

# Seed-bank contribution in maintaining phytoplanktonic biodiversity

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## Introduction

How the high biodiversity of plant communities maintains is still an unresolved question for both experimental and theoretical ecologists. Terrestrial plants and phytoplanktonic communities can present hundreds of species relying on similar resources. Early theoreticians have proposed that environmental fluctuations only [ref] could sustain coexistence but further research showed that this could not explain the order of magnitude of species richness [ref]. Other mechanisms such as niche differentiation[ref], demography [ref] and life history traits [ref] have completed explanation by the stochastic environmental variations and demographic processes.

Analyses of coexistence in terrestrial plant communities often take into account several life stages [refs]. Considering at least two stages, seeds/juveniles and adults, different models have uncovered mechanisms that might explain long-term coexistence. Examples of such mechanisms are the bet-hedging strategy, the storage effect and the Janzen-Connell effect. Bet-hedging is a long-term strategy relying on the creation of seeds which can remain dormant for a long period of time (over a year, often much longer). Dormant seeds can tolerate harsher years during which adults cannot maintain, but they also reduce part of the population that could germinate from one year to another (in case of an annual plant). The storage effect has first been defined by the presence of a long-lived life stage and temporal variation in recruitment from this long-lived life stage that helps escape interspecific competition (Chesson, 1986; Cáceres, 1997). This has been later generalized as a negative correlation between the effect of the environment and the effect of competition (Ellner *et al.*, 2016). In good environmental conditions, competition between individuals is stronger as seeds might germinate and therefore use the same resources at the same time. Finally, models and experiments suggest that adults can have a negative effect on seed survival, through the Janzen-Connell effect (Comita *et al.*, 2014). Therefore, neglecting explicit modeling of this life stage can modify the understanding we have of the dynamics of the populations (Nguyen *et al.*, 2019).

Even though different coexistence mechanisms have been unveiled through the use of several life stages and a focus on the youngest stage (seeds) for terrestrial plants, aquatic plants, and more specifically phytoplanktonic algae, have not been modeled with the same precision. Although ecologists have proposed for a long time that the blooms (peaks in abundances that can cover several orders of magnitude) may initiate after the resuspension and germination of seeds (Patrick, 1948; Marcus & Boero, 1998), it is unusual to see an explicit model of such process (but see Hinnert *et al.*, 2019). The classical view behind phytoplankton dynamics is that bloom formation is mostly seasonal, due to the variation in light and temperature, assuming vegetative cells remaining in the environment can duplicate enough to attain bloom amplitude. However, a recent review (Ellegaard & Ribeiro, 2018) suggests that seeds/cysts might another player .

Phytoplankton communities in coastal environments may benefit from seed banks even more than the oceanic communities [REF-find back], as the distance to the sea bottom is smaller allowing frequently recolonization of the pelagic environment from the shallow sea bottom. Also, and similarly to the seed bank approach in the terrestrial

plant literature, Smayda (2002) has proposed the term “pelagic seed bank” to characterize the contribution of the ocean to coastal communities. This has been noticed for dinoflagellate especially [[ref Dinophysis, check what we have on diatoms]]. Conversely, we can wonder to which extent the seed banks can contribute to the biodiversity in the ocean, especially in the long term. Indeed, spores are able to germinate again after tens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy, which can have a long-term effect on biodiversity in both oceanic and coastal environments.

Here we build on the discrete metacommunity model by Shoemaker & Melbourne (2016), completed by Wisnoski *et al.* (2019) who included exchanges with a seed bank. The growth rate in this model is temperature-dependent and inspired by a metabolism-based model (Scranton & Vasseur, 2016), which we adapted to the specific phenology of modeled phytoplankton groups (Picoche & Barraquand, 2020). Empirical interactions between organisms are informed by previous analyses of field data (Picoche & Barraquand, 2019, 2020). In a first step, we use linear interaction effects, then tweak the Beverton-Holt model to introduce saturating interactions. With these different elements, we aim to examine the effect of exchanges between different compartments (ocean and coastal water column and the seed bank at the bottom of the water column) on coexistence.

## Methods

### Models

Our models builds atop those developed by Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019). These discrete-time models are designed for metacommunities with multiple species competing and unfold as follow: first, individuals increase with a Beverton-Holt (BH) density-dependence (eqs. 1 and 2), then exchanges occur between the different compartments or patches part constituting the metacommunity (eq. 3).

