parameter regime of moderate competition, contain many species in a stable equilibrium (i.e., due to the assembly process). Our methodology thus differs from the extensive literature that has considered models with random interactions in order to study stability-complexity relationships [34], including more recent works in a spatial context [35,36], as we rather focus on the abundance and diversity patterns arising from community assembly."

D3. 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.

We thank the reviewer for raising this comment, which in some ways mirrors comments raised about what 'cells' vs 'patches' are (previous comment by this reviewer) and how their treatment here adds biological realism that generalize to a number of competitive systems (comment by another reviewer). We have added new text to the Discussion (l. 479-483):

"Predictions of our model could be best tested empirically in microcosm or mesocosm setups or using data synthesis, for example, examining the spatial structure of species richness and biomass depending on process scales of focal taxa (e.g., small vs large-bodied animals using remotely sensed data, experiments with insects where mobility is restricted)."

For a very specific example, one could work with *Tribolium* flour beetles, a system where individuals actively forage in flour but also make decisions about when and where to disperse - mobility and dispersal can be augmented by removing legs or hampering the sensory structures used to make dispersal decisions; landscape structure can be easily augmented by creating landscapes with different spatial patterns of flour types.

The most relevant revised text is (l. 175-183): "Although at face value cells in our model resemble patches in traditional metacommunity models, given that discrete populations are necessary to simulate Lotka-Volterra dynamics, here it is best to interpret cells as neighborhoods on a landscape. Each neighborhood may take on a unique environmental value and hold unique densities of individuals of different species. Viewed in this way, landscape dynamics can be simulated more continuously, with the numerical limitation of needing to discretize dynamics at their finest resolution. Whike "patches" can emerge in autocorrelated environments (i.e., a spatial clustering of cells that are suitable to a given species), our model is also generalizable to landscapes with a diversity of environmental structures."

Like many of the classic metapopulation and metacommunity models, we present our model as a general theoretical model not calibrated to a specific system. By referring to spatial scales as 'local', 'regional' or 'global' as opposed to a specific unit (meter, kilometer, or hectare) we retain flexibility if one wanted to test the framework in an empirical setting (the spatial units of a microcosm experiment would be drastically different from a grassland experiment, for example). The same idea holds true for the temporal scale (timescales of growth rates for microbes is drastically faster than plants or mammals). That said, it is likely easier to empirically test the framework in a micro- or mesocosm setup (e.g. O'Gorman&Emmerson 2009, Gonzalez&Chaneton 2002, Thompson&Shurin 2012), mainly because field experiments can become more unwieldy and costly in terms of time, personpower, and equipment.

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 literature has advanced such that several of these parameters have been calibrated for certain systems, such as the work of Gonzalez&Chaneton (2002), who measured the effects of dispersal on species biomass, controlling for environmental variation. When estimating species growth rates, researchers often control for environmental conditions and dispersal by the experimental setup (e.g. mesocosm experiment) or statistically (i.e., field surveys), allowing one to measure the effect of the environment or dispersal, and possibly their interaction, on growth rates. What is primarily lacking is the experimental measurement of the effects of the spatial scale of interactions on ecological processes. We clarify these points in the Introduction (l. 104-107) and Discussion (mentioned earlier in this response, l.479-483), including suggestions on how to test the framework empirically . However, we prefer to keep the model general rather than calibrate the model and parameters to a specific system.

In the introduction: "Resolving these issues will be useful for both basic and applied biodiversity problems, for instance allowing us to scale up to landscape scales our predictions of biodiversity loss and its effect of ecosystem productivity, that are often based on local scales [30]."

In the discussion: "Predictions of our model could be best tested empirically in microcosm or mesocosm setups or using data synthesis, for example, examining the spatial structure of species richness and biomass depending on process scales of focal taxa (e.g., small vs large-bodied animals using remotely sensed data, experiments with insects where mobility is restricted)."

The parameters ρ and kc 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.

More details on the creation of the landscape, and how they relate to species growth rates, have been added to the Appendix (section A2)

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?

Deriving practical management suggestions from this study is difficult, but we now added a more concrete example of pest suppression in agricultural landscapes, in hopes of inspiring future work (l.496-497).

This can, for instance, be relevant for managing predation of pest herbivores in agricultural landscapes [16].

REFS:

O'Gorman, E. J. and M. C. Emmerson (2009). "Perturbations to trophic interactions and the stability of complex food webs." Proceedings of the National Academy of Sciences 106(32): 13393-13398.

Gonzalez, A. and E. J. Chaneton (2002). "Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem." Journal of Animal Ecology 71(4): 594-602.

Thompson, P. L. and J. B. Shurin (2012). "Regional zooplankton biodiversity provides limited buffering of pond ecosystems against climate change." Journal of Animal Ecology 81: 251-259.

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.