

Stabilizing niche differences are required to maintain  
species-rich communities in temporally variable  
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 stabilizing niche differences (SNDs). SNDs occur when intraspecific competition is stronger than interspecific, and we tuned the competition ratio based on empirical data. Although SNDs maintained more species than the storage effect (50% w.r.t 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. 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.

**Number of words: 240**

**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, and 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) 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 (Vernon 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 (or temporal niche partitioning, that is an equivalent

53 concept for forced Lotka-Volterra models, Barabás et al, 2012; Scranton and Vasseur, 2016) that  
54 increases the possibility of coexistence by making the interaction strength covary positively with  
55 a fluctuating environment (see also Barabás et al, 2012).

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

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

81 In an empirical study combining phytoplankton community-level time series and multivariate  
82 autoregressive models (Barraquand et al, 2018), we found that despite a large influence of the  
83 environment (including temperature, irradiance, and other factors), intraspecific (or intragenus)  
84 competition was most likely the key driver of species coexistence. In other words, stabilizing niche  
85 differences had a large role to play in maintaining species diversity in coastal phytoplankton (Bar-  
86 raquand et al, 2018)<sup>1</sup>. These SNDs mirror those found in a number of terrestrial plant communities  
87 (Adler et al, 2018) and in animal communities (Mutshinda et al, 2009).

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

## 93 **2 Methods**

### 94 ***Models description***

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

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<sup>1</sup>Preprint version available: (Barraquand et al, 2017)

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

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

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

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

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

Table 1: Parameter definition and values of the model described in Eq. 1-4

Name	Definition	Value (unit)
$S$	Number of species	60
$N_i$	Biomass density of the $i$ th species	(kg/area)
$\tau$	Temperature	K
$r_i(\tau)$	Growth rate of species $i$ as a function of temperature	$\frac{\text{kg}}{\text{kg}^*\text{year}}$
$\alpha_{ij}$	Strength of competition of species $j$ on species $i$	0.001 area/kg
$b_i$	Normalization of the thermal decay rate	
$m$	Mortality rate	$15 \frac{\text{kg}}{\text{kg}^*\text{year}}$
$\tau_0$	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	
$\mu_\tau$	Mean temperature	293 K
$\sigma_\tau$	Standard deviation for temperature	5 K
$\tau_{\min}$	Minimum thermal optimum	288K
$\tau_{\max}$	Maximum thermal optimum	298 K
$A$	Niche breadth	$10^{3.1} \frac{\text{kg}}{\text{kg}^*\text{year}}$
$\tau_i^{opt}$	Thermal optimum for growth of the $i$ th species	K
$\theta$	Scaling between white noise and seasonal signal	$[0, \sqrt{(2)}]$
$\rho$	Ratio of intra-to-intergroup competition strengths	(1;10)

104 We kept the mean and standard deviation of the forcing signal but included a lower-frequency  
 105 component using a sinusoidal function with a period of 365 days (1 time unit being one day, Eq.5).  
 106 We tune the ratio of low-to-high frequency with the variable  $\theta$  so as to keep the same energy  
 107 content - i.e., equal total variance - in the forcing signal.

$$\tau(t) = \mu_\tau + \theta\sigma_\tau \sin\left(\frac{2\pi t}{365}\right) + \epsilon_t, \text{ where } \epsilon_t \sim \mathcal{N}(0, \sigma_\tau \sqrt{1 - \frac{\theta^2}{2}}) \quad (5)$$

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

112 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies a  
 113 storage effect, as the competition strengths covary positively with the growth rate values  $r_i(\tau)$  (Chesson,  
 114 1994; Ellner et al, 2016). To test for the effect of an explicit storage effect in the model, we for-  
 115 mulated a new version of this model, where we removed this assumption by using the mean value  
 116 of a species' growth rate ( $\bar{r}_i$ ) to weight the interaction coefficients (see Table 2).

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

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

119 Stabilizing niche differences are ensured by the addition of the coefficient  $\rho$ , which is the ratio  
 120 of intra-to-intergroup competition strength. We can therefore re-write the interaction coefficients  
 121  $\alpha_{ij}$  in Eq. 7

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

122 where  $\delta_{ij}$  is the Kronecker symbol, equal to 1 if  $i = j$  and to 0 otherwise. The value of the  
 123 parameter  $\rho = 10$  was chosen from analyses of phytoplanktonic data (Barraquand et al, 2018) <sup>2</sup>.

