

~~Stabilizing niche differences are required to maintain
species-rich communities in temporally variable
environments~~How self-regulation, storage effect and their
interaction contribute to coexistence in stochastic and
seasonal environments

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Abstract

Explaining coexistence in species-rich communities of primary producers remains a challenge for ecologists because of the likely competition for shared resources. Following Hutchinson's seminal suggestion, many theoreticians have tried to create diversity through a fluctuating environment, which impairs or slows down competitive exclusion. There are now several fluctuating-environment models allowing coexistence, but they often produce only a dozen of coexisting species at best. Here, we investigate how to create even richer communities in fluctuating environments, using an empirically parameterized model. Building on the forced Lotka-Volterra model of Scranton and Vasseur (2016) inspired by phytoplankton communities, we have investigated the effect of two coexistence mechanisms, namely the storage effect and differences in intra- and interspecific competition strength. We tuned the competition ratio on empirical data, in which self-regulation supersedes interspecific interactions in phytoplankton dynamics. ~~stabilizing niche differences (SNDs). SNDs occur when intraspecific competition is stronger than interspecific; we tuned the competition ratio based on empirical data.~~ Although ~~SNDs~~ a strong self-regulation maintained more species (50%) than the storage effect (25%), we show that none of the two coexistence mechanisms considered could, by itself, ensure the coexistence of all species present at the beginning of our simulations. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to ~~white noise~~ a random environment. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which mechanism explains best the observed diversity levels. Our results on community composition (formation of clumps, biomass distribution) in the different scenarios give further hints about likely coexistence mechanisms at work.

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Keywords: coexistence; seasonality; competition; phytoplankton; Lotka-Volterra; storage effect

1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives on species coexistence (Gravel et al, 2006; Carmel et al, 2017). Under the neutral perspective, all species have equal birth and death rates and compete equally (since space is limited) whilst under the niche perspective, birth and death rates can vary between species and various mechanisms contribute to increasing intraspecific over interspecific competition (Hubbell, 2001). However, as it has been pointed out repeatedly, niche and neutral processes are not mutually exclusive: they may actually act together to produce observed species coexistence (Gravel et al, 2006; Mutshinda et al, 2009; Götzenberger et al, 2012).

For instance, Scheffer and van Nes (2006) put forward the concept of ‘clumpy coexistence’, whereby a simultaneous influence of both niche and neutral processes create several clumps of similar species along a single trait axis. Classical stabilizing niche differences (SNDs), [such as stronger net intraspecific competition](#), enable coexistence of multiple clumps ~~through stronger net intraspecific competition~~ (Chesson, 2000), while within-clump coexistence occurs through neutral processes (Hubbell, 2001; Munoz and Huneman, 2016), as species that differ too little in their fitnesses cannot exclude themselves out on reasonable timeframes. Indeed, clumps on the trait axis eventually thin out in absence of immigration, but transient coexistence can last for extended periods of time. This ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying concept for the niche and neutral theories. The findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013). Hidden niches emerge through stronger intraspecific competition mediated by a an additional intraspecific predation-like term (Barabás et al, 2013). This makes coexistence in the Scheffer and van Nes model more similar to that of the classical Lotka-Volterra model (Barabás et al, 2016), so that coexistence within clumps is not exactly neutral. Still, the idea that niche and neutral assembly can mould communities stays potent (Vergnon et al, 2013). Since then, several studies have suggested that ‘clumpy coexistence’ can occur in theoretical models, most notably models incorporating temporal variation (Scranton and Vasseur, 2016; Sakavara et al, 2018). In these temporal-variation models, equal competitive strengths are combined with other mechanisms like the storage effect

55 (or temporal niche partitioning, that is an equivalent concept for forced Lotka-Volterra models,
56 Barabás et al, 2012; Scranton and Vasseur, 2016). The storage effect increases the possibility of
57 coexistence by making the interaction strength covary positively with a fluctuating environment
58 (see also Barabás et al, 2012).

59 Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of
60 coexistence through species response to fluctuating environments. Our enthusiasm for the Scranton
61 and Vasseur (2016) model stems from our interest in phytoplankton communities, that inspired
62 their thermal preference curves modeling intrinsic growth rates. However, Scranton and Vasseur
63 (2016) described temperature as a ~~white~~random noise, i.e., independent and identically distributed
64 Gaussian random variates over time. This appeared to us a key assumption to relax. Under most
65 latitudes, temperature is indeed a seasonal signal, and seasonal forcing can strongly affect the
66 dynamics of the community considered (Vesipa and Ridolfi, 2017). Hence, over short timescales,
67 random temporal variations often only add noise to a largely deterministic seasonal trend. Our
68 present work can therefore be seen as an attempt to blend Scranton and Vasseur (2016)’s framework
69 with the periodic environments of Barabás et al (2012), to better represent the mixture of stochastic
70 and deterministic environmental forces affecting phytoplankton community dynamics.

71 Because many phytoplankton species or genera respond in similar ways to temperature despite
72 having different optimas (Moisan et al, 2002), we hypothesized that a large seasonal variation
73 might not necessarily foster species coexistence. In fact, similar responses to seasonal fluctuations
74 should lead to an increased synchrony of species abundances which, in turn, should theoretically
75 mitigate the expected temporal partitioning. How seasonality affects coexistence (as opposed to a
76 purely randomly fluctuating environment) is therefore a key feature of this paper. In particular,
77 we contrast cases where the storage effect is present vs. absent, which conveniently maps to
78 two different parameterizations of the forced Lotka-Volterra model. Moreover, the overall diversity
79 obtained at the end of the simulations with Scranton and Vasseur (2016)’s model was relatively low
80 compared to what we usually observe in phytoplankton communities (several dozens to hundreds
81 of species). We have therefore sought out which mechanisms would foster a truly species-rich
82 community for extended periods of time.

