

1 Intro

The continued maintenance of diversity in spite of widespread competition has bewildered ecologists, especially for primary producers such as phytoplankton that share the same basic resources (Hutchinson, 1961). The first solution that has been proposed for the ‘paradox of the plankton’ was the temporal variation of the environment. However, inclusion of temporal variability per se in competition models is not sufficient for maintaining a realistic diversity (Fox, 2013). Additional mechanisms such as the storage effect Chesson (1994); Ellner et al (2016) or relative nonlinearity of competition (Chesson, 2000; Fox, 2013) need to be introduced. Richness rarely exceeds a dozen of species in this type of model, except when external inputs such as immigration maintain the dynamics (Jabot and Lohier, 2016). To our knowledge, the effect of temporal variability on persistence in competition models has mostly been tested in theoretical communities of 2 to 3 species (Chesson and Huntly, 1997; Litchman and Klausmeier, 2001) .

One of the richest modeled communities that we identified is the model of Scranton and Vasseur (2016), which is based on temperature variation and different thermal optima for each species (Moisan et al, 2002). In this model, the synchronizing effect of the environment and the storage effect can maintain 12 phytoplankton-like species on average. Scranton and Vasseur (2016) described daily temperature as a random noise, i.e., independent and identically distributed Gaussian random variates over time. However, under most latitudes, seasonality drives part of the environmental variation: over short timescales, random temporal variations often only add noise to a largely deterministic seasonal trend.

Seasonality can indeed strongly affect the dynamics of communities, whether it be in models (Miller and Klausmeier, 2017; Vesipa and Ridolfi, 2017) or in empirical analyses (Boyce et al, 2017; Barraquand et al, 2018). How seasonality affects coexistence, as opposed to a purely randomly fluctuating environment, is therefore a key feature of this paper. Our present work can be seen as an attempt to blend Scranton and Vasseur (2016)’s stochastic framework with the periodic environments of Barabás et al (2012), to better represent the mixture of stochastic and deterministic environmental forces affecting phytoplankton community dynamics.

Niche differences between species, leading to intraspecific interaction stronger than interspecific interactions, has recently been confirmed as a key mechanism in terrestrial plant communities (Adler et al, 2018), animal communities (Mutshinda et al, 2009), and phytoplanktonic communities (Barraquand et al, 2018). The interaction between environment variability and niche overlap has been investigated by Abrams (1976) but their relative contribution to coexistence was not evaluated.

Niche models have often been opposed to the neutral theory (Hubbell, 2001). An intriguing offshoot of the niche vs neutrality debate is the concept of ‘clumpy coexistence’ (Scheffer and van Nes, 2006), whereby simultaneous influences of both niche and neutral processes create several clumps of similar species along a single trait axis. Niche differences enable coexistence of multiple clumps (Chesson, 2000) while within-clumps coexistence occurs through neutral processes. This ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying concept

for niche and neutral theories even though the neutrality of such model has been disputed due to hidden niches (Barabás et al, 2013). Since then, clumpy coexistence has appeared in theoretical models incorporating temporal variations (Scranton and Vasseur, 2016; Sakavara et al, 2018). These models, and the biomass-trait distributions that they output, may provide some understanding of multimodal trait patterns (D’Andrea and Ostling, 2016).

Here, we therefore try to establish what are the relative contributions to coexistence of the storage effect vs strong self-regulation, in a phytoplankton-like theoretical community model. We consider both species richness and the distribution of these species. This led us to cross different combinations of seasonality in the forcing signal, presence of the storage effect or not, and intra- vs interspecific competition intensity, in order to disentangle the contributions of all these factors to biodiversity maintenance.

References

- Abrams PA (1976) Niche overlap and environmental variability. *Mathematical Biosciences* 28(3):357–372, doi:10.1016/0025-5564(76)90133-4
- Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, Meiners JM, Tredennick AT, Veblen KE (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters* 21(9):1319–1329, doi:10.1111/ele.13098
- Barabás G, Meszéna G, Ostling A (2012) Community robustness and limiting similarity in periodic environments. *Theoretical Ecology* 5(2):265–282, doi:10.1007/s12080-011-0127-z
- Barabás G, D’Andrea R, Rael R, Meszéna G, Ostling A (2013) Emergent neutrality or hidden niches? *Oikos* 122(11):1565–1572, doi:10.1111/j.1600-0706.2013.00298.x
- 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* In press, doi:10.1101/171264
- Boyce DG, Petrie B, Frank KT, Worm B, Leggett WC (2017) Environmental structuring of marine plankton phenology. *Nature Ecology & Evolution* doi:10.1038/s41559-017-0287-3
- Chesson P (1994) Multispecies Competition in Variable Environments. *Theoretical Population Biology* 45:227–276, doi:10.1006/tpbi.1994.1013
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics* 31:343–366, doi:10.1146/annurev.ecolsys.31.1.343
- Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150(5):519–553, doi:10.1086/286080

- D’Andrea R, Ostling A (2016) Challenges in linking trait patterns to niche differentiation. *Oikos* 125(10):1369–1385, doi:10.1111/oik.02979
- Ellner SP, Snyder RE, Adler PB (2016) How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters* 19(11):1333–1342, doi:10.1111/ele.12672
- Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology & Evolution* 28(2):86–92, doi:10.1016/j.tree.2012.08.014
- Holt R (2006) Emergent neutrality. *Trends in Ecology & Evolution* 21(10):531–533, doi:10.1016/j.tree.2006.08.003
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (MPB-32). Princeton University Press
- Hutchinson GE (1961) The paradox of the plankton. *The American Naturalist* 95(882):137–145
- Jabot F, Lohier T (2016) Non-random correlation of species dynamics in tropical tree communities. *Oikos* 125(12):1733–1742, doi:10.1111/oik.03103
- Litchman E, Klausmeier CA (2001) Competition of phytoplankton under fluctuating light. *The American Naturalist* 157(2):170–187
- Miller ET, Klausmeier CA (2017) Evolutionary stability of coexistence due to the storage effect in a two-season model. *Theoretical Ecology* 10(1):91–103, doi:10.1007/s12080-016-0314-z
- Moisan JR, Moisan TA, Abbott MR (2002) Modelling the effect of temperature on the maximum growth rates of phytoplankton populations. *Ecological Modelling* 153(3):197–215, doi:10.1016/S0304-3800(02)00008-X
- Mutshinda CM, O’Hara RB, Woivod IP (2009) What drives community dynamics? *Proceedings of the Royal Society B: Biological Sciences* 276(1669):2923–2929, doi:10.1098/rspb.2009.0523
- Sakavara A, Tsirtsis G, Roelke DL, Mancy R, Spatharis S (2018) Lumpy species coexistence arises robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences* 115(4):738–743, doi:10.1073/pnas.1705944115
- Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences* 103(16):6230–6235, doi:10.1073/pnas.0508024103
- Scranton K, Vasseur DA (2016) Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. *Theoretical Ecology* 9(3):353–363, doi:10.1007/s12080-016-0294-z
- Vesipa R, Ridolfi L (2017) Impact of seasonal forcing on reactive ecological systems. *Journal of Theoretical Biology* 419:23–35, doi:10.1016/j.jtbi.2017.01.036