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<sup>2</sup>The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2018) are somewhat higher than here (and  $\rho$  lower, closer to 4) because the best-fitting model actually set to zero some

124 In addition to two types of environmental forcings (white noise with  $\theta = 0$ , and seasonal  
125 forcing with  $\theta = 1.3$ ), we therefore compare the results for four formulations of the model: with  
126 and without an explicit storage effect (Eq. 1 and Eq. 6, respectively) ; with and without stabilizing  
127 niche differences ( $\rho = 10$  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	$r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha (1 + 9\delta_{ij}) N_j\right)$	$N_i \left(r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha (1 + 9\delta_{ij}) N_j\right)$
No stabilizing niche differences	$r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha N_j\right)$	$N_i \left(r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha N_j\right)$

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

128

## 129 Set-up

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

137 All simulations were ran with Matlab's ode45 algorithm, an explicit Runge-Kutta (4,5) algo-  
138 rithm with an absolute error tolerance of  $10^{-8}$ , and relative error tolerance  $10^{-3}$ . The code is  
139 available in a GitHub repository <sup>3</sup>

## 140 3 Results

141 Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016),  
142 with both the environmental signals described in Eq. 1 (original choice of Scranton and Vasseur,

intergroup competition coefficients; using a model where all  $\alpha_{ij}$  are non-zero leads in contrast to  $\rho = 10$ .

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



143 2016 ; Fig. 1a) and Eq. 5 (our variant, Fig. 1b), are shown in Fig. 1c and d. A sinusoidal  
 144 forcing produces the strongly seasonally structured dynamics that are typical of phytoplankton.  
 145 Even though only 5 species can be seen in Fig. 1c), there were 14 species still present at the end  
 146 of the simulation forced by a white noise, with large disparities in the range of variation of their  
 147 biomasses. A third of the species kept a biomass above 10 kg/area (setting area = 1 ha, with a  
 148 depth of a few meters, produce a realistic standing biomasses Reynolds, 2006) while 6 out of the  
 149 14 remained below the unit. All persisting species in the white noise simulations were clustered  
 150 within a 3.2°C-range of thermal optima (see the biomass distribution as a function of the thermal  
 151 optimum in Fig. A1 in the Supplementary Material). No obvious temporal patterns (e.g., cycles)  
 152 could be seen in the communities forced by white noise. On the contrary, seasonal cycles were clear  
 153 in the seasonally-forced case of Fig. 1d). Only 4 species coexisted at the end of the simulation with  
 154 seasonal forcing, gathered in two groups with large thermal optimum differences (5.7°C between  
 155 the maximum thermal optimum of the first group and the minimum thermal optimum of the  
 156 second group). When temperatures are high, the group with higher thermal optima reaches its  
 157 maximum biomass, then as temperature decreases through the season, these species leave room  
 158 for the growth of the low-temperature group.