In this paper, individuals are phytoplanktonic cells that move between the upper layer of coastal water, its bottom layer where a seed bank accumulates (hereafter called a cyst bank to remain consistent with phytoplankton terminology) and the ocean. Only oceanic and coastal cells are subject to BH-density dependence. Cysts are only affected by mortality  $m$  and burial due to sedimentation  $\zeta$ . Parameters and state variables are defined in Table 1 [[Table is false]]

The BH formulation is the Lotka-Volterra equivalent for discrete-time models and is often used to represent terrestrial plant growths. In our model, the species-specific maximum achievable growth rate  $r_i$  is modified by positive and negative interactions  $\alpha_{ij}$ . In the most classical formulation of the BH competition model, which is also our first model (model I), interaction effects increase linearly with the abundances (eq. 1). We subsequently defined saturating interactions (model II, eq. 2). More specifically, in our case, the first step of the first model is written as

$$\begin{cases} N_{t',i,c} &= \frac{e^{r_i(T)} N_{t,i,c}}{1 + \sum_j \alpha_{ij} N_{t,j,c}} - l N_{t,i,c} \\ N_{t',i,o} &= \frac{e^{r_i(T)} N_{t,i,o}}{1 + k_{c2o} \sum_j \alpha_{ij} N_{t,j,o}} - l N_{t,i,o} \\ N_{t',i,b} &= N_{t,i,b} (1 - m - \zeta) \end{cases} \quad (1)$$

In contrast, in model II, oceanic and coastal dynamics are governed by eq. 2.

$$N_{t',i,c/o} = \frac{e^{r_i(T)} N_{t,i,c/o}}{1 + \sum_{j/\alpha_{ij} \in \mathbb{C}} \frac{a_C N_{t,j,c/o}}{H_{ij} + N_{t,j,c/o}} + \sum_{j/\alpha_{ij} \in \mathbb{F}} \frac{a_F N_{t,j,c/o}}{H_F + N_{t,j,c/o}}} - l N_{t,i,c/o} \quad (2)$$

#####DEFINE THE REST here

As we assume that competition for nutrients is stronger in the ocean than along the coast [ref], a coefficient  $k_{c2o} > 1$  is applied to competitive interactions and facilitation is removed from the oceanic interaction matrices. [[NO]] Here, the growth rate  $r_i(T)$  varies with the temperature, and this variation depends on the genus of interest (see eq. 4). Abundances are also affected by a density-independent loss term  $l$  which can cover all other lethal processes such as a natural mortality or predation. During the same first step, the abundance of cells present at the bottom of the water column in coastal areas (hereafter called cysts) decreases with cyst mortality ( $m$ ) and burial resulting from sedimentation ( $\zeta$ ).

During the second step, exchanges take place between the three compartments (eq. 3) [[Check that formula are still ok]]

$$\begin{cases} N_{t+1,i,c} &= N_{t',i,c}(1 - s_i - e) + \gamma N_{t',i,b} + e N_{t',i,o} \\ N_{t+1,i,o} &= N_{t',i,o}(1 - s_i - e) + e N_{t',i,c} \\ N_{t+1,i,b} &= N_{t',i,b}(1 - \gamma) + s_i N_{t',i,c} \end{cases} \quad (3)$$

Param	Name	Value (unit)
$N_{t,i,c/o/b}$	Abundances of species $i$ at time $t$ in the coast ( $c$ ) or ocean ( $o$ ) water column, or in the benthos ( $b$ )	NA (Number of cells)
$T$	temperature	NA (K)
$r_i(T)$	growth rate of species $i$	NA
$b_i$	Normalization constant for the thermal decay rate	( $K^3$ )
$\tau_0$	Reference temperature	293 (K) / 20 ( $^{\circ}C$ ) (Scranton & Vasseur, 2016)
$a_r(\tau_0)$	Growth rate at reference temperature	$386(\frac{kg}{kg \times year})$ (Scranton & Vasseur, 2016)
$E_r$	Activation energy	0.467 (eV) (Scranton & Vasseur, 2016)
$T_{min}$	Minimum thermal optimum	0
$T_{max}$	Maximum thermal optimum	30 (approximate of the range in Edwards <i>et al.</i> (2016))
$T_i^{opt}$	Optimal temperature for species $i$	Adapted from Picoche & Barraquand (2020)
$\alpha_{ij,c/o}$	interaction strength of species $j$ on $i$	Adapted from Picoche & Barraquand (2020)
$k_{c2o}$	conversion coefficient from coastal to oceanic interactions	1.5 [arbitrary]
$A_i, b_i$	Niche area, width	NA
$g$	gain in growth rate	0.2 [this study, based on Edwards <i>et al.</i> (2016)]
$s_i$	sinking rate of species $i$ in a coastal environment	$\{0.1; 0.3; 0.5\} \beta(0.55, 1.25)$ (Passow, 1991)
$e$	exchange rate between ocean and coast	$\{0.4; 0.6; 1\}$ (Ascione Kenov <i>et al.</i> , 2015)
$l$	loss of vegetative phytoplankton (predation, mortality...)	0.04 (Scranton & Vasseur, 2016)
$m$	cyst mortality	$\approx 10^{-4}/10^{-5}$ (McQuoid <i>et al.</i> , 2002)
$\zeta$	cyst burial	$\{0.01; 0.1; 0.3\}$ [arbitrary]
$\gamma$	germination $\times$ resuspension rate of species	$\{0.1; 0.01; 0.001\} * \{10^{-5}; 0.1\}$ [arbitrary]

Table 1: Definition of main variable states and parameters of the model. Fixed values or distributions are estimated from the literature. When a set or a range of values is given, the sensitivity of the model related to changes in parametes has been assessed (see text).

