

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

Coralie Picoche and Frederic Barraquand

Associate Editor’s comments:

Two reviewers provided quite positive comments on this study. However, reviewer 2 also raised some important concerns about the assumption and robust of the model constructed, and I agree with him. The author should carefully revise their manuscript by taking the reviewer’s comments into account.

Dear Editor,

We have now revised our manuscript according to the constructive remarks of the two referees, for which we are very thankful. We present our responses to their questions and the modifications to the main text (that we implemented in response to their suggestions) in blue below.

The referees wanted to know if the structure we imposed on our interaction matrices could influence our results. We have addressed this question in two ways. First, we highlighted in this response both the biological rationale behind our choices and the previous thorough analyses of the consequences of such choices in a similar context in Barraquand *et al.* (2018). Second, we also added some new analyses in the response letter, on interactions found in absence of constraints on the structure of the matrices. These analyses show that our results are robust to the choices made in the main text.

An additional point has been brought up by referee 2, who was not convinced by our argument regarding the (absence of) stability-complexity relationship, and suggested to skip these results and discussion altogether. As we answer referee 2, while we have taken onboard his many thoughtful comments on the comparison to adequate theory, the stability-complexity *sensu* May or Allesina is but a small part (4 lines) of the corresponding section in the results. We have therefore kept this section but modified it in response to the referee’s remarks, and added more discussion to avoid any misinterpretation. Even though we understand the referee’s concern that the metrics and models used here may not match exactly that of random matrix theory or be limited by community size (which we now recognise explicitly), we believe that (1) the match does not need to be exact for comparison to theory to be attempted and (2) for the broad readership of Journal of Ecology, showing the probable absence of complexity - stability relationship, while mentioning potential caveats in the Discussion, is probably more useful than just avoiding to mention it and let the reader guess. In our opinion, one way to promote an improved connection between empiricism and theory is to try to make that connection while also carefully highlighting where it could be improved.

A point of form: we have decided to modify slightly the title, from “Strong self-regulation and widespread facilitative interactions between genera of phytoplankton” to “Strong self-regulation and widespread facilitative interactions in phytoplankton communities”. It seemed that the initial title could have been confusing, since strong self-regulation occurs *within* a genus.

We hope that you will find the corrections and disambiguations that we provided satisfying, and that the manuscript may now be fit for publication in Journal of Ecology.

Sincerely,

Coralie Picoche & Frederic Barraquand

Reviewers' comments:

Reviewer: 1

The principal question of the paper is, what the competition interactions that exist between phytoplankton genera is.

The paper is an analysis of the competition mechanism between genera using interactions networks on phytoplankton community. The authors use a multivariate autoregressive (MAR) model to reveal the interactions type existing within the community. The analysis was done on empirical data from 10 sampling location in France from Brittany to the Mediterranean Sea. Each site has a long-term time series, 20 years for the majority of sampling every two weeks. The main identified plankton used in paper are diatoms and dinoflagellates. The best interaction models used in the paper is the scenario with differentiated pennate and centric diatoms. The results show a strong self-regulation and facilitation, mainly mutualism in intragenus interactions in the phytoplankton community.

I found this paper really interesting and valuable for a large community in the field, of community ecology and microbial ecology that together try to understand the large subject of plankton community dynamics. I'm impressed by the resolution and the time series of data. I have few comments to address.

In comparison with other systems, I'm not sure about the value of added comparisons with terrestrial and fish system. Is it comparable to terrestrial interaction on insects, Lynx/Hare with phytoplankton? Another point of view about these questions is; are predator-prey interactions comparable with competition interactions in planktonic system?

The strong predator-prey interactions in fish and interacting terrestrial insects/mammals are included in the plot to provide a *lower bound* to the interaction strength ratio: they indicate, using interactions *that are known to be strong*, how strong could interspecific interaction strengths be for a given number of species. They are, in a sense, "for illustration only". From a previous simulation and estimation study on two-species models, we have not detected massive differences in the possible intra/inter coefficients between competition and predation (Certain *et al.*, 2018) although obviously, caution is always warranted when comparing the two. We now plot those interactions "for illustration only" in another colour to highlight this, and edited the legend accordingly (Fig 4, Figs. S9 & S10). To sum up, interactions with completely different taxa than phytoplankton are only meant to give an interpretable scale to the interaction ratios found in this paper.

And if you compare predator-prey interactions with competition in plankton community, you need to take into account that plankton like a majority of dinoflagellates are mixotrophs. Especially the ones in the data, who will be the prey and predator at the same time.

We completely agree, and we actually constrained, in Barraquand *et al.* (2018) [a previous paper on one region only], the sign of the interaction matrix based on known biotic interactions between dinoflagellates and cryptophytes. However, these were never of substantial magnitude, so they were not kept in the model selection process here.