83 In an empirical study combining phytoplankton community-level time series and multivariate
84 autoregressive models (Barraquand et al, 2018)¹, we found that despite a large influence of the
85 environment (including temperature, irradiance, and other factors), intraspecific (or intragenus)
86 competition was most likely the key driver of species coexistence. In other words, a stabilizing niche
87 differencesstrong self-regulation had a large role to play in maintaining species diversity in coastal
88 phytoplankton (Barraquand et al, 2018). These SNDshigh intraspecific interaction strengths mir-
89 ror those found in a number of terrestrial plant communities (Adler et al, 2018) and in animal
90 communities (Mutshinda et al, 2009).

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

96 2 Methods

97 *Models description*

98 The model described in Scranton and Vasseur (2016) is based on a variant of the Lotka-Volterra
99 competition model. Fluctuations in the environment are introduced in the model by temperature-
100 dependent intrinsic growth rates (see Eq. 1-2, all coefficients are defined in Table 1) so that species
101 growth rates can be expressed as:

¹Preprint version available: see Barraquand et al (2017) in the reference list

$$\frac{dN_i}{dt} = r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha_{ij}N_j\right) - mN_i \quad (1)$$

$$r_i(\tau) = a_r(\tau_0)e^{E_r \frac{(\tau - \tau_0)}{k\tau\tau_0}} f_i(\tau) \quad (2)$$

$$\text{where } f_i(\tau) = \begin{cases} e^{-|\tau - \tau_i^{opt}|^3/b_i}, & \tau \leq \tau_i^{opt} \\ e^{-5|\tau - \tau_i^{opt}|^3/b_i}, & \tau > \tau_i^{opt} \end{cases} \quad (3)$$

$$\text{and } b_i \text{ defined by numerically solving } \int r_i(\tau)d\tau = A \quad (4)$$

102 Model parameters are detailed in Table 1, and we set their values to match the features of
 103 phytoplankton communities as in Scranton and Vasseur's work (2016). The niche of each species is
 104 defined by its thermal optimum τ_i^{opt} . Thermal performance curves defined in Eq. 3 are parameter-
 105 ized so that all species share the same niche area (Eq. 4), which sets a trade-off between maximum
 106 growth rates and niche width.

Table 1: Parameter definition and values of the model described in Eq. 1-4. Parameter values are not specified when they vary with time and/or the species considered.

Name	Definition	Value (unit)
S	Number of species	60 ()
N_i	Biomass density of the i th species	(kg/area)
τ	Temperature	(K)
$r_i(\tau)$	Growth rate of species i as a function of temperature	($\frac{\text{kg}}{\text{kg}^*\text{year}}$)
α_{ij}	Strength of competition of species j on species i	0.001 (area/kg)
b_i	Normalization of the thermal decay rate	(K^3)
m	Mortality rate	$15(\frac{\text{kg}}{\text{kg}^*\text{year}})$
τ_0	Reference temperature	293 (K)
$a_r(\tau_0)$	Growth rate at reference temperature	$386(\frac{\text{kg}}{\text{kg}^*\text{year}})$
E_r	Activation energy	0.467 (eV)
k	Boltzmann's constant	$8.6173324 \cdot 10^{-5}(\text{eV} \cdot \text{K}^{-1})$
$f_i(\tau)$	Fraction of the maximum rate achieved for the i th species	()
μ_τ	Mean temperature	293 (K)
σ_τ	Standard deviation for temperature	5 (K)
τ_{\min}	Minimum thermal optimum	288 (K)
τ_{\max}	Maximum thermal optimum	298 (K)
A	Niche breadth	$10^{3.1}(\frac{\text{kg}}{\text{kg}^*\text{year}})$
τ_i^{opt}	Thermal optimum for growth of the i th species	(K)
θ	Scaling between whiterandom and seasonal noise and seasonal signal	$[0, \sqrt{(2)}]$ ()
ρ	Ratio of intra-to-intergroup competition strengths	(1;10) ()

107 The original environmental forcing is a normally distributed variable centered on 293 K, with
108 a 5K dispersion. This variable varies from one day to another but is kept constant throughout the
109 day. At the macro-temporal scale usually used in ecological studies, temperature could therefore
110 be considered as a white noise (Vasseur and Yodzis, 2004) but it is slightly auto-correlated as the
111 integration process goes below the daily time step. We have therefore chosen to use the word
112 'random noise' to describe this forcing and remain coherent with the 'seasonal noise' described
113 hereafter. We ~~kept~~keep the mean and standard deviation of the forcing signal but included a
114 lower-frequency component using a sinusoidal function with a period of 365 days (~~1 time unit~~
115 ~~being one day~~, Eq. 5). We tune the ratio of low-to-high frequency with the variable θ so as to keep
116 the same energy content - i.e., equal total variance - in the forcing signal.

$$\tau(t) = \mu_\tau + \theta \sigma_\tau \sin(2\pi t) + \epsilon_t, \text{ where } \epsilon_t \sim \mathcal{N}(0, \sigma_\tau \sqrt{1 - \frac{\theta^2}{2}}) \quad (5)$$

117

118 Note that the upper limit for θ , $\sqrt{2}$, corresponds to a completely deterministic model which we
 119 do not explore here (but see Zhao (1991) proving bounded coexistence). We choose to keep the
 120 stochasticity in the signal and to model a plausible temperature signal with $\theta = 1.3$ (see Fig. 1b)
 121 when considering a seasonal forcing of the dynamics.

