Response to comments (3) – Strong self-regulation and widespread facilitative interactions in phytoplankton communities

Coralie Picoche and Frederic Barraquand

Dear Prof. Rees and Associate Editor,

We are thankful for this opportunity to revise and improve our manuscript. We explain below our changes in response to the AE's remarks. We have also checked thoroughly the reference list and found no references cited in the text but not in the list.

We hope that the manuscript is now fit for publication in Journal of Ecology,

With our best regards,

Coralie Picoche and Frédéric Barraquand.

Associate Editor's comments:

The manuscript has largely been improved after two rounds of revision. However, I found that there are still some concerns that should be fixed before the acceptance for publication:

1) the authors should check carefully to ensure they cited the correct references. For example, Line 9, both Volkov et al 2003 and 2007 papers advocate the neutral model, not niche differentiation. Also see line 342.

This point is more challenging than it looks; we therefore provide a detailed response. Volkov *et al.* (2007), cited l. 9 and l. 342 in the previous version of the manuscript is not, in fact, a neutral model in the sense of Hubbell (2001). It is an *extension* of the neutral theory that does include extreme niche differentiation, as interactions between species are shut off (exactly zero). By contrast, the original neutral theory implies that a randomly chosen individual will exert equal competition towards all other individuals (conspecifics and heterospecifics alike), irrespective of their species identity.

With hindsight, it was probably not ideal to suggest that Volkov *et al.* (2007) belongs to the family of neutral models, even if it originated from them. Indeed, the good fit of this model to forest biodiversity data supports niche differentiation. We previously hinted at this by suggesting that neutral theory assumed equal competitive abilities "though there are exceptions, see Volkov et al. (2003, 2007)".

However, the AE is correct that Volkov *et al.* (2003) is probably not the right reference here: although there is no restriction for equal birth and death rate across species, it is very close to the original neutral model. Volkov *et al.* (2005), promoting as an alternative models without competition between species (niche differentiation), rather than neutrality, would have been a better reference.

Re-reading that series of papers, it has occurred to us that Volkov *et al.* (2009) [not previously cited] is in fact an ideal reference to show that weak interactions between species and strong interactions within species occur. Indeed it does so by actually estimating interactions. We have therefore added this reference together with the 2007 paper cited in the introduction (now in the second paragraph) and the discussion, and removed the 2003 reference which was less relevant.

The corrected sentence in the introduction now reads (l. 7-11):
"Neutral theory, assuming that all individuals have equal birth and death rates and exert equal competitive pressure on conspecifics and heterospecifics alike, produces a non-equilibrium coexistence maintained by dispersal from a regional pool. It has been proposed as a solution to the puzzle presented by highly diverse communities (Hubbell, 2001; Rosindell *et al.*, 2011)."

In the second paragraph, we now cite Volkov *et al.* (2007, 2009) (l. 15) in support of niche differentiation.

We thank the AE for this remark, which will no doubt help to clarify the introduction.

2) some papers cited in the text are missing from the Reference list.

We have carefully checked that each cited paper in the text is both (1) referenced in the reference list and (2) adequate (following the first comment of the Associate Editor). Both authors have performed these checks independently.

In spite of this, we have not found any reference in the text that was not in the reference list. We have corrected one reference though, by García-Callejas *et al.* (2018) (we had two references in the list instead of one).

3) I would mention that many studies conclude that both niche differentiation and neutral theory are operating in community assembly and species coexistence in line 11-15, as stochastic process cannot be excluded in this study system as well.

There are two main elements within neutral theory, as we summarize in the introduction:

1. The presence of some dispersal, with recolonisation from a common pool.
2. No niche differentiation, i.e., equal competitive strengths within and between taxa.

As we summarized in our response to the first comment, a model is truly neutral if it matches criterion 2. We agree that the contribution of dispersal can be important, but it is perfectly possible for a community to be somewhat regionally-influenced and yet strongly niche-differentiated locally, with competition occurring mostly within species. We therefore discuss only criterion 2 in the following, which is what we mean by neutrality, and what most theoreticians mean by neutrality (e.g., Loreau & de Mazancourt (2008), who extend theory to varying total community size).

Some authors, and that is perhaps what the AE is referring to, consider that a blend of niche differentiation and neutral coexistence is likely (Scheffer & van Nes, 2006; Scranton & Vasseur, 2016). Within these "emergent neutrality models", species are organised along one or several traits. Coexistence occurs through niche differentiation *between* clusters of species in trait space and neutrally *within* clusters of species. We have actually just published a theoretical paper which tackles this "emergent neutrality" (Picoche & Barraquand, 2019) [not cited], with a parameterisation tuned to the ecology of phytoplankton species. Our theoretical model has shown that for strongly seasonal phytoplankton-like communities, this neutral coexistence within trait clusters is fairly unlikely. As a consequence, we would prefer to avoid suggesting that neutral competition could contribute to transient coexistence. Moreover, it is also noteworthy that the original "emergent neutrality" model has actually hidden niches (Barabás *et al.*, 2013).

On empirical grounds, an important element to test reliably the strength of intra vs intertaxa interaction is the presence of long-term temporal data. To our knowledge, there is no analysis of long-term time series in plants (terrestrial or aquatic) which suggests unequivocally neutral-like coexistence (i.e., that interactions strength between and within taxa are similar). In our previous publication, Barraquand *et al.* (2018), we discussed another publication claiming neutrality in phytoplankton and argued that it could not be conclusive, in absence of estimation of intra- vs inter-interaction strengths.

In light of all the elements above, we feel that the edited second paragraph communicates fairly to the reader that in most communities – with the current evidence – interactions between species are

often much weaker than within species, which implies that communities are not neutral.

Finally, we note that nowhere in this study do we exclude stochastic processes. The models have a noise term to represent precisely stochastic variation over time. Responses to temperature and precipitation that vary across species additionally contribute to making population densities and community composition fluctuate.

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