Cryptophytes, one of the main preys of dinoflagellates, were counted consistently in only one region (Arcachon). However, as data in the other sites did not consistently include cryptophytes, and we are not aware of cases of predation or kleptoplasty of dinoflagellates on diatoms their size, we have not specifically considered predation from dinoflagellates on diatoms by blocking the sign. Note that these effects are weak anyway so that they would not be retained by the model selection process.

The interactions that we did compute, i.e., intragenus regulation and intergenus interactions within dinoflagellates, can implicitly represent direct predation in addition to resource-based or apparent competition. Predation within dinoflagellates is therefore implicitly taken into account, even though it cannot be disentangled from competition/mutualism in the MAR(1) coefficients.

In the discussion, I suggest putting the section 'Ghosts of competition past and present' before the section 'No complexity-stability relationship but connections between self-regulation and intergroup interactions'. It seems that your argument about why the ghost competition couldn't work for plankton is supported by your results on mutualistic interactions.

We understand the logic behind the referee’s suggestion - substantial mutualism suggests that it may contribute to coexistence rather than interspecific interactions simply vanishing - but we would rather unfold the discussion so that broad perspectives conclude the discussion, which motivated us to keep the current order. Indeed, we think that the paragraphs about the ghost of competition past and present open to a broader and more timely discussion towards current research needs. However, to account for the sensible suggestion put forward by the referee, we now do mention facilitation in the ghost of competition section, l. 350-352.

Your discussion about the high self-regulation of rare taxa seems not appropriate (l 281 to l 289). Abundance was determined by microscopy, where the technique is only able to highlight the abundant species. Even if a microorganism was determined rare under the microscope it can be very abundant in the water.

Indeed, all species considered in this paper are relatively common – while it is appropriate to speak of *relative rarity*, it was not correct to talk about rare species – we therefore corrected to “least common, rarer, ...” whenever appropriate in this manuscript (note that when referring to other papers such as Yenni *et al.* (2017), we still use “rare”, as these authors consider different techniques and species). We thank the referee for this much-needed correction.

Continuously with my previous comments how you manage the abundance between genus and species into a genus, in the model? This difference has an impact on the results?

Some genera that we considered have many species (CHA, i.e. *Chaetoceros* spp.) and other few or mostly one (AST, i.e. *Asterionellopsis glacialis*), both being fairly abundant. Therefore, the number of species in one genus was not correlated to the total abundance of the genus. Also, we have not found more or less competition for those genera that have less species, although one could expect from theory that the closer taxa are, phylogenetically, the more they compete (but see Narwani *et al.* 2017, now added to the manuscript l. 109 and 235, for data contradicting such assumption). We discuss this l. 232-244.

Reviewer: 2

The manuscript of Picoche & Barraquand uses a long-term phytoplankton abundance time series dataset to infer the structure of intra- and interspecific interactions in several different phytoplankton communities. They do so at the genus level, using MAR(1) multivariate one-step autoregressive models. The Authors show that intraspecific effects are overwhelmingly stronger than interspecific ones. Furthermore, interspecific interactions, contrary to naive (or even reasonable) first expectations, are more often positive than not, highlighting a large fraction of mutualistic cross-species (or, in this case, cross-genus) interactions.

Overall, I found this to be an excellent study using a time series dataset of fantastic length and quality, at least by ecological standards. Below, I raise a few questions, the answering of which will hopefully improve the manuscript further. I then finish with some more specific comments and suggestions.

First, to simplify model fitting, the Authors assumed a certain interaction structure between the different genera (page 6; also Supplement, “MAR(1) models”). If I am correct, the most parsimonious model has the consequence that certain genera are only allowed to interact within themselves, decomposing the interaction matrix into independent sub-blocks (this is also visible on Figure 1). Would this not be over-restrictive? Is it reasonable to assume that certain groups of genera really do have negligible interactions? I am wondering if the Authors have any thoughts on this.

The goal of the preliminary comparison between models was indeed to restrict the number of parameters to estimate. The unconstrained or “full” model, which allows all interactions, can require to estimate up to 224 parameters for a 500-point time series. This leads to high uncertainties in parameter values. It is therefore common practice in MAR-based analyses of interactions to reduce the number of parameters to avoid this issue. In the past, this has been done by a combination of AIC-based selection and random selection of matrix coefficients (Ives *et al.*, 2003). Here, we have opted

to build contrasted interaction matrices on phylogenetic grounds, which in our view fits better the philosophy of model selection (Burnham & Anderson, 2002), that is comparing a handful of biological hypotheses.

