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Dear Editor,

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

How many species of primary producers can coexist in spite of competition for shared resources is a key puzzle of ecology. This coexistence problem can be found in plants as varied as grasslands, tropical trees or microscopic algae. Phytoplanktonic communities are a quintessential example: they exhibit high diversity in spite of a seemingly homogeneous environment and similar nutrient resources, which usually favors competitive exclusion.

In this manuscript, we seek to tackle the phytoplankton paradox using long-term field-based data, in contrast to the many experimental studies on this topic. 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. The estimated interaction matrices then enable us to unveil the structure of interactions through network analyses, and coexistence conditions are found by examining intra- and inter-taxa interaction strengths.

Although past experimental work on phytoplankton has suggested that non-equilibrium dynamics (temporal variation in resources, neutral coexistence,...) might be behind phytoplankton coexistence, we show instead the crucial importance of classic niche differentiation (i.e., stabilizing niche differences sensu Chesson 2000, updated in Chesson 2018). Recently, Adler et al. (Ecology Letters, 2018) suggested a ratio of intra/interspecific interaction strength of 4 or 5 in land plants. Our estimates are in this range (the ratio being at least 10), suggesting greater niche differentiation in phytoplankton. This result, based on our spatially replicated dataset, is confirmed by a re-analysis of published interaction matrices using identical time series techniques. We therefore conclude that there is widespread niche differentiation in phytoplanktonic communities, just as in land plants, and our discussion explores what those niches may be (notably natural enemies, as well as spatial differentiation).

More surprisingly, and this is a key novel feature of our paper, we show that facilitative interactions are to be expected for phytoplanktonic communities (>50% on average, and always above 40%). To our knowledge, this is the first time that widespread facilitation is shown as

clearly in phytoplankton. It is likely that such positive net effects between taxa greatly help their coexistence as well.

Finally, our manuscript also sheds a new light on the stability-complexity debate: we show that while direct links between network resilience and complexity are absent, indicators of a taxon vulnerability to interspecific interactions covary with self-regulation strength and rarity. This helps the less common taxa to persist, and therefore contributes as well to biodiversity maintenance.

Overall, our manuscript provides empirical, field-based answers to the plankton paradox - as opposed to the overwhelmingly experimental evidence so far, which usually favours non-equilibrium theories. We found instead a strong niche differentiation (self-regulation), many facilitative interactions, and a covariance between intra- and inter-taxa interactions, that seem to be key features of coexisting phytoplanktonic communities in the field.

We therefore believe that our manuscript will be able to appeal to all ecologists (terrestrial and marine alike) interested in how diversity maintains. We hope that our manuscript constitutes a suitable match for Journal of Ecology, and we look forward to hearing from you,

Sincerely yours,

Frédéric Barraquand & Coralie Picoche

References cited in the cover letter:

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Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, 106, 1773–1794.

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