122 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies a
 123 storage effect, as the net effect of competition on a given species is the product of the temperature-
 124 related growth rate and the sum of competitive strengths exerted by other species. Therefore,
 125 ~~competition strengths~~ net competition covaries positively with the growth rate values $r_i(\tau)$ (Chesson,
 126 1994; Ellner et al, 2016). ~~To test for the effect of an explicit storage effect in the model, we~~
 127 ~~formulated a new version of this model, where~~ we removed this assumption of an explicit storage
 128 effect in another version of the model by using the mean value of a species' growth rate (\bar{r}_i) to
 129 weight the interaction coefficients (see Table 2). The mean growth rate value was computed by
 130 first generating the temperature time series and averaging all r_i over the corresponding simulation.

$$\frac{dN_i}{dt} = N_i \left(r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha_{ij} N_j \right) - m N_i \quad (6)$$

131 In this way, competition strengths remain unaffected by the environmental conditions, in con-
 132 trast to growth rates (Eq. 6), while preserving the same average magnitude as in Eq. 1.

133 ~~Stabilizing niche differences are~~ Strong self-regulation is ensured by the addition of the coefficient
 134 ρ , which is the ratio of intra-to-intergroup competition strength. We can therefore re-write the
 135 interaction coefficients α_{ij} in Eq. 7

$$\alpha_{ij} = \alpha (1 + (\rho - 1) \delta_{ij}) \quad (7)$$

137

138 where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. The value of the
 139 parameter $\rho = 10$ was chosen from analyses of phytoplanktonic data (Barraquand et al, 2018)

140 ². Hereafter, the phrase “strong (and respectively, weak) self-regulation” characterizes dynamics

²The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2018) are

where the intraspecific competition strength is 10 times higher than (and respectively, equal to) the interspecific competition strength. When we use the word “strong”, we therefore consider a “relatively stronger” self-regulation but do not wish to compare our interaction values to those used outside of our framework.

In addition to two types of environmental forcings (~~white~~random noise with $\theta = 0$, and seasonal ~~foreign~~noise with $\theta = 1.3$), we ~~therefore~~ compare the results for four formulations of the model: with and without an explicit storage effect (Eq. 1 and Eq. 6, respectively) ; with and without ~~stabilizing niche differences~~strong self-regulation ($\rho = 10$ or $\rho = 1$, respectively). These are summed up in Table 2

$\frac{dN_i}{dt} + mN_i$	Storage effect	No storage effect
Stabilizing niche differences Strong self-regulation	$r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha (1 + 9\delta_{ij}) N_j\right)$	$N_i \left(r_i(\tau) - \sum_{j=1}^S \alpha N_j\right)$
No stabilizing niche differences Weak self-regulation	$r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha N_j\right)$	$N_i \left(r_i(\tau) - \sum_{j=1}^S \alpha N_j\right)$

Table 2: Growth rate of species i in the four formulations of the model we present

Set-up

We replicate the ‘Species sorting’ experiment of Scranton and Vasseur (2016) so as to investigate how the structure of synthetic phytoplankton communities varies under the different scenarios we described above. We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval $[15^\circ\text{C}, 25^\circ\text{C}]$, and with the same initial density ($\frac{1}{\alpha S}$). Each simulation was run for 5000 years in 1-day intervals. When the density of a species dropped below 10^{-6} , it was considered extinct. For each combination of parameters (type of environmental signal, storage effect and stabilizing niche differences), we ran 100 simulations.

All simulations were ran with Matlab’s ode45 algorithm, an explicit Runge-Kutta (4,5) algorithm with an absolute error tolerance of 10^{-8} , and relative error tolerance 10^{-3} . The code is available in a GitHub repository ³.

somewhat higher than here (and ρ lower, closer to 4) because the best-fitting model actually set to zero some intergroup competition coefficients; using a model where all α_{ij} are non-zero leads in contrast to $\rho = 10$.

³<https://github.com/CoraliePicoche/Seasonality>, will be made public upon acceptance or at the reviewer’s

3 Results

Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016), with both the environmental signals described in Eq. 1 (original choice of Scranton and Vasseur, 2016; Fig. 1a) and Eq. 5 (our variant, Fig. 1b), are shown in Fig. 1c and d. A sinusoidal forcing produces the strongly seasonally structured dynamics that are typical of phytoplankton. Even though only 5 species can be seen in Fig. 1c, there were 14 species still present at the end of the simulation forced by a **whiterandom** noise, with large disparities in the range of variation of their biomasses. A third of the species kept a biomass above 10 kg/area (setting area = 1 ha, with a depth of a few meters, produce a realistic standing biomasses; Reynolds, 2006) while 6 out of the 14 remained below the unit. All persisting species in the **whiterandom** noise simulations were clustered within a 3.2°C-range of thermal optima (see the biomass distribution as a function of the thermal optimum in Fig. A1 in the Supplementary Material). No obvious temporal patterns (e.g., cycles) could be seen in the communities forced by **whiterandom** noise. On the contrary, seasonal cycles were clear in the seasonally-forced case of Fig. 1d. Only 4 species coexisted at the end of the simulation with seasonal **foreingnoise**, gathered in two groups with large thermal optimum differences (5.7°C between the maximum thermal optimum of the first group and the minimum thermal optimum of the second group). When temperatures are high, the group with higher thermal optima reaches its maximum biomass, then as temperature decreases through the season, these species leave room for the growth of the low-temperature group.