Based on our previous work in Barraquand *et al.* (2018) on a subset of this data, we have two independent reasons to think that these phylogenetically informed networks make biological sense. First, our model selections of network structure are consistent between all sites. That is, the model ranking is identical at all sites. Second, in our previous work, we have looked in detail at those “forbidden interactions” (absent blocks) in the best-fitting model. For instance, *Chaetoceros* (centric diatom) and *Asterionellopsis* (pennate diatom), the most abundant genera across the French coast, belonging to different clusters in our best-fitting network, did not show interactions significantly different from zero even when considered as a two-species pair. On these grounds, we have therefore reason to view the phylogenetic interaction scenario as robust.

However, in order to be thorough, we did look additionally at the full (unconstrained) model results for all study sites. We present those results below in the response letter (Fig. 1 and in Table 1 of this letter) and in the Supplementary Information.

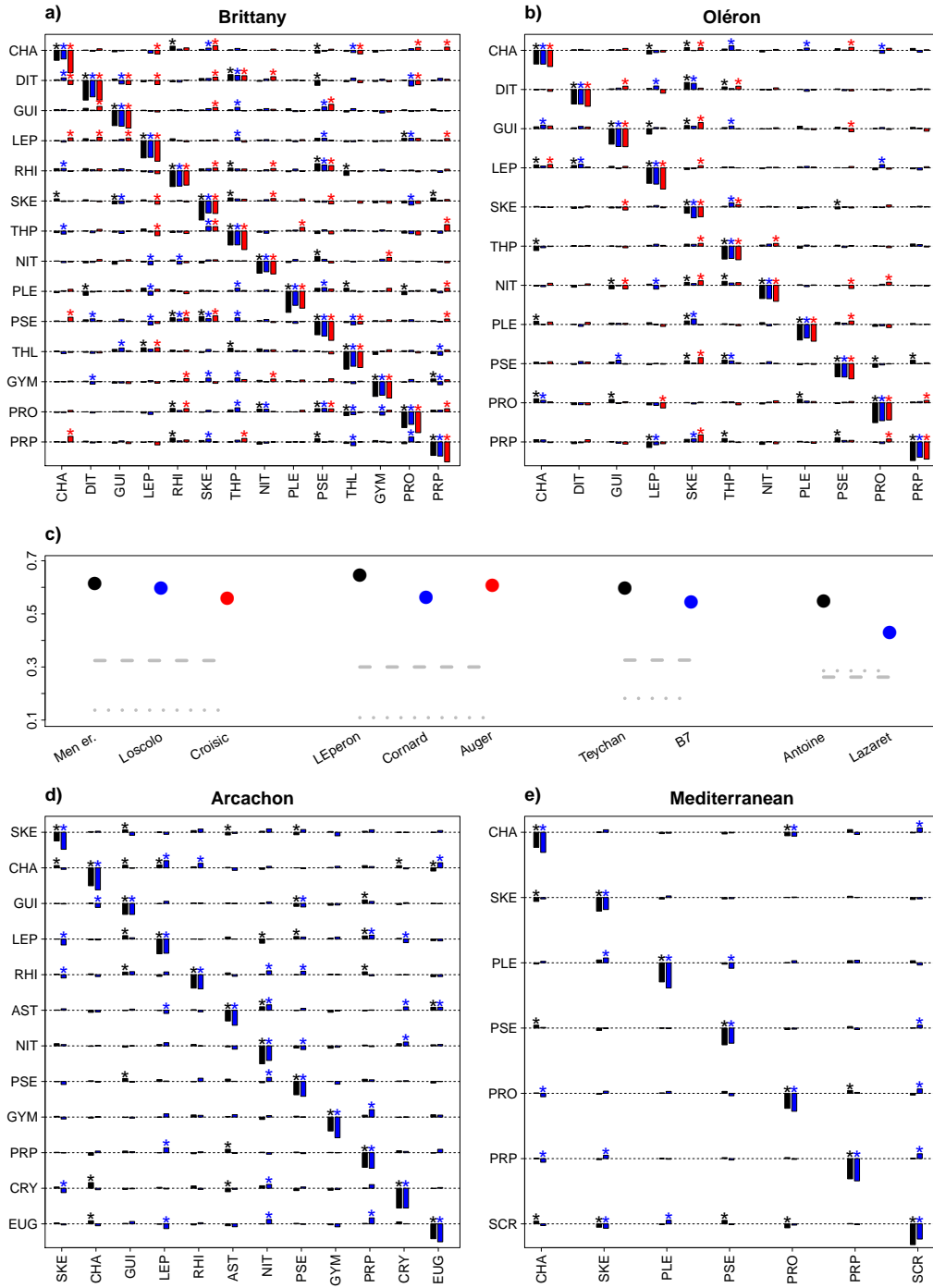


Figure 1: Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). There is no constraint on the structure (modularity) of the interaction matrices. The fraction of positive interactions in each matrix is given by points in c) while the dashed (resp., dotted) line represents the ratio of interactions remaining positive (resp., negative) for all sites of a given region.

