

Dear Ms. Picoche:

We have received the reports from our advisors on your manuscript, "How self-regulation, the storage effect and their interaction contribute to coexistence in stochastic and seasonal environments", which you submitted to Theoretical Ecology.

Based on the advice received, your manuscript could be accepted for publication should you be prepared to incorporate minor revisions. When preparing your revised manuscript, you are asked to carefully consider the reviewer comments which are attached below and submit a list of responses to the comments.

The important point about differences between species raised by reviewer 2 needs to be addressed, as well as other more minor comments.

Your list of responses should be uploaded as a file in addition to your revised manuscript.

In order to submit your revised manuscript electronically, please access the following web site:

<https://thee.editorialmanager.com/>

Click "Author Login" to submit your revision.

Please make sure to submit your editable source files (i.e. Word, Tex).

We look forward to receiving your revised manuscript on or before 08 Feb 2019.

Sincerely yours,

Alan Hastings  
Theoretical Ecology

**Dear Pr. Hastings,**

**We have now revised our manuscript according to the reviewers comments. We are grateful for their suggestions that helped to better highlight our results and to clarify the message of the manuscript. We answer their questions and remarks below, in bold font.**

**The referees required two major changes: sharpening the introduction, and checking the robustness of our results to the addition of between-species variability in the mortality parameter.**

**We reframed the introduction so that it better reflects the structure and contents of the article, as required by the referees. We now focus more on coexistence mechanisms in a**

temporally variable environment and only briefly touch upon the niche vs neutral debate, which seemed superfluous to both reviewers.

Our analysis of new simulations with added between-species variability in the mortality rate did not alter any of our conclusions. These additional results are therefore reported only in the Electronic Supplementary Material.

We thank again the referees for the constructive feedback, and hope that the revised manuscript will now be up to the standards of Theoretical Ecology.

Sincerely,

Coralie Picoche and Frédéric Barraquand

#### COMMENTS FOR THE AUTHOR:

There is additional documentation related to this decision letter. To access the file(s), please click the link below. You may also login to the system and click the 'View Attachments' link in the Action column.

<https://thee.editorialmanager.com/l.asp?i=16440&l=E376JRNJ>

Reviewer #1: I have a clearer understanding of what this paper is about now. However, I think the framing could be crisper still. Right now, the final paragraph of the introduction --- the "here's what we're going to do" paragraph --- doesn't have a strong connection to the set-up at the beginning of the introduction. I think the last paragraph is pretty motivating, but you may lose readers before they get there. Or if they do get there, they will wonder, as I did, how the second half of the intro. connects to the first. My understanding is that the big story is what happens with various coexistence mechanisms present with various forcing types --- the 2x2x2 factorial experiment done here. And the main(?) point of that experiment is to understand how we can observe the diversity of species that we do, especially since at least for phytoplankton assemblages in temperate zones, there is likely to be seasonal forcing. A nice secondary issue is the biomass-trait distribution, but that's secondary. Is that right? To be clear, I'm not suggesting that you take anything out of the paper, just that you frame it more clearly.

**>> We are grateful for this careful reading of our article. We have now rewritten the introduction to start with the effect of temporal variability in competition models, and then discuss the two coexistence mechanisms that we explore. The biomass-trait distribution is mentioned towards the end of the introduction as an aside. We hope this makes the introduction more focused on the core objectives of the paper and easier to follow. We made minor edits to the discussion in the same spirit.**

I'm still a little confused about inferring mechanisms from biomass-trait distributions. My understanding is that if both the storage effect and strong self-regulation are present, the trait-biomass distribution is multi-modal if there is seasonal forcing and unimodal otherwise.

**>> Yes, this is correct.**

However, if only one of these coexistence mechanisms is present, the biomass distribution is multimodal if it's the storage effect and uniform if it's strong self-regulation, regardless of seasonality.