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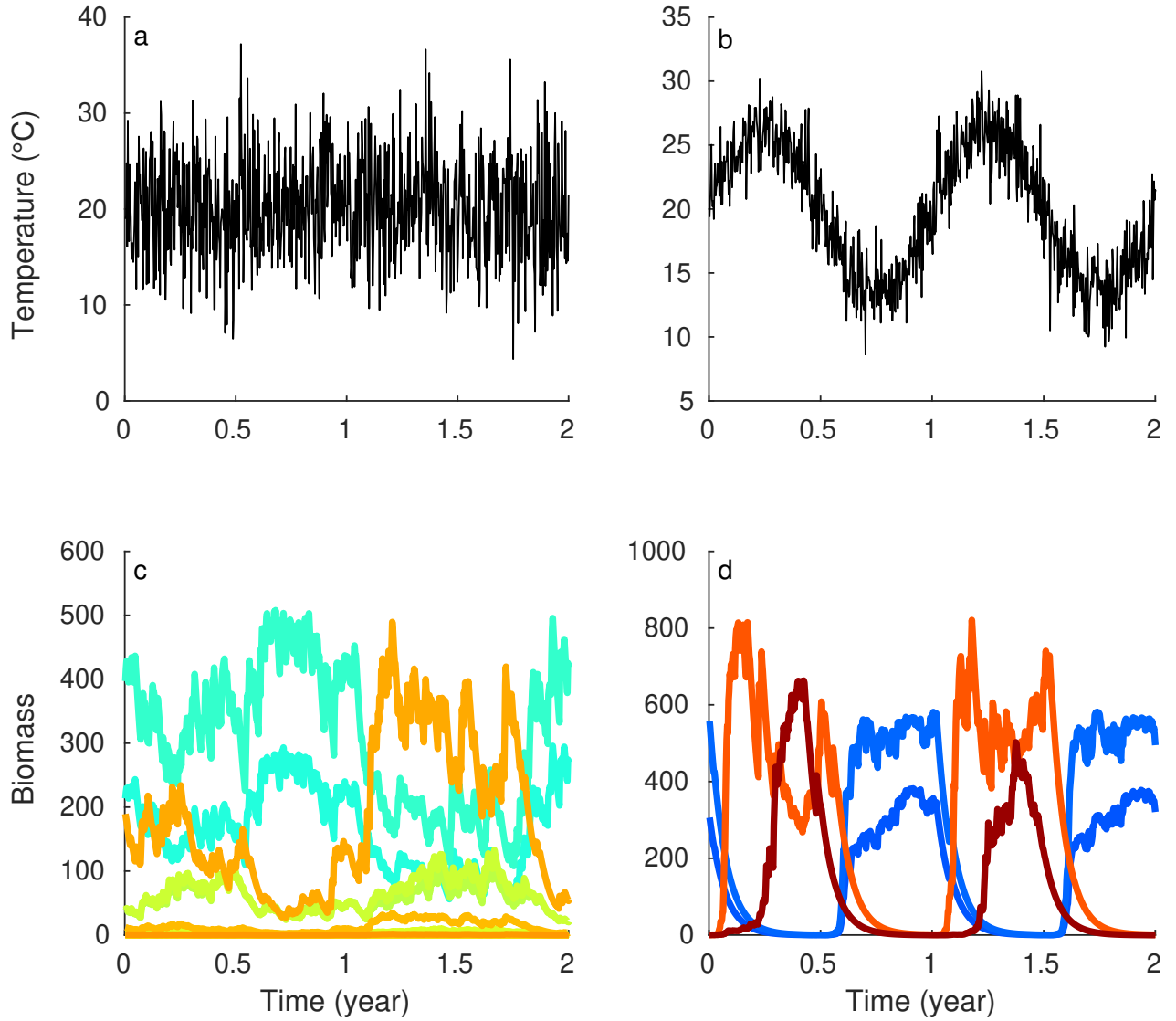


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000 years simulation, with storage effect and ~~no stabilizing niche differences~~ ~~no differences between intraspecific and interspecific competition strengths~~. The forcing temperature is either a ~~white~~ random noise (a) or a ~~noisy~~ seasonal ~~signal~~ noise (b), leading to community dynamics with more erratic fluctuations (c) vs seasonally structured fluctuations (d). Line colors of species biomasses correspond to their thermal optimum (from blue, corresponding to low thermal optimum, to red, corresponding to high thermal optimum).

181 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our simu-
 182 lations (Fig. 2). In cases where final species richness varied from one simulation to another (namely,
 183 the two middle cases in Fig. 2: with storage effect but without ~~stabilizing niche differences~~ ~~strong~~
 184 ~~self-regulation~~, or without storage effect but with ~~stabilizing niche differences~~ ~~strong~~ self-regulation),
 185 seasonality reduced the number of extant species to, on average, 27% and 48% of their original

186 values, respectively (Fig. 2). A seasonal signal therefore led to a much smaller average persistence.
187 There was also less variance in persistence between seasonally forced simulations when compared
188 to ~~white~~random noise simulations.

189 Both ~~the~~ ~~stabilizing niche differences~~strong self-regulation and the storage effect markedly
190 increased persistence. Without any of these coexistence mechanisms, only one species persisted at
191 the end of the simulations. When only the storage effect was present, the number of extant species
192 varied between 8 and 20 (14.8 ± 2.4) with a white noise, or 2 and 6 (4.1 ± 0.7) with a seasonal
193 signal. On the other hand, when only ~~stabilizing niche differences~~a strong self-regulation~~were~~was
194 present, the number of extant species nearly doubled, varying between 20 and 32 (27.5 ± 2.4), or 12
195 and 15 (13.3 ± 0.6), with a ~~white~~random noise~~or~~ a seasonal ~~signal~~noise, respectively. Remarkably,
196 when the storage effect and ~~SND~~s a strong self-regulation both affected the community dynamics,
197 all species persisted in the community, while neither of these mechanisms was able to produce that
198 result alone, for either ~~white~~random~~noise~~ and seasonal ~~foreign~~noise.

