Coralie Picoche University of Bordeaux, Integrative and Theoretical Ecology 33615 Pessac France

Dear Editor,

We hereby submit our manuscript entitled "Strong self-regulation and widespread facilitative interactions between genera of phytoplankton" for consideration as an article in Nature Ecology and Evolution.

Understanding how many species coexist in spite of competition has presented a challenge to ecologists for years. Phytoplanktonic communities are a quintessential example of the coexistence problem: they exhibit both high diversity and seemingly homogeneous resources. Theoreticians have proposed quite a few models to explain coexistence, but the proposed mechanisms are seldom compared to species-rich experimental data, and even less to field data.

In this manuscript, we seek precisely to tackle the phytoplankton paradox using field-based data. We analyse the interactions governing the dynamics of 10 coastal phytoplanktonic communities, using long-term time series (>20 years, sampled every two weeks) of the abundance of up to 14 phytoplanktonic genera. We estimate interaction networks (i.e., community matrices) using a dynamic multivariate autoregressive model, a technique thoroughly tested and validated on real and simulated data (Ives 2003, Hampton et al. 2013, Barraquand et al. 2018). Community matrices then enable us to unveil the structure of interactions and coexistence conditions.

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). 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, has then been 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 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 as purely competitive. 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 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 matrix models, with strong niches and many facilitative interactions. We therefore believe that our manuscript may be able to appeal to both empirically- and theoretically-driven sides of ecology, and that our focus on how species coexist within rich communities, with many references to the general literature, can reach Nature Ecology & Evolution's broad readership, well beyond plankton ecologists and theoreticians.

We hope that you will find our manuscript a good fit for Nature Ecology & Evolution, and we look forward to hearing from you,

Sincerely yours,

Coralie Picoche & Frédéric Barraquand

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

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

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

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

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