Thus, even if we chose to select the full interaction model, there would be no difference in our main conclusions: intragenus interactions are still much stronger than intergenus interactions and positive interactions are still the rule. There is at most 18% of interactions significantly different from zero outside of the pennate and centric blocks and those interactions are on average 3.5 times lower than the interactions inside the pennate and centric blocks (Table 1 of this letter).

	signif outside	positive	ratio intra/inter	ratio in/out block	transfo sign
Men er Roue	0.09	0.57	11.06	3.03	0.04
Loscolo	0.14	0.56	8.42	2.65	0.07
Croisic	0.13	0.52	10.15	2.89	0.09
LEperon	0.13	0.59	8.78	2.75	0.04
Cornard	0.08	0.51	10.32	3.64	0.06
Auger	0.07	0.55	9.66	3.10	0.06
Antoine	0.10	0.47	11.18	5.21	0.00
Lazaret	0.18	0.37	8.67	4.30	0.00
Teychan	0.11	0.55	10.46	3.68	0.14
B7	0.11	0.50	8.29	3.59	0.14

Table 1: Descriptors of coefficients in unconstrained interaction matrices and comparison to best-fitting pennate-centric structures: ratio of coefficients significantly different from 0 outside of the pennate-centric blocks vs total number of coefficients in the unconstrained matrix, proportion of positive interactions in the unconstrained matrix, ratio of mean intragroup interaction strength and mean intergroup interaction strength in the unconstrained matrix, ratio of mean interaction strength inside the pennate-centric modules vs outside the pennate-centric modules in the unconstrained matrix and proportion of interactions changing sign between the two structures.

In sum, our results seem very robust to the restriction to block-diagonal interaction matrix structured by phylogeny.

Second, the Authors have given considerable attention to making sure that their model fitting procedure is robust. I do have some questions regarding this though. The estimates of the model parameters do not come with any uncertainty, since maximum likelihood estimates are point estimates. Would it be possible to characterize the uncertainty? I have some ideas; some may be easier than others to implement. One way is to go Bayesian: assign priors to the parameters and estimate their distributions, instead of just a single value. Another, much simpler way is to estimate the breadth of the likelihood surface. Near the optimum, this can be done via the Hessian matrix (which the Authors have used for another purpose anyway): if all eigenvalues of the Hessian are strongly negative (or positive, in case the Authors used negative log-likelihoods), then there is no direction in parameter space in which the likelihood surface is flat, supporting the idea that there is only a low level of parameter uncertainty. Yet another, complementary method is to integrate the (non-log) likelihood function and see if most of it is indeed concentrated around the maximum. The point of doing all or any of this is to get at least a rough idea about whether 1) intraspecific effects are indeed so much stronger than interspecific ones; and 2) if the weaker interspecific effects “survive” the uncertainty - e.g., if the predicted high prevalence of positive interactions would be washed out by the uncertainty.

For all sites, we computed 95% confidence intervals (CIs) based on a bootstrap method with 1000 bootstraps. The significance of the parameters (stars in Fig. 1 in the manuscript, present in the previous version as well) is actually based on these bootstrapped CIs values. We acknowledge that the 95% CI is a convention that can be discussed, and could provide other CI should the referee ask for those (unfortunately, even if 50% CIs might perhaps make more sense as uncertainty measures here, we do not think these would be as easily accepted by most readers). In the meantime, we present below the uncertainty measures as 95% CIs (Fig. 2 in this letter); as one can see, uncertainties can be fairly broad (which is to be expected, Certain *et al.*, 2018).