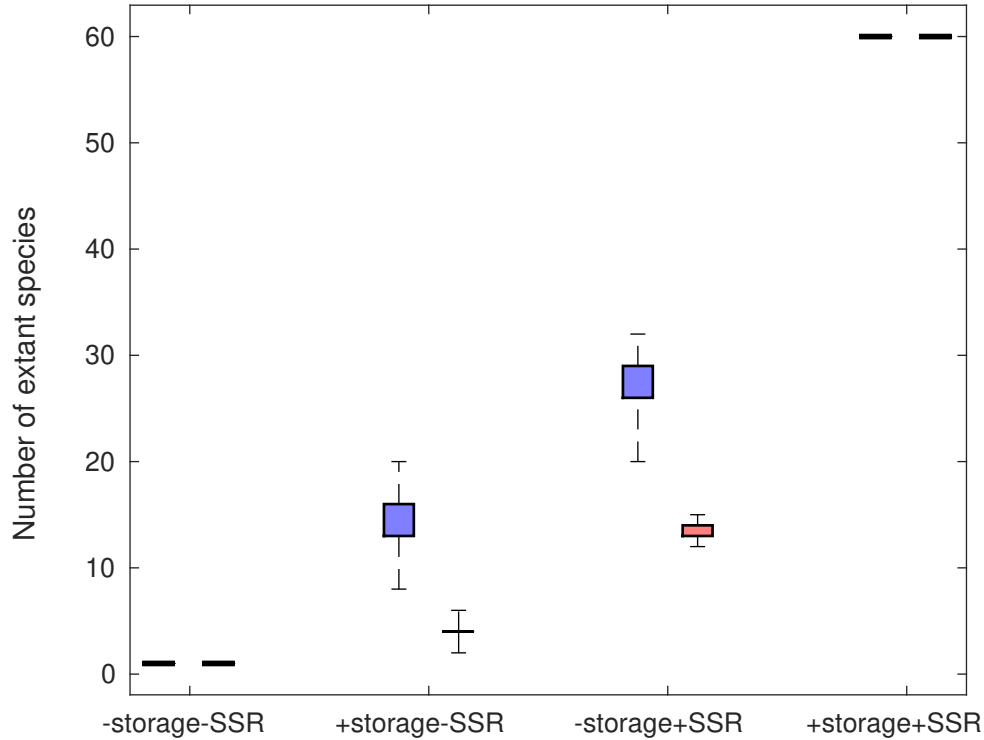


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a ~~white~~random noise forcing signal (blue) or a ~~noisy~~-seasonal ~~signal~~noise (red). The signs + or - storage refer to presence or absence of a storage effect, respectively; + / - ~~SND~~SSR, presence or absence of ~~Stabilizing Niche Differences~~Strong Self-Regulation, respectively. Community compositions are stable in the cases -storage-~~SND~~SR and +storage+~~SND~~SR, for which 1 or 60 species are still present at the end of all simulations, respectively. Due to low variance, the whiskers here represent min and max rather than 1.5 interquartile range.

When the richness of the community was stable (either 1 or 60 species at the end of the simulation), there were still large differences in the structure of the community with respect to temperature, due to both stochasticity and the type of forcing (Fig. 3). The trait pattern of the community was affected by the type of forcing even when the richness of the community was stable (Fig. 3). Without storage effect nor ~~SND~~sstrong self-regulation, there was only one species left at the end of a simulation. ~~a~~A ~~white~~random noise ~~forcing~~-favored species with intermediate thermal optima; the final species had a thermal optimum between 18.9°C and 21.4°C (only a fourth of the initial range of thermal optima) for two simulation out of three and the maximum final biomasses over 100 simulations was reached in this range ~~with two thirds of the simulations ending with a species with a thermal optimum between 18.9°C and 21.4°C (corresponding to only one fourth of~~

the range of thermal optima present at the beginning of the simulation) and reaching a maximum average biomass in this range (Fig. 3a). [[[This distribution can be related to a selection for the highest long-term growth rates, averaged over time (see scaled growth rates in Fig. 3).]]] On the contrary, sSeasonality with no coexistence mechanisms also tended to favor led to a single final species but, in this case, the species always had a with larger higher maximum growth rates (thermal optima above 22°C). - Species with a higher thermal optimum are were more likely to persist and to reach a higher biomass at the end of the simulation. 38% of the simulations therefore ended with the species having the highest temperature optimum, 25°C. The shift in trait distribution towards higher maximum growth rates with seasonality vs. higher average growth rates with a random noise was consistent in all sets of simulations (see below). -38% of the simulations therefore ended with the species having the highest temperature optimum, 25°C.

When both ~~coexistence mechanisms~~ storage effect and strong self-regulation were present, the 60 initial species coexisted with small variations in biomasses for each species over the 100 simulations (mean CV=0.008 across simulations with either a white noise random or a seasonal forcing signal noise, Fig. 3b and d). The forcing signal modified only the distribution of biomasses resulting in contrasted community structures despite equal richness in both simulation types. With a white random noise, the distribution was unimodal with a maximum biomass reached for the second best long-term average growth rate (corresponding to a thermal optimum of 20.2°C). On the contrary, a seasonal signal led to a bi-modal distribution (centered on 17.0°C and 24.4°C), each corresponding to one season, with highest biomasses for higher thermal optima (Fig. 3d). The minimum biomass was reached for the best long-term average growth rate at an intermediate temperature (20.4°C), one species apart from the maximum biomass in the white random noise case.