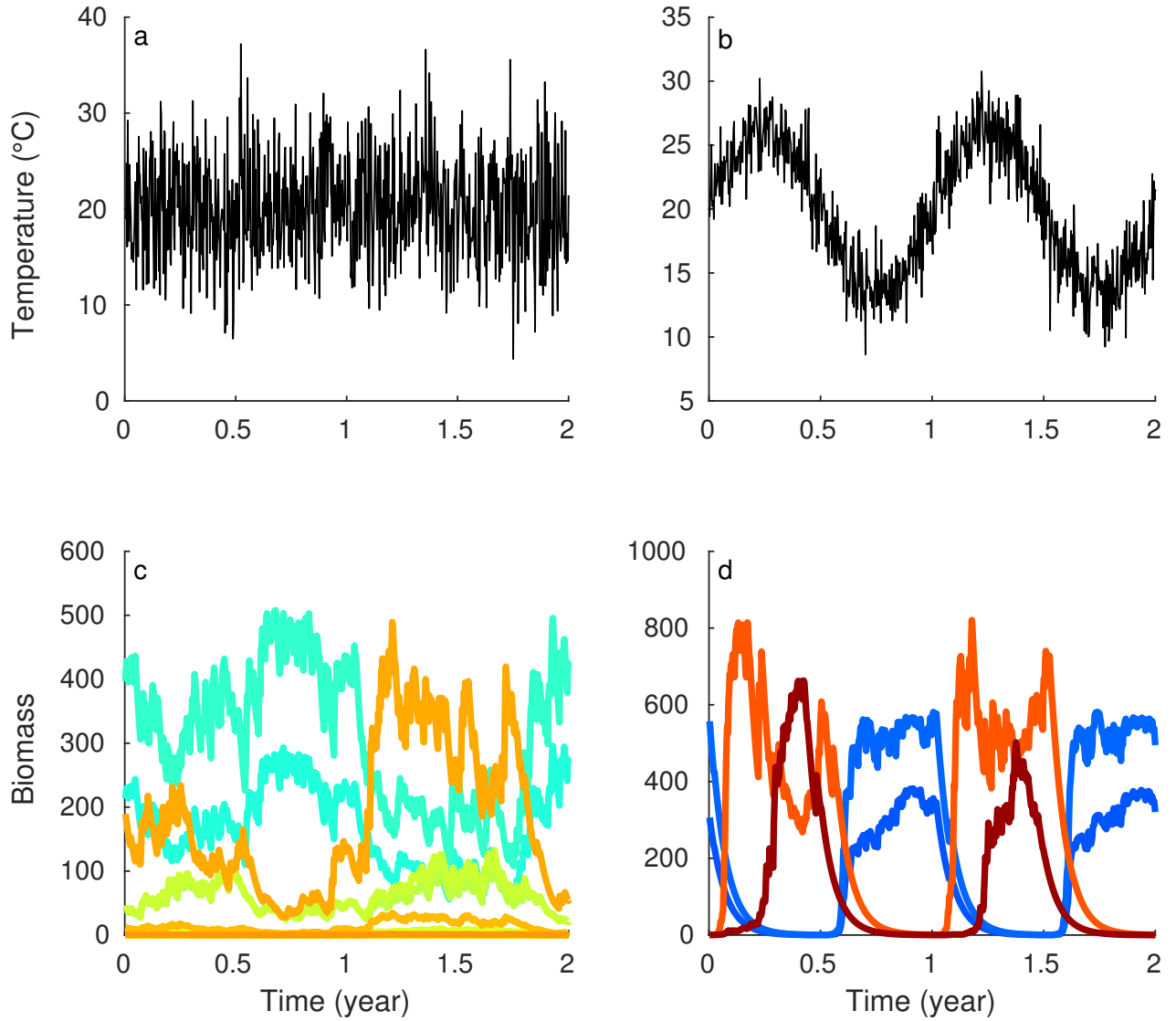


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000 years simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (a) or a noisy seasonal signal (b), leading to community dynamics with more erratic fluctuations (d) 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).

159 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our  
160 simulations (Fig. 2). In cases where final species richness varied from one simulation to another  
161 (namely, the two middle cases in Fig. 2: with storage effect but without stabilizing niche differences,  
162 or without storage effect but with stabilizing niche differences), seasonality reduced the number  
163 of extant species to, on average, 27% and 48% of their original values, respectively (Fig. 2). A  
164 seasonal signal therefore led to a much smaller average persistence. There was also less variance

165 in persistence between seasonally forced simulations when compared to white noise simulations.

166 Both the stabilizing niche differences and the storage effect markedly increased persistence.

167 Without any of these coexistence mechanisms, only one species persisted at the end of the simu-

168 lations. When only the storage effect was present, the number of extant species varied between 8

169 and 20 ( $14.8 \pm 2.4$ ) with a white noise, or 2 and 6 ( $4.1 \pm 0.7$ ) with a seasonal signal. On the other

170 hand, when only stabilizing niche differences were present, the number of extant species nearly

171 doubled, varying between 20 and 32 ( $27.5 \pm 2.4$ ), or 12 and 15 ( $13.3 \pm 0.6$ ), with a white noise or

172 a seasonal signal, respectively. Remarkably, when the storage effect and SNDs both affected the

173 community dynamics, all species persisted in the community, while neither of these mechanisms

174 was able to produce that result alone, for either white noise and seasonal forcing.