More precisely, in eq. 1, the coefficients  $\alpha_{ij}$ , i.e. the strength of the effect of species  $j$  on species  $i$  for all  $i$  and  $j$ , are inferred from a previous work on coastal data with a Multivariate AutoRegressive (MAR) model (Picoche & Barraquand, 2020). The shift from MAR to BH- interaction matrices is described in SI. The change in growth rate  $r_i(T)$  is based on the formula by Scranton & Vasseur (2016) (eq. 4). [[NO. We need Eppley]]

$$\begin{aligned} r_i(T) &= a_r(\tau_0) e^{E_r \frac{(T - \tau_0)}{kT\tau_0}} f_i(T) + g \\ \text{where } f_i(T) &= \begin{cases} e^{-|T - T_i^{opt}|^3 / b_i}, & T \leq T_i^{opt} \\ e^{-5|T - T_i^{opt}|^3 / b_i}, & T > T_i^{opt} \end{cases} \\ \text{and } b_i &\text{ is defined by numerically solving } \int r_i(\tau) d\tau = A_i \end{aligned} \quad (4)$$

In this model, species are therefore defined by their thermal optimum  $T_i^{opt}$ . The equation by Scranton & Vasseur (2016) was modified to account for two more processes. Taxa roughly divide between generalists and specialists, with more or less tolerance to variations in the temperature. Generalists have a larger niche width than specialists,

which can be roughly translated by a larger  $A_i$  (for more details on the modeling of generalist and specialist, see specific section in SI). Field-based estimation of the niche area  $A_i$  is described in the next section. However, apart from a radical and unrealistic change in  $A_i$  value, the resulting growth rate decreases very rapidly with the distance from  $T_i^{opt}$ , leading to values close to 0 for temperatures in which phytoplankton can normally grow. The meta-analysis by Edwards *et al.* (2016) can be used to correct at least qualitatively the growth rate for temperature outside the range of the considered taxa, by adding a gain  $g$  in the final growth rate (see a comparison of the original and final versions of the growth rates in SI, Fig. S??). Finally, the temperature at each time step is a repetition of the temperatures observed over 20 years in our example dataset [[NO]]

Each compartment (ocean, coast, seed bank) contains  $10^3$  cells at the beginning of the simulation, which is run for 10000 time steps. [[NO]]

## Parameterisation

### Empirical dataset used for calibration

[[Write here]]

### Parameter values

**Phenology** In eq. 4, the growth rate is mainly defined by two parameters: the thermal optimum  $T_i^{opt}$  and the niche area  $A_i$ , which drive the phenology of the genus. Each year, the dynamics of phytoplanktonic organisms is characterized by a blooming period and a lower concentration during the rest of the year. The bloom can be triggered by a combination of nutrient and light input, as well as a sufficient temperature. All parameters being more or less dependent on seasonality, it is reasonable to restrain this study to the effect of temperature.

We base estimates of  $T_i^{opt}$  and  $A_i$  on field observations. For each genus and each year, the beginning of the bloom of a given genus is defined by the date at which its abundance exceeds its median abundance over the year. The duration of the bloom is the number of days between the beginning and the date where abundance fall below the median value. Generalists are characterized by one long bloom in the year or several blooms when the abundances oscillate around their median. Specialists tend to appear only once or twice in the year for shorter amounts of time. A genus is therefore defined as a generalist if its cumulated blooms last more than the average duration (137 days) for at least 15 years over the 20 years of the time series.

With these values in mind, we can define two range of values for the niche width (5-10 for specialists, 12-17 for the generalists) and then order the species in these ranges as a function of the mean sum of their bloom length, i.e.  $\sum \bar{L}_{i,b} > \sum L_{j,b} \Rightarrow A_i > A_j$  where  $\bar{L}$  is the mean over 20 years of the annual cumulated lengths of the bloom.

The thermal optimum  $T_i^{opt}$  is defined as the mean minimum value [[CHECK]] of the temperature at the beginning bloom throughout the whole time series. <sup>1</sup>

**Loss rate** The loss rate of vegetative cells is defined according to Scranton & Vasseur (2016).

**