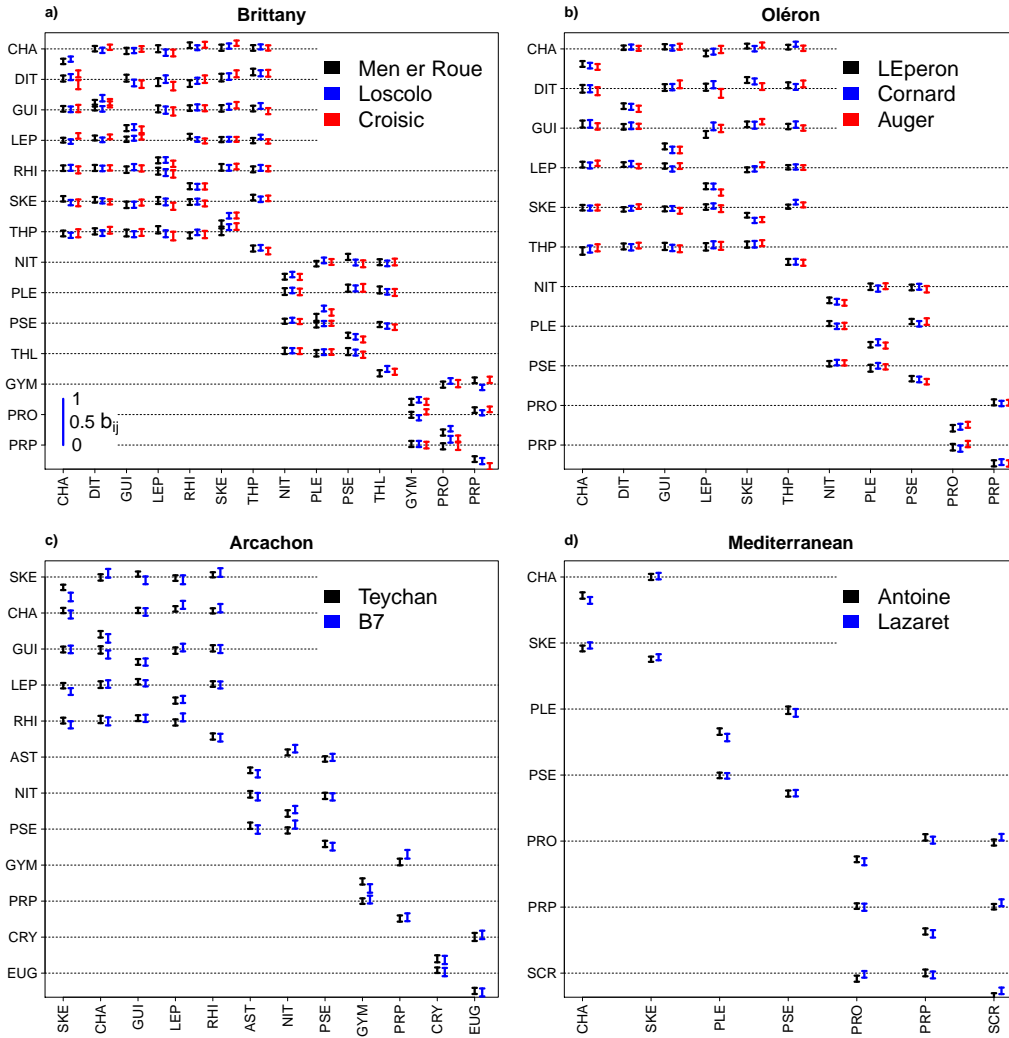


Figure 2: Confidence intervals at the 95% threshold for interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (c) and the Mediterranean Sea (d).

Another simple question related to model robustness: if one uses half of the data to estimate the parameters, and then uses the model to predict the rest of the time series, does one get qualitatively the same dynamics as the observed one?

Such analysis would require an estimation of about 100 parameters on time series made of 250 points at most, which appears to us a too risky endeavour. We already know that this is not achievable without large uncertainties (Certain *et al.*, 2018).

A third point I wanted to bring up concerns putting the Authors' results in the context of the stability-complexity debate. I would actually encourage omitting this discussion, for multiple reasons. First, the original measure of “complexity” introduced by May (1972 Nature) is bound not to work, for reasons explained in e.g. Tang & Allesina (2015 Popul Ecol) or Allesina *et al.* (2015 Nature Commun). Instead, the way to go is to compare with appropriate random matrix predictions that are more sophisticated than May's original one (again, see the above two articles). Second, the communities studied by the Authors are small, containing a maximum of 14 taxa. This is further exacerbated by the fact that each community decouples into smaller sub-communities (Figure 1); the largest interacting block has only 7 taxa. Even if such a system happened to conform to random matrix expectations, one would not be able to see this, because random matrix results only start converging for large systems. Third, the question of which complexity metrics to use is itself nontrivial. The ones in Figure 2 are partial metrics whose connection with the predicted leading eigenvalue of a corresponding random

matrix are tenuous (e.g., “% positive values” has no known simple relationship to the magnitude of the leading eigenvalue, since that depends on the relative strengths of the interactions, not just their prevalence). Fourth, if positive interspecific interactions are indeed the rule, then their mean will also be positive, indicating that the eigenvalue with the largest real part may be an outlier from the bulk of the spectrum, and to determine the position of such an outlier, a different formula is needed than the “standard” measures (see e.g. my paper Barabás et al. 2017, Supplement, Section 2.1). Fifth, the random matrix metrics in the literature, to my knowledge, assume exclusively continuous-time models where the eigenvalue with the largest real part determines stability. Whereas here, a discrete-time model is used, where stability is governed by the eigenvalue with the largest modulus.