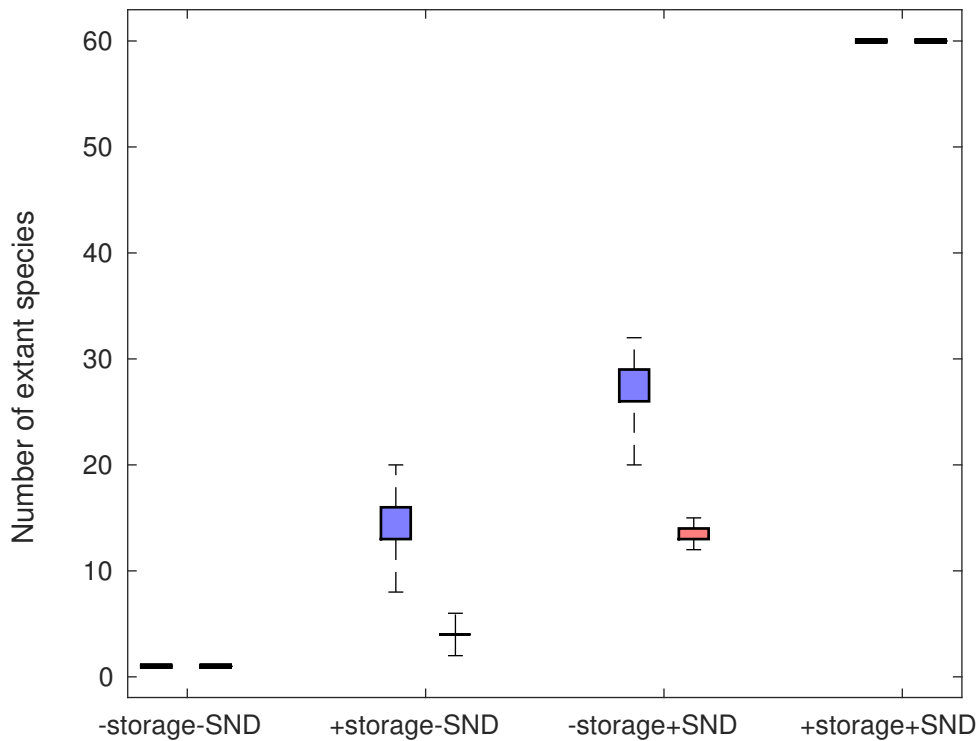


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). The signs + or - storage refer to presence or absence of a storage effect, respectively; + / - SND, presence or absence of Stabilizing Niche Differences, respectively. Community compositions are stable in the cases -storage-SND and +storage+SND, 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.

175 When the richness of the community was stable (either 1 or 60 species at the end of the  
 176 simulation, Fig. 3), there were still large differences in the structure of the community with  
 177 respect to temperature, due to both stochasticity and the type of forcing (Fig. 3). Without storage  
 178 effect nor SNDs, a white noise forcing favoured species with intermediate thermal optima, with two  
 179 thirds of the simulations ending with a species with a thermal optimum between 18.9°C and 21.4°C  
 180 (corresponding to only one fourth of the range of thermal optima present at the beginning of the  
 181 simulation) and reaching a maximum average biomass in this range (Fig. 3 a). This distribution  
 182 can be related to a selection for the highest long-term growth rates, averaged over time (see scaled  
 183 growth rates in Fig.3). On the contrary, seasonality tended to favor species with larger maximum  
 184 growth rates (thermal optima above 22°C). Species with a higher thermal optima are more likely  
 185 to persist and to reach a higher biomass at the end of the simulation. 38% of the simulations  
 186 therefore ended with the species having the highest temperature optimum, 25°C.