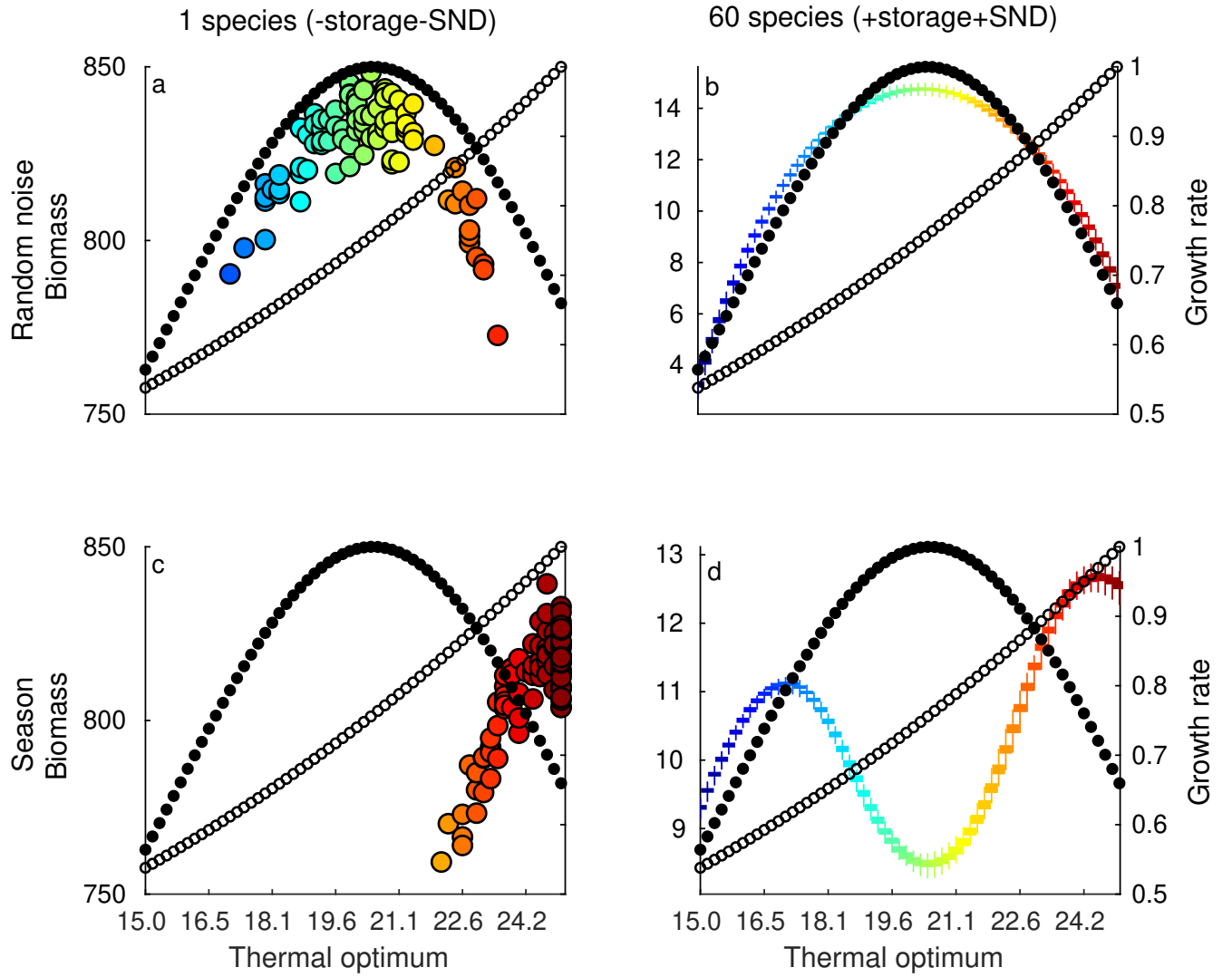


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor **stabilizing niche differences** **strong self-regulation** are presented. Only one species is present at the end of the simulations and its mean value is represented by one large colored circle per simulation. There can be several circles for the same species, corresponding to multiple simulations ending with this species alone. On the right column, simulations with storage effect and **stabilizing niche differences** **strong self-regulation** are represented. All species are present at the end of the simulations and small boxplots present the variation in the temporal average of biomass with a given trait, for 100 simulations. The forcing signal is either a **white random noise** (top) or a seasonal **signal noise** (bottom). Each species is identified by its thermal optimum through its color code. Scaled (divided by maximum) average and maximum growth rates are shown as small filled and open circles, respectively, and are indexed on the right y-axis.

232 In cases where the richness of the community varied, the overall shape (multimodal vs. uni-
 233 modal) of the marginal distribution of extant species with respect to the trait axis were similar
 234 for both types of environmental forcings (Fig. 4). By contrast, the type of coexistence mechanism

235 generated different shapes. Indeed, the storage effect led to a multimodal biomass distribution
 236 with respect to thermal optima. We always observed 3 modes with a ~~whiterandom~~ noise and 3
 237 modes in 95% of the seasonal simulations (Fig. 4a). With a ~~whiterandom~~ noise, extant species are
 238 grouped in rather similar clumps regarding species thermal optima (between 18.8°C and 22.2°C)
 239 whereas clumps tended to be further apart in the seasonal case, covering a total range of 7.7°C,
 240 with species grouping in the higher part of the thermal range, above 22°C. On the other hand,
 241 ~~stabilizing niche differences~~strong self-regulation led to a quasi-uniform biomass distribution (Fig.
 242 4 b). Species characterising communities forced by a ~~whiterandom~~ noise stayed in the lower range
 243 of temperatures (in 96% of the simulations, the highest thermal optimum was 22.4°C, see Fig. A2
 244 in the Supplementary Material) while they were filtered out in communities subjected to a seasonal
 245 fluctuation of their environment, for which species with thermal optima above 20.5°C persisted.
 246 As before (Fig. 3), seasonality promoted species with a higher maximum growth rates since the
 247 autocorrelated temperatures enabled them to achieve this highest growth rate for a longer period
 248 of time than a random noise would have.