While Figure 2 could probably be adjusted to account for all these complications, I am not sure it would pay off, especially in light of the smallness problem. For these reasons, I think the parts on stability-complexity could simply be dropped. Even in their absence, the current study has more than enough substance, and reveals many highly valuable things about real community structure - such as the very strong diagonals, and the unexpectedly many mutualistic interactions.

We thank the referee for his positive comments, it feels good to know that the manuscript would be interesting even without one of its sections! However, if possible, we would really like to keep this part. Instead of removing it, we feel that it is possible to improve a bit the discussion by adding more connection to the theoretical literature.

Two general points about this aspect of the manuscript might be good to recall:

Firstly, our stability analyses are partially inspired by May, Allesina, and others but also by the work of Ives and colleagues on diversity - stability in discrete-time systems (Ives, 1995; Ives *et al.*, 1999, 2003; Ives & Carpenter, 2007).

Secondly, only a small part of the results (4 lines) and the discussion (14 lines) in the stability-complexity sections actually referred to how resilience relates to complexity metrics in the previously submitted version. Most of the developments in that section referred in fact to how self-regulation and intergenus interaction strength covary. We do already agree that a resilience - complexity perspective has its limits in this case.

But on a more philosophical level, if a goal of research should be to progress and avoid mistakes from the past, we feel that it would be more efficient to show readers that there is no relationship to connectance and explain why we can expect that, both theoretically and biologically, rather than avoid talking about connectance altogether. To our knowledge, there are very few articles (except Jacquet *et al.*, 2016) who actually tackle this absence of stability - connectance link in the empirical literature, where the standards of connection to theory are usually much weaker than what we attempt here.

In light of the above considerations, we have opted for the following strategy to deal with the referee’s abovementioned five criticisms:

1. We have modified the figure so that the largest modulus of the eigenvalues is plotted against the mean and variance (multiplied by the number of taxa S) of the interaction coefficients, as suggested by Random Matrix Theory (RMT) *sensu* Allesina & Tang (2015). We agree that May’s binary connectance metric is not relevant here; our connectance metric was weighted connectance. We agree that it is not a perfect match to current theory; however, this is nonetheless an important global descriptor of the interaction matrix, and thus we kept it in the multipanel figure. We do present the correlation between species interaction pairs in Fig. S5 (already in the SI of the previous version). Perhaps disappointingly from a theoretical standpoint, Fig. S5 shows no correlation, so correlation between matrix elements does not need to be considered here.
2. We now mention that the absence of link between the resilience metrics and “complexity metrics” (we know, this is an imperfect designation...) could also occur because communities are small, l. 290-292, as rightly remarked by the referee.
3. Although we do agree with the referee that the percentage of positive interactions may be affected by the strength of these interactions, there is also influential literature (e.g. Coyte *et al.*, 2015) suggesting that more positive interactions lead in general to less stability *sensu* resilience... We cite three references discussing this l. 298-299. We do need to address such findings in a paper showing many positive interactions, hence we have kept the graph with %positive interactions.