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

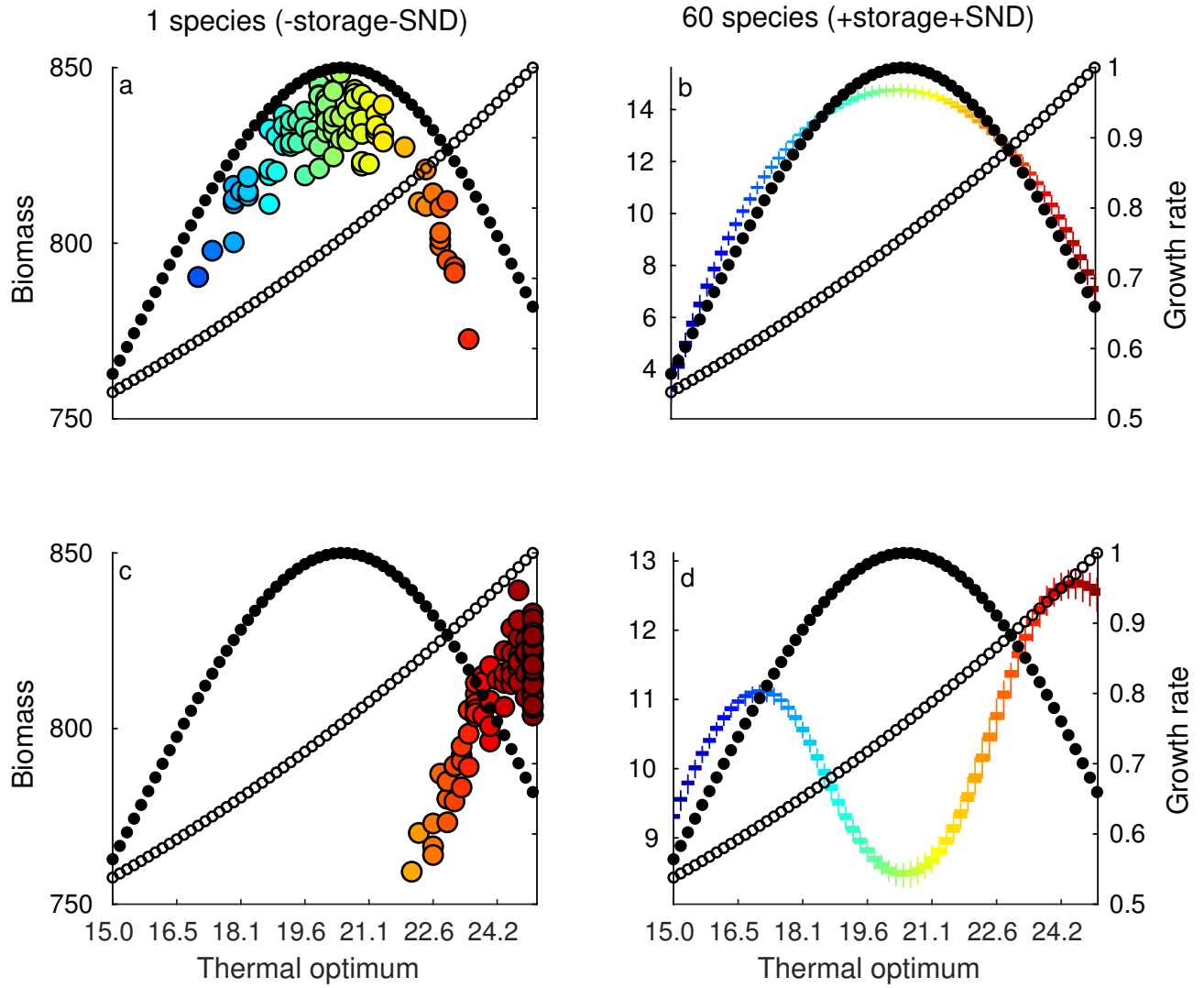


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor stabilizing niche differences are presented. Only one species is present at the end of the simulations and its mean value is represented by one point per simulation. There can be several dots 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 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 noise (top) or a seasonal signal (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 filled and open circles, respectively, and are indexed on the right y-axis.

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

201 generated different shapes. Indeed, the storage effect led to a multimodal biomass distribution with  
202 respect to thermal optima. We always observed 3 modes with a white noise and 3 modes in 95% of  
203 the seasonal simulations, Fig. 4a. With a white noise, extant species are grouped in rather similar  
204 clumps regarding species thermal optima (between 18.8°C and 22.2°C whereas clumps tended to  
205 be further apart in the seasonal case, covering a total range of 7.7°C, with species grouping in the  
206 higher part of the thermal range, above 22°C. On the other hand, stabilizing niche differences led  
207 to a quasi-uniform biomass distribution (Fig. 4 b). Species characterising communities forced by  
208 a white noise stayed in the lower range of temperatures (in 96% of the simulations, the highest  
209 thermal optimum was 22.4°C, see Fig. A2 in the Supplementary Material) while they were filtered  
210 out in communities subjected to a seasonal fluctuations of their environment, for which species  
211 with thermal optima above 20.5°C persisted.