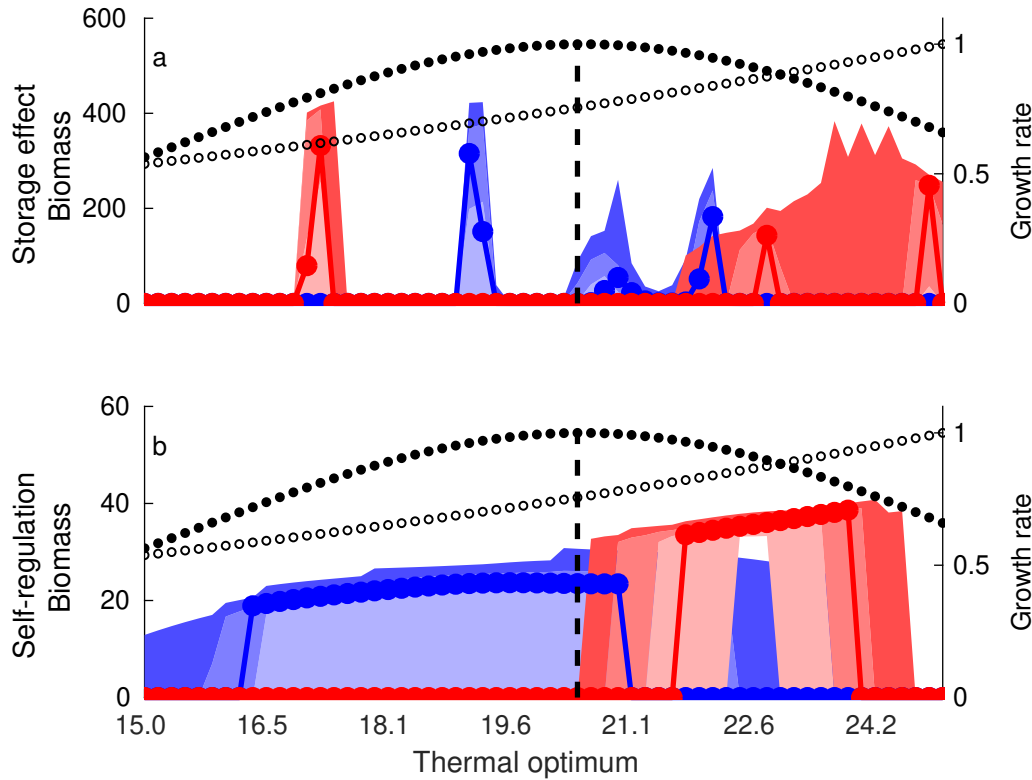


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and ~~weak self-regulation–no stabilizing niche differences~~ (a) and without storage effect, with ~~stabilizing niche differences~~~~strong self-regulation~~ (b). The forcing signal is either a ~~white noise~~~~random~~ (in blue) or a seasonal ~~signal~~~~noise~~ (in red). Shades of the same color correspond to the 50th, 90th and 100th percentiles of the distributions while colored lines correspond to one representative simulation. Scaled (divided by maximum) average (whose maximum is indicated by the dashed line) and maximum growth rates are shown as filled and open circles, respectively, and indexed on the right y-axis.

4 Discussion

We have simulated competitive Lotka-Volterra dynamics forced by a fluctuating environment (e.g., temperature fluctuations) under a range of scenarios allowing more or less coexistence. Two coexistence mechanisms, the storage effect and ~~stabilizing niches differences~~~~strong self-regulation~~, could be either present or absent, which led to four scenarios. These four scenarios were crossed with two possibilities for the forcing signal, a ~~white~~~~random~~ noise and a stochastic yet seasonal signal, both with equal temporal variance. Our investigation therefore built on the model of Scranton

and Vasseur (2016), which included a ~~white noise forcing~~noisy forcing and a storage effect, but considered seven additional combinations of mechanisms. This was motivated by our wish to include two observed features of phytoplankton dynamics: seasonal cycles (Winder and Cloern, 2010) and ~~stabilizing niche differences~~strong self-regulation (Chesson, 2000; Adler et al, 2010; Barraquand et al, 2018). ~~Stabilizing niche differences, that occur whenever i~~Many mechanisms can lead to intraspecific competition ~~isbeing~~ stronger than interspecific competition, ~~can arise from many mechanisms~~ : nonlinearities in the functional forms of competition or mutualism that contribute to increasing self-regulation (Kawatsu and Kondoh, 2018), predation or parasitism (see e.g., the generalist predators in Haydon, 1994), etc. They seem nonetheless an ubiquitous feature in primary producers (Adler et al, 2018).

We have found that first, temporally forced Lotka-Volterra dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the structure is geared to include either a storage effect or a ~~SNDs~~strong self-regulation. Although this absence of diversity-enhancing effect of “pure” environmental variation has already been stated by other authors (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth rate alone cannot help coexistence within competitive communities. A nice point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized for phytoplankton communities, could lead to some degree of coexistence. Our investigation reproduced these results, using the ~~white~~random noise ~~forcing~~considered by Scranton and Vasseur (2016). However, an arguably more lifelike noisy and seasonal temperature forcing considerably lessened the richness of the community after 5000 years, decreasing from 15 to 4 species on average. Even imagining that groups represented here are genera or classes rather than species, this is a fairly low diversity for a phytoplankton-like community (see Chapter 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own, be sufficient to maintain species-rich communities (e.g., dozens to hundreds of species). We have therefore sought out whether ~~stabilizing niche differences~~a stronger self-regulation could maintain a higher diversity, using field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al, 2018), where the intragroup density-

dependence was chosen 10 times stronger. The comparison of both coexistence mechanisms, the storage effect and a strong self-regulation, depends on the intensity of self-regulation of each species and the type of dynamics considered, which calls for further analyses on different networks before drawing a general conclusion. On their own, in a Lotka-Volterra model applied to phytoplankton species, a stronger self-regulation produced a higher level of diversity than the storage effect (almost double for white random noise), which not only aligns with our results on phytoplankton but also with results on perennial plants (Adler et al, 2010).