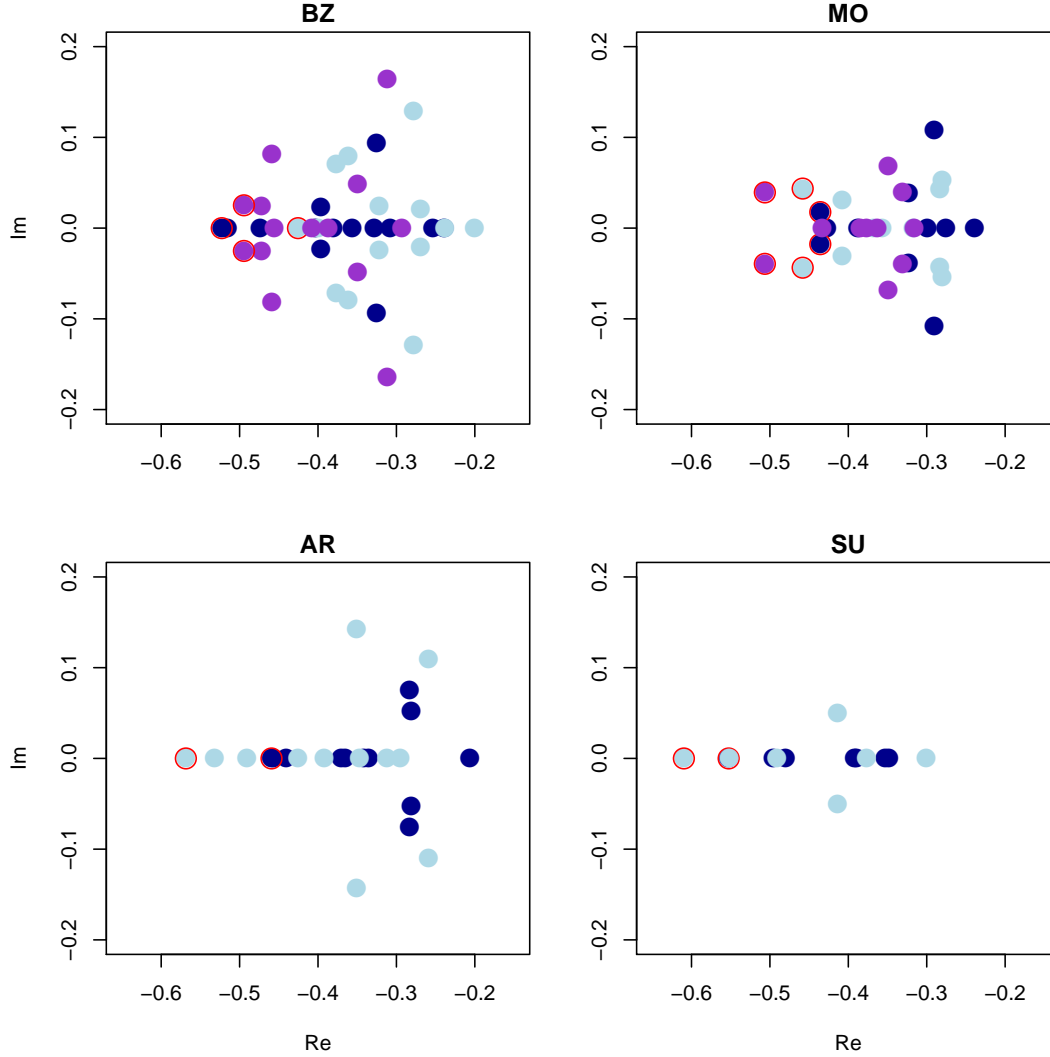


Figure 3: Eigenvalue spectrum of the community matrices for four regions (BZ=Brittany, MO=Marennes-Oléron, AR=Arcachon, SU=Mediterranean Sea. Each color within a panel corresponds to a different sites. The eigenvalue(s) with the maximum modulus for a given matrix have a red outline.

4. We are not sure about the referee's fourth point, as we do not see immediately why a more positive mean would lead to the largest modulus being an outlier. In any case, there does not seem to be an outlier (see Fig. 3 in this letter)
5. Indeed, we do consider the largest modulus - we now mention explicitly in the Discussion (l. 292-295) that this is less standard than using a continuous-time model though not unheard of (outside of papers by AR Ives, see e.g. Cohen & Newman 1984). In fact, a lot of the literature on RMT uses the spectral radius (i.e., largest modulus), which is tightly related in many cases to the largest real part of the eigenvalues. The main difference (in our view) is that the matrix B whose stability is investigated here is a little different than the matrix A in continuous-time since $A = B - I$, as noted by Cohen & Newman (1984).

Additionally, I have a few more specific suggestions:

- 1.5: These two references should probably be lumped with the ones at the end of the sentence, as neither article argues that exclusion is "likely" with shared resources - in fact, both point out ways in which this naive expectation can be violated.

We agree and have now gathered all references at the end of the sentence (l. 6-7).

- 1.14: Forest trees - is there actually solid evidence for those (comparable to annual plants)?

Evidence is indeed less convincing for forest trees than for other terrestrial plants, from which comes most of the evidence. We have removed this system from our examples (l. 14).

- 1.60-62: Does this mean that the current results were also tested, and are robust with respect to this way of handling missing data?

Results presented in this manuscript have not been as thoroughly tested regarding missing data than they have been in Barraquand *et al.* (2018), which analyses a subset of the data used here. In Barraquand *et al.* (2018), an entire section of the Appendix 1 was dedicated to the comparison of several methods to reconstruct time series with missing values. However, the time series in Arcachon Bay are extremely similar in kind to the new ones (e.g., Brittany) included in our analyses. Furthermore, the method chosen has been used many times for MAR(1) interaction analyses in planktonic ecosystems previously (Hampton *et al.*, 2006, 2008; Scheef *et al.*, 2013; Griffiths *et al.*, 2015; Gsell *et al.*, 2016). In sum, we are using a method to deal with missing values that is both completely standard and tested on a subset of the data. We have no reason to anticipate any issue, and it is important to note that we have excluded most of the time series with long gaps of missing data susceptible to cause problems (l. 44-47).

- Eq.(1): the definition of \mathbf{e}_t could go in the explanatory text right after the equation, instead of in the equation itself.