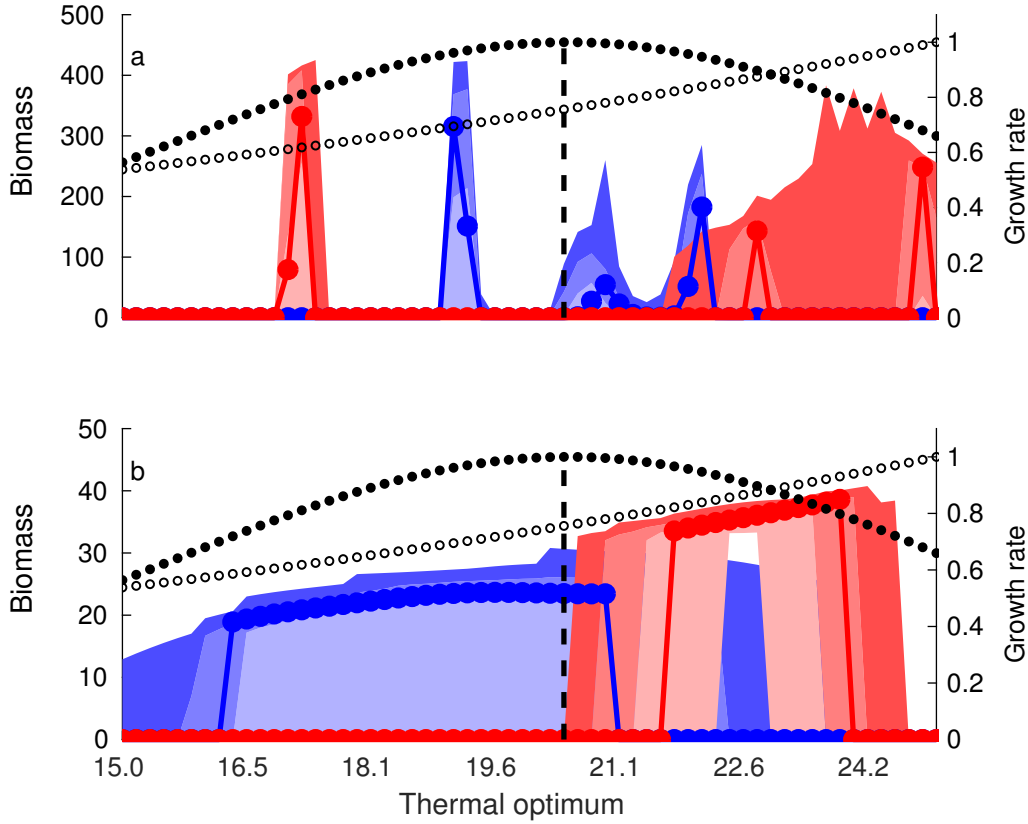


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (a) and without storage effect, with stabilizing niche differences (b). The forcing signal is either a white noise (in blue) or a seasonal signal (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, 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 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

219 included a white noise forcing and a storage effect, but considered seven additional combinations  
220 of mechanisms. This was motivated by our wish to include two observed features of phytoplankton  
221 dynamics: seasonal cycles (Winder and Cloern, 2010) and stabilizing niche differences (Chesson,  
222 2000; Adler et al, 2010; Barraquand et al, 2018). Stabilizing niche differences, that occur whenever  
223 intraspecific competition is stronger than interspecific competition, can arise from many mech-  
224 anisms: nonlinearities in the functional forms of competition or mutualism that contribute to  
225 increasing self-regulation, predation or parasitism (see e.g. the generalist predators in Haydon,  
226 1994), etc. They seem nonetheless an ubiquitous feature in primary producers (Adler et al, 2018).

227 We have found that first, temporally forced Lotka-Volterra dynamics cannot sustain any di-  
228 versity with our phytoplankton-based set of parameters, unless the structure is geared to include  
229 either a storage effect or SNDs. Although this absence of diversity-enhancing effect of “pure” en-  
230 vironmental variation has already been stated by other authors (Barabás et al, 2012; Fox, 2013;  
231 Scranton and Vasseur, 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress  
232 it once more: temporal variation in growth rate alone cannot help coexistence within competitive  
233 communities. A nice point made by Scranton and Vasseur (2016) was that a built-in storage ef-  
234 fect in a forced Lotka-Volterra model, parameterized for phytoplankton communities, could lead  
235 to some degree of coexistence. Our investigation reproduced these results, using the white noise  
236 forcing considered by Scranton and Vasseur (2016). However, an arguably more lifelike noisy and  
237 seasonal temperature forcing considerably lessened the richness of the community after 5000 years,  
238 decreasing from 15 to 4 species on average. Even imagining that groups represented here are gen-  
239 era or classes rather than species, this is a fairly low diversity for a phytoplankton-like community  
240 (see Chapter 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own,  
241 be sufficient to maintain species-rich communities (e.g., dozens to hundreds of species). We have  
242 therefore sought out whether stabilizing niche differences could maintain a higher diversity, using  
243 field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al,  
244 2018), where the intragroup density-dependence was chosen approximately 10 times stronger. On  
245 their own, SNDs produced a higher level of diversity than the storage effect (almost double for  
246 white noise), which not only aligns with our results on phytoplankton but also with results on



247 perennial plants (Adler et al, 2010).

248       However, the seasonal forcing still considerably reduced diversity when SNDs were considered,  
249 especially the “neutral” kind of diversity, i.e., diversity within clumps of similar traits. This diversity  
250 reduction occurs because within a season, the signal autocorrelation gives long, contiguous time  
251 intervals to the best competitor to exclude its less adapted heterospecifics. This makes the results  
252 likely to hold not only for seasonal environments, but also autocorrelated ones, i.e., “red” noise (this  
253 could be relevant for species whose population dynamics occurs at timescales largely above one  
254 year). In contrast, a white noise generates large temperature shifts more frequently, and thereby  
255 forbid such competitive exclusion. In a seasonal setting, a species with the highest long-term  
256 averaged growth rate may not be the best competitor, and can disappear as a result of a strong  
257 competition from both low- and high-temperature tolerant species. This holds with or without a  
258 storage effect.