**>> Indeed.**

If we only observe a multimodal distribution, how do we know there's a storage effect? I guess both situations involve a storage effect, but one also requires seasonal forcing?

**>> Previously, we suggested to regard multimodality only as a clue pointing towards a mechanism: there is definitely no one-to-one mapping between biomass-trait distributions and coexistence mechanisms. We now make this clearer 1.344-348, where we added “However, when both strong self-regulation and the storage effect were at play, the biomass-trait distribution could either be unimodal or multimodal depending on the type of noise (random or seasonal, respectively) driving the community dynamics. This implies that the mere observation of multimodality in a thermal preference trait-biomass distribution is not a proof of a storage effect, or conversely, the proof of the influence of a seasonal environment.”**

The idea of superadditivity doesn't come up until the discussion section. That surprised me. Any result I see discussed in the Discussion, I also expect to see analyzed in the results.

**>> The word ‘superadditivity’ was indeed only implicit in the previous sentence: ‘neither of these mechanisms was able to produce that result alone, for either random and seasonal noise’. We corrected the sentence so that superadditivity is explicitly mentioned 1. 184 - 187: “the number of species coexisting with both mechanisms present is greater than the sum of the species coexisting with either mechanism alone. The two mechanisms therefore combine superadditively, as their interaction has a positive effect on the richness of the community.”**

Also, when Chesson or Ellner et al. 2018 talk about contributions to coexistence from various mechanisms, they mean contributions to invader growth rate from various mechanisms (and their interactions). You haven't measured this, so I think what you mean by superadditivity is that the number of species coexisting with both mechanisms present is greater than the sum of the number of species present with either mechanism alone. Is this correct? If so, it would be worth explicitly mentioning in the results that the number of species coexisting with both mechanisms present is greater than the sum of species coexisting with either mechanism acting

alone. It would also be worth briefly defining what you mean by superadditivity (numbers of species, not strength of contribution to a single invader growth rate).

**>> We now give the definition of superadditivity according to Chesson and Ellner et al. (2019) in the Discussion, and clarify the differences with our use of the term in the manuscript (l. 381-383).**

Ellner, Stephen P., Snyder, Robin E., Adler, Peter B., Hooker, Giles. An expanded modern coexistence theory for empirical applications. Ecology Letters, 2018

Reviewer #2: I thank the Authors for considering my earlier comments and thoroughly addressing them. I think the article has definitely improved. I still have a few points I would like to revisit - please see them below.

**>> We greatly appreciated your appraisal of the manuscript and constructive suggestions.**

1) In my mind, this is the most important point. I suggested to the Authors to introduce a slight species-specific variation in the mortalities  $m_i$ , which were set equal across species. The Authors objected, on the grounds that this would introduce new niche differences between species, making their Figure 4 uninterpretable. In fact, extra density-independent mortalities do not introduce any niche differences. Take basic  $R^*$  competition as an example. A set of species compete for one single resource  $R$  (a single niche), with per capita growth rates  $r_i = b_i R - m_i$ , where  $b_i$  is the amount of growth generated from one unit of resource, and  $m_i$  is the mortality rate. The  $R^*$  of species  $i$  is then  $m_i / b_i$ . If all  $b$ 's and  $m$ 's were equal, then there would be neutral coexistence. Introducing variation in the mortalities means that the  $R^*$ -values will vary, and all but the single most adapted species will go extinct. Far from introducing new niches and coexistence, an extra density-independent mortality term exacerbates competitive exclusion by resolving model degeneracy caused by parameter fine-tuning.

The Authors claim that introducing variation in the  $m$ 's would change the emergent neutrality pattern. I have not checked this myself, but I am sure the Authors are right (though, importantly, not because this introduces any new niches; see above). But if so, that just goes on to show that making all  $m$ 's equal is an overly special parameter choice. In nature, we do not expect precisely equal mortalities. If some predicted pattern critically depends on this strict equality, then we do not expect the pattern to be a relevant prediction at all.