However, self-regulation was still insufficient to maintain the whole community diversity by itself, especially when the seasonal forcing ~~forcing still considerably reduced diversity when only SNDs were considered. , especially t~~ The “neutral” kind of diversity, i.e., diversity within clumps of similar values of ~~traits~~ growth rates was considerably decreased. This diversity reduction occurs because within a season, the signal autocorrelation gives long, contiguous time intervals to the best competitor to exclude its less adapted heterospecifics. ~~This makes the results likely to hold not only for seasonal environments, but more generally for autocorrelated ones, i.e., “red” noise.~~ This could be relevant for species whose population dynamics occurs at timescales largely above one year. In contrast, a white random noise generates large temperature shifts more frequently, and thereby forbid such competitive exclusion. In a seasonal setting, a species with the highest long-term averaged growth rate may not be the best competitor, and can disappear as a result of a strong competition from both low- and high-temperature tolerant species. This holds with or without a storage effect.

Our results may appear at odds with recent proposals that seasonal forcing in itself would help maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to that of other forcing signals while controlling for total variance. Thus, the contrast between our results and those of Sakavara et al (2018) may be due to the role of forcing variance over time (we compare scenarios under a constant total variance). Overall, while seasonality may be slightly better than no forcing at all in maintaining diversity, seasonal forcing of parameters does not improve coexistence: diversity within clumps is lower when seasonality is included.

In addition to community diversity, the biomass-trait relationship also varied from one sim-

312 ulation to another. Some regularities did emerge across simulations though. The storage effect
 313 begot several clumps along the trait space (as observed by Scranton and Vasseur, 2016). The
 314 seasonality that we added to the temperature signal led to more distant clumps on the trait axis
 315 (as said above, less species per clump). Conversely, **SNDs**strong self-regulatory mechanisms alone
 316 led to relatively uniform biomass distributions, with species forming a single large cluster, which
 317 covers a fraction of the initial trait space. Therefore, the shape of the disitribution was affected
 318 by the coexistence mechanism at stake while the average trait value was modified by the type of
 319 environmental forcing, even though the mean value of the environmental signal did not change.
 320 The relationships between trait patterns and filters applied on local communities are complex and
 321 still need to be clarified but they constitute an additional clue on species dynamics (D’Andrea
 322 and Ostling, 2016; Loranger et al, 2018). The identification of multiple modes in biomass-trait
 323 relationships and SADs is relatively recent (Dornelas and Connolly, 2008; Matthews et al, 2014)
 324 and is a rare pattern in theoretical models (McGill et al, 2007). Barabás et al (2013) convincingly
 325 argued that multimodality could arise from the demographic stochasticity of a single model run
 326 (with either **SNDs**self-regulation or neutrality, but without the clumpy coexistence emerging from
 327 a storage effect). However, our results are based on many model runs, for which either the storage
 328 effect alone or a storage effect + **SNDs**strong self-regulation in a seasonal context consistently pro-
 329 duced multimodal distributions, while simulations without the storage effect always led to a single
 330 cluster along the trait axis. Our suggestion for empirical studies is as follows: if only one spatial
 331 location is observed, caution in interpreting multiple clumps on the trait axis is of course required,
 332 as Barabás et al (2013) highlighted. However, with several locations - or in a theoretical context -
 333 one could average across locations to reproduce similar graphs to the ones produced here. Clumps
 334 in the trait axis when averaged across model runs/locations is therefore a signature of the storage
 335 effect for the cases that we considered in the article. Of course, other mechanisms that we did not
 336 include in our models may produce similar patterns (Rael et al, 2018)-. Still, clustering on the
 337 trait axis, in scenarios where the environment fluctuates strongly in time, suggests that storage
 338 effects could be at work-.

339 In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2018),

we did not find any storage effect (which does not mean that it could not be observed in other systems). Given the results on species richness and composition presented here, we are skeptical that the storage effect alone could help explaining phytoplankton diversity. However, our results suggest that in phytoplankton-like seasonal environments, even though empirically-based **SNDsself-regulation** produce much more diversity than the storage effect when considered in isolation, the storage effect can help diversity maintenance when combined to other mechanisms. Indeed, the combination storage effect + **SNDsstrong self-regulation** is non-additive: the cases were both **SNDsself-regulation** and the storage effect were present showed more diversity than generated by any mechanism on its own.

The above results suggest the very exciting idea that multiple coexistence mechanisms might combine superadditively, thus helping us to better understand the astounding diversity of primary producers. This logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial structure, specialized natural enemies, that could be as important here for plankton as they are for tropical trees, see Bagchi et al, 2014; Comita et al, 2014; Stump and Chesson, 2015; Barraquand et al, 2017). Previous research has however demonstrated that generalist seed predation could weaken the storage effect (Kuang and Chesson, 2009, 2010) thus different mechanisms might not always combine superadditively as we found here. That said, superadditivity has been found in some cases, i.e., pathogens could enhance the storage effect (Mordecai, 2015). Better explaining plant or microbial diversity would then not be about selecting the best unique mechanism susceptible to explain the observed diversity, but rather better combining those mechanisms together. This may obviously be an annoyance for those who like to sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate synergies between coexistence mechanisms in highly diverse communities. Aside from the synergies between predator diversity-enhancing effects and SNDs or storage effects (on the temporal axis), one obvious follow-up of this research would be interactions with spatial structure. Spatial structure occurs both endogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial variation in environmental covariates (Bolker, 2003). Numerous studies (e.g., Bolker and Pacala, 1999; Murrell and Law, 2002) have shown that spatially restricted movements and interactions - very

small-scale spatial structure - can help coexistence, which we believe would be especially important for phytoplankton since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2018). Moreover, although temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall, pH in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main factor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies, spatial limits to competition and temporal niche partitioning all interact to promote the very high-dimensional coexistence observed in the field seem much higher than for any of those mechanisms alone. Whether the diversity-enhancing effects of these mechanisms combine sub-additively (as in Kuang and Chesson, 2010) or super-additively like here is therefore worthy of further research.

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