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

266       In addition to community diversity, the biomass-trait relationship also varied from one simula-  
267 tion to another. Some regularities did emerge across simulations though. The storage effect begot  
268 several clumps along the trait space (as observed by Scranton and Vasseur, 2016). The seasonality  
269 that we added to the temperature signal led to more distant clumps on the trait axis (as said above,  
270 less species per clump). Conversely, SNDs alone led to relatively uniform biomass distributions,  
271 with species forming a single large cluster, which covers some fraction of the initial trait space.  
272 The identification of multiples modes in biomass-trait relationships and SADs is relatively recent  
273 (Dornelas and Connolly, 2008; Matthews et al, 2014) and is a rare pattern in theoretical models  
274 (McGill et al, 2007). Barabás et al (2013) convincingly argued that multimodality could arise from

the demographic stochasticity of a single model run (with either SNDs or neutrality, but without the clumpy coexistence emerging from a storage effect). However, our results are based on many model runs, for which either the storage effect alone or a storage effect + SNDs in a seasonal context consistently produced multimodal distributions, while simulations without the storage effect always led to a single cluster along the trait axis. Our suggestion for empirical studies is as follows: if only one spatial location is observed, caution in interpreting multiple clumps on the trait axis is of course required, as Barabás et al (2013) highlighted. However, with several locations - or in a theoretical context - one could average across locations to reproduce similar graphs to the ones produced here. Clumps in the trait axis when averaged across model runs/locations is therefore a signature of the storage effect for the cases that we considered in the article. Of course, other mechanisms that we did not include in our models may produce similar patterns (Rael et al, 2018). Still, clustering on the trait axis, in scenarios where the environment fluctuates strongly in time, suggests that storage effects could be at work.

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 SNDs 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 + SNDs is non-additive: the cases where both SNDs 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 (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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## References

- Adler PB, Ellner SP, Levine JM (2010) Coexistence of perennial plants: an embarrassment of niches. *Ecology letters* 13(8):1019–1029
- 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* doi:10.1111/ele.13098
- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506(7486):85–88, doi:10.1038/nature12911
- Barabás G, Mészéna 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, Mészéna G, Ostling A (2013) Emergent neutrality or hidden niches? *Oikos* 122(11):1565–1572, doi:10.1111/j.1600-0706.2013.00298.x
- Barabás G, Michalska-Smith MJ, Allesina S (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist* doi:10.1086/686901
- Barraquand F, Picoche C, Maurer D, Carassou L, Auby I (2017) Weak interactions between groups and physical drivers of community dynamics in coastal phytoplankton. *bioRxiv* doi:10.1101/171264
- 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 Accepted*, doi:10.1101/171264
- Bolker B, Pacala S (1999) Spatial Moment Equations for Plant Competition: Understanding Spatial Strategies and the Advantages of Short Dispersal. *The American Naturalist* 153(6):575–602
- Bolker BM (2003) Combining endogenous and exogenous spatial variability in analytical population models. *Theoretical Population Biology* 64(3):255–270, doi:10.1016/S0040-5809(03)00090-X

354 Carmel Y, Suprunenko YF, Kunin WE, Kent R, Belmaker J, Bar-Massada A, Cornell SJ (2017)  
 355 Using exclusion rate to unify niche and neutral perspectives on coexistence. *Oikos* 126(10):1451–  
 356 1458, doi:10.1111/oik.04380

357 Chesson P (1994) Multispecies Competition in Variable Environments. *Theoretical Population*  
 358 *Biology* 45:227–276

359 Chesson P (2000) Mechanisms of maintenance of species diversity. *Annual review of Ecology and*  
 360 *Systematics* pp 343–366

361 Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, Beckman N, Zhu Y  
 362 (2014) Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental  
 363 evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*  
 364 102(4):845–856, doi:10.1111/1365-2745.12232

365 Dornelas M, Connolly SR (2008) Multiple modes in a coral species abundance distribution. *Ecology*  
 366 *Letters* 11(10):1008–1016, doi:10.1111/j.1461-0248.2008.01208.x

367 Ellner SP, Snyder RE, Adler PB (2016) How to quantify the temporal storage effect using simula-  
 368 tions instead of math. *Ecology Letters* doi:10.1111/ele.12672

369 Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology*  
 370 *& Evolution* 28(2):86–92, doi:10.1016/j.tree.2012.08.014

371 Götzenberger L, de Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, Lepš J, Lindborg  
 372 R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Zobel K, Zobel M (2012) Ecological  
 373 assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews*  
 374 87(1):111–127, doi:10.1111/j.1469-185X.2011.00187.x

375 Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality:  
 376 the continuum hypothesis: Reconciling niche and neutrality. *Ecology Letters* 9(4):399–409,  
 377 doi:10.1111/j.1461-0248.2006.00884.x

378 Haydon D (1994) Pivotal assumptions determining the relationship between stability and com-  
379 plexity: an analytical synthesis of the stability-complexity debate. *The American Naturalist*  
380 144(1):14–29