Therefore, I would like to ask the Authors again to consider implementing this suggestion. I think they would also agree that any result which critically depends on a precise equality of mortalities is not to be taken seriously. Including such results would simply make an otherwise strong article weaker than it could be.

**>> We agree and we have performed new analyses adding a mortality rate that varies between species. The results are reported in the Electronic Supplementary Material Section B: the figures are all very similar and our conclusions are therefore robust to the addition of variable mortality.**

2) This point is somewhat minor, but still has relevance for the big picture. I would be careful with making the case for exactly 5000-year-long simulations on the basis of the importance of transients. Brushing off 10000-year-long simulations on the basis of ecological relevance sounds reasonable - until one realizes that 5000-year-long ones are susceptible to the exact same criticism. Are 5000 years "just right", or maybe too long? And how about 1000 years? Or 500? And so on... To rigorously account for transients, one must include simulation time,  $t$ , as an extra control parameter, and explore everything as a function of  $t$ . Unless this is done, the arbitrary simulation time of 5000 years is no better justified than looking for equilibrium solutions. At least, equilibria and their stability do tell us something about model behavior even when the system is far away from them (as in topological analyses of phase plots using equilibrium points and their stability), and they do reveal how many species could in principle coexist indefinitely.

For these reasons, I would stick to the (admittedly weaker, but honest and still good-enough) argument that 5000-year intervals were chosen for better comparison with Scranton & Vasseur (2016 TE). I would revise lines 264-273 accordingly.

**>> We have done just that, writing at l. 252-259 : “We could have considered longer time intervals, but comparison with the values reported by Scranton & Vasseur (2016) would then have been compromised [...] All things considered, we therefore kept the 5000-year time window for integration.”**

(Incidentally, would performing simulations for more than 5000 years really be that much more challenging computationally? I have written my own R script, which integrates 5000 years in just a few minutes on my desktop. On a computing cluster, by running different parameterizations in parallel, all simulations could be done quite fast, or so I imagine. I might have made a mistake in my code, or the Authors may not have access to a computing cluster - I am attaching my code for reference, in any case.)

**>> It looks like the integration scheme with adaptive timestep of ode45 may be largely responsible for slowing down the numerical integration, by comparison to Runge Kutta (4). In Matlab, 1 simulation with ode45 takes 40 mins on an (average) laptop with ode45. Your original R code runs in 8 mins. Using your code but switching the solver to ode45 in R, the computation time increases to 3h (!). This incidentally suggests that we may be able to get an even faster code with RK4 in Matlab.**

**We will definitely keep in mind (for future work) to be wary of adaptive timesteps when speed is important. Many thanks for providing your code, this was most welcome to compare speeds and pinpoint what part most slows down the integration.**

3) I think the Introduction could still be improved by making it more direct. Right now, one could cut practically all of lines 28-59 without loss of content or context. I would cut or shorten this part, and maybe move it towards the end of the Introduction (which would reflect its position in the main text better as well).

**>> As referee #1 also highlighted, the first two paragraphs of the introduction could have induced the reader into thinking that our paper was mostly about niche vs neutrality or biomass-trait distribution. We have therefore re-centered the first paragraph of the introduction on coexistence in fluctuating environments and kept the niche vs neutral debate to the bare minimum, towards the end of the introduction. We think that this still gives some background to the concept of 'clumpy coexistence' and the biomass-trait distribution which we analyze later on.**

One minor comment: in line 276, erase "or interspecific competition strength".

**>> In the manuscript, competition strength refers to  $\alpha_{i,j}$ . We would prefer to keep mentioning that we did not introduce "variability in either intraspecific competition strength or interspecific competition strength", because many authors have tried to introduce only variability in interspecific interaction strength (e.g. Kokkoris et al. 2002) while intraspecific interaction strength variability may be equally important (see e.g. the recent paper by Stump et al. Ecology Letters 2018).**

Sincerely,  
Gyuri Barabás