

Frédéric Barraquand
Institute of Mathematics of Bordeaux, CNRS
Integrative and Theoretical Ecology Chair, University of Bordeaux
33615 Pessac
France

Dear Editor,

We would like to submit our manuscript entitled “*Strong self-regulation and widespread facilitative interactions between genera of phytoplankton*” for consideration as a primary research article for the PLOS Biology.

Understanding how very many species can coexist in spite of competition still presents a great challenge to biology. Phytoplanktonic communities are a quintessential example of this coexistence problem: they exhibit high diversity in spite of a seemingly homogeneous environment and similar resources, which usually favors competitive exclusion. Theoreticians have then proposed various models to solve the “plankton paradox”, but these are seldom compared to species-rich experimental data, and even less to long-term observational datasets.

In this manuscript, we seek precisely to tackle the phytoplankton paradox using field-based data. We uncover the interactions governing the dynamics of 10 phytoplanktonic communities along the whole French coastline, using long-term time series (>20 years, sampled every two weeks). We estimate interaction networks using a dynamic multivariate autoregressive model, a technique thoroughly tested on both real and simulated data (Ives 2003, Hampton et al. 2013, Barraquand et al. 2018). The estimated interaction matrices then enable us to unveil the structure of interactions through network analyses and coexistence conditions by comparing intra- to inter-genus interaction strength.

We confirm the crucial importance of niche differentiation to coexistence (“stabilizing niche differences”, *sensu* Chesson 2000), exceeding previous estimates of the strength of intraspecific interactions relative to interspecific interactions (Adler et al. 2018 suggested 4 or 5), and definitely rejecting more neutral explanations of coexistence (*sensu* Hubbell 2001). The ratio of intra- to inter-specific interaction strength is indeed at least 10, and possibly more. The plausibility of this result, based on our 10-sites dataset, is confirmed by a re-analysis of published interaction matrices, estimated with the same statistical technique in 12 articles. We conclude that there is widespread niche differentiation in phytoplanktonic communities, just as in land plants, and our discussion explores what those niches may be, with a notable focus on natural enemies.

More surprisingly, we show that facilitative interactions and even mutualism are to be expected for phytoplanktonic communities (between 40 to 70% of positive interactions), which are often perceived a contrario as purely competitive. Finally, we also contribute to the stability-complexity debate: while links between network stability and connectivity are absent, indicators of species

vulnerability and impact on heterospecifics covary with self-regulation and rarity at the species level, showing how rarer species can in fact persist.

Our manuscript therefore provides empirical, field-based answers to the plankton paradox (as opposed to the overwhelmingly experimental empirical evidence so far) and offer new suggestions to structure interaction matrices in theoretical models, by including strong niches and many facilitative interactions.

We therefore believe that our manuscript will be able to appeal to all scientists interested in how diversity maintains (including ecologists of course, but also microbiologists and applied mathematicians). We hope that our manuscript constitutes a suitable match for PLOS Biology, and we look forward to hearing from you,

Sincerely yours,

Frédéric Barraquand & Coralie Picoche

References cited in the cover letter:

Adler, P. B., Smull, D. , Beard, K. H., Choi, R. T., Furniss, T. , Kulmatiski, A. , Meiners, J. M., Tredennick, A. T. and Veblen, K. E. (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecol Lett*, 21: 1319-1329. doi:[10.1111/ele.13098](https://doi.org/10.1111/ele.13098)

Barraquand, F. , Picoche, C. , Maurer, D. , Carassou, L. and Auby, I. (2018) Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127: 1834-1852. doi:[10.1111/oik.05361](https://doi.org/10.1111/oik.05361)

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Evol. Syst*, 31(1), 343-366. doi:[10.1146/annurev.ecolsys.31.1.343](https://doi.org/10.1146/annurev.ecolsys.31.1.343)

Hampton, S. E., Holmes, E. E., Scheef, L. P., Scheuerell, M. D., Katz, S. L., Pendleton, D. E. and Ward, E. J. (2013) Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, 94: 2663-2669. doi:[10.1890/13-0996.1](https://doi.org/10.1890/13-0996.1)

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.

Ives, A. R., Dennis, B. , Cottingham, K. L. and Carpenter, S. R. (2003), Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73: 301-330. doi:[10.1890/0012-9615\(2003\)073\[0301:ECSAEI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2)