The parameter \mathbf{e}_t is defined l.73-75

- 1.70: I might mention right here that $V=2$, and what those variables are (temperature and salinity).

This has been corrected accordingly (l. 73)

- 1.84-86: Is the model in Eq. (1) actually capable of producing either a storage effect or relative nonlinearity? Is the reason for not finding any that a model of this form is not actually capable of it (a problem that was retrospectively discovered in Adler *et al.* 2010 *Ecol Lett*), or that these mechanisms are actually absent?

It is true that Eq. 1 is not able to produce such effects (although it can be debated regarding relative nonlinearity, depending on whether we think of linearity in log-scale or untransformed scale). We had already mentioned this l.85-86, but we rephrased to make it more explicit (l. 87-89 and 92-96). Note that in Barraquand *et al.* (2018) we have also tested threshold-MAR models (with two phases), which do include nonlinearities by allowing interaction strengths to change with densities or environmental factors. In short, we did not find any nonlinearities that could not be captured by the MAR(1) framework, since estimates per phase were near-identical.

- 1.99-102: I might mention here, just for the record, that the parameters to be fitted are the $S \times S$ entries of the matrix B and the $V \times S$ entries of C . Then it is clear that $63 = 7 \times 7 + 2 \times 7$, so the 7 taxa give 63 parameters altogether.

We now make this precise l. 105-106. We thank the referee for this useful suggestion.

- Figure 2: I am wondering if, instead of plotting complexity metrics against the dominant eigenvalue, it is more worthwhile to plot the actual spectra of the obtained community matrices? Either just the expected spectra (based on the point estimates of the matrix entries), or, if the Authors feel so inclined, with regions of uncertainty around each spectral point (which can be done by e.g. repeatedly drawing matrices based on some confidence or credibility intervals of the matrix entries, and recalculating the eigenvalues).

Spectra are presented in Fig. 3 of this response letter, but it is unclear to us exactly how to interpret the whole spectrum, thus we only report the modulus of the lead eigenvalue (quantifying resilience) in

the main text of the article. We can include these full spectra in the SI if need be.

Sincerely, Gyuri Barabás

References

- Allesina, S. & Tang, S. (2015). The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology*, 57, 63–75.
- Barraquand, F., Picoche, C., Maurer, D., Carassou, L. & Auby, I. (2018). Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127, 1834–1852.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. Springer, New York.
- Certain, G., Barraquand, F. & Gårdmark, A. (2018). How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution*, 9, 1975–1995.
- Cohen, J. & Newman, C. (1984). The stability of large random matrices and their products. *The Annals of Probability*, 12, 283–310.
- Coyte, K., Schluter, J. & Foster, K. (2015). The ecology of the microbiome: Networks, competition, and stability. *Science*, 350, 663–666.
- Griffiths, J., Hajdu, S., Downing, A., Hjerne, O., Larsson, U. & Winder, M. (2015). Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*, 125, 1134–1143.
- Gsell, A.S., Özkundakci, D., Hébert, M.P. & Adrian, R. (2016). Quantifying change in pelagic plankton network stability and topology based on empirical long-term data. *Ecological Indicators*, 65, 76–88.
- Hampton, S., Izmet’Eva, L., Moore, M., Katz, S., Dennis, B. & Silow, E. (2008). Sixty years of environmental change in the world’s largest freshwater lake - Lake Baikal, Siberia. *Global Change Biology*, 14, 1947–1958.
- Hampton, S., Scheuerell, M. & Schindler, D. (2006). Coalescence in the lake washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography*, 51, 2042–2051.
- Ives, A., Gross, K. & Klug, J. (1999). Stability and Variability in Competitive Communities. *Science*, 286, 542–544.
- Ives, A.R. (1995). Measuring Resilience in Stochastic Systems. *Ecological Monographs*, 65, 217–233.
- Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, 73, 301–330.
- Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P. & Gravel, D. (2016). No complexity-stability relationship in empirical ecosystems. *Nature Communications*, 7.
- Narwani, A., Bentlage, B., Alexandrou, M., Fritschie, K., Delwiche, C., Oakley, T. & Cardinale, B. (2017). Ecological interactions and coexistence are predicted by gene expression similarity in freshwater green algae. *Journal of Ecology*, 105, 580–591.
- Scheef, L., Hampton, S. & Izmet’eva, L. (2013). Inferring plankton community structure from marine and freshwater long-term data using multivariate autoregressive models. *Limnology and Oceanography: Methods*, 11, 475–484.
- Yenni, G., Adler, P. & Ernest, S.K.M. (2017). Do persistent rare species experience stronger negative frequency dependence than common species? Asymmetric NFD and persistent rare species. *Global Ecology and Biogeography*, 26, 513–523.