381 Holt R (2006) Emergent neutrality. *Trends in Ecology & Evolution* 21(10):531–533,  
382 doi:10.1016/j.tree.2006.08.003

383 Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (MPB-32).  
384 Princeton University Press

385 Kuang JJ, Chesson P (2009) Coexistence of annual plants: generalist seed predation weakens the  
386 storage effect. *Ecology* 90(1):170–182

387 Kuang JJ, Chesson P (2010) Interacting coexistence mechanisms in annual plant communities:  
388 frequency-dependent predation and the storage effect. *Theoretical population biology* 77(1):56–  
389 70

390 Matthews TJ, Borges PAV, Whittaker RJ (2014) Multimodal species abundance distributions:  
391 a deconstruction approach reveals the processes behind the pattern. *Oikos* 123(5):533–544,  
392 doi:10.1111/j.1600-0706.2013.00829.x

393 McGill BJ, Etienne RS, Gray JS, Alonso D, Anderson MJ, Benecha HK, Dornelas M, Enquist  
394 BJ, Green JL, He F, Hurlbert AH, Magurran AE, Marquet PA, Maurer BA, Ostling A, Soykan  
395 CU, Ugland KI, White EP (2007) Species abundance distributions: moving beyond single pre-  
396 diction theories to integration within an ecological framework. *Ecology Letters* 10(10):995–1015,  
397 doi:10.1111/j.1461-0248.2007.01094.x

398 Moisan JR, Moisan TA, Abbott MR (2002) Modelling the effect of temperature on the  
399 maximum growth rates of phytoplankton populations. *Ecological Modelling* 153(3):197–215,  
400 doi:10.1016/S0304-3800(02)00008-X

401 Mordecai EA (2015) Pathogen impacts on plant diversity in variable environments. *Oikos*  
402 124(4):414–420

403 Munoz F, Huneman P (2016) From the neutral theory to a comprehensive and multiscale theory  
404 of ecological equivalence. *The Quarterly Review of Biology* 91(3):321–342

405 Murrell DJ, Law R (2002) Heteromyopia and the spatial coexistence of similar competitors. *Ecol-*  
406 *ogy Letters* 6(1):48–59, doi:10.1046/j.1461-0248.2003.00397.x, [https://onlinelibrary.wiley.](https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1461-0248.2003.00397.x)  
407 [com/doi/pdf/10.1046/j.1461-0248.2003.00397.x](https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1461-0248.2003.00397.x)

408 Mutshinda CM, O’Hara RB, Woiwod IP (2009) What drives community dynamics? *Proceedings*  
409 *of the Royal Society B: Biological Sciences* 276(1669):2923–2929, doi:10.1098/rspb.2009.0523

410 Rael RC, D’Andrea R, Barabás G, Ostling A (2018) Emergent niche structuring leads to increased  
411 differences from neutrality in species abundance distributions. *Ecology*

412 Reynolds CS (2006) *The ecology of phytoplankton*. Cambridge University Press

413 Sakavara A, Tsirtsis G, Roelke DL, Mancy R, Spatharis S (2018) Lumpy species coexistence arises  
414 robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences*  
415 115(4):738–743, doi:10.1073/pnas.1705944115

416 Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of  
417 similar species. *Proceedings of the National Academy of Sciences* 103(16):6230–6235

418 Scranton K, Vasseur DA (2016) Coexistence and emergent neutrality generate synchrony among  
419 competitors in fluctuating environments. *Theoretical Ecology* doi:10.1007/s12080-016-0294-z

420 Snyder RE (2008) When does environmental variation most influence species coexistence? *Theo-*  
421 *retical Ecology* 1(3):129–139

422 Stump SM, Chesson P (2015) Distance-responsive predation is not necessary for the Janzen-Connell  
423 hypothesis. *Theoretical population biology* 106:60–70

424 Vergnon R, van Nes EH, Scheffer M (2013) Interpretation and predictions of the Emergent  
425 neutrality model: a reply to Barabás et al. *Oikos* 122(11):1573–1575, doi:10.1111/j.1600-  
426 0706.2013.00790.x

- 427 Vesipa R, Ridolfi L (2017) Impact of seasonal forcing on reactive ecological systems. Journal of  
428 Theoretical Biology 419:23–35, doi:10.1016/j.jtbi.2017.01.036
- 429 Winder M, Cloern JE (2010) The annual cycles of phytoplankton biomass. Philo-  
430 sophical Transactions of the Royal Society B: Biological Sciences 365(1555):3215–3226,  
431 doi:10.1098/rstb.2010.0125
- 432 Zhao XQ (1991) The qualitative analysis of n-species lotka-volterra periodic competition systems.  
433 Mathematical and Computer Modelling 15(11):3–8