

1 Intro

The diversity of communities has bewildered ecologists for years, especially for primary producers such as phytoplankton (Hutchinson, 1961). One of the first solutions that have been proposed for the ‘paradox of the plankton’ was the temporal variation of the environment. However, inclusion of temporal variability in competition models is not sufficient for maintaining a realistic diversity Fox (2013) as richness never exceeds a dozen of species in this type of model (Dakos, 2009), except when the dynamics are maintained by immigration (Jabot et al. 2016). Coexistence mechanisms such as the storage effect Chesson (1994); Ellner et al (2016) [DEFINE storage effect?] can help to increase the persistence of species in the community, but, to our knowledge, this was mostly tested on theoretical communities of 2 to 3 species (Litchman and Klausmeier 2001, Chesson and Huntly 1997).

One of the richest modeled communities we identified is the model of Scranton and Vasseur (2016), which is based on temperature variation and different thermal optima defining 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, empirical analysis investigating the effect of a variable environment do not always identify the storage effect while still showing the importance of seasonal variation on the dynamics of phytoplanktonic communities (Barraquand et al, 2018).

Seasonality, which is a common feature under most latitudes, can indeed strongly affect the dynamics of a community (Vesipa and Ridolfi, 2017, Miller and Klausmeier). How seasonality affects coexistence (as opposed to a purely randomly fluctuating environment) is a key feature of this paper. Our present work can therefore 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. In particular, we contrast cases where the storage effect is present vs absent. Moreover, the overall diversity obtained at the end of the simulations with Scranton and Vasseur (2016)’s model was relatively low compared to what we usually observe in phytoplankton communities (several dozens to hundreds of species). We have therefore sought out which mechanisms would foster a truly species-rich community for extended periods of time.

Niche differences, leading to intraspecific interaction stronger than interspecific interactions, has recently been confirmed as 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 et al. 1976 [which inspired SV] but their relative contribution to coexistence was not evaluated. Here, niche differences are both explicit (through growth-temperature relationship) and implicit (through the interaction coefficients), enabling us to isolate different effects.

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. This 'emergent neutrality' within groups (Holt, 2006) has been proposed as a unifying concept for niche and neutral theories even though the concept has been disputed (Barabás et al, 2013). Clumpy coexistence appears in theoretical models incorporating temporal variations (Scranton and Vasseur, 2016; Sakavara et al, 2018) and may provide some clues to the questions behind 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 also consider 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

- 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
- Chesson P (1994) Multispecies Competition in Variable Environments. *Theoretical Population Biology* 45:227–276, doi:10.1006/tpbi.1994.1013
- 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
- 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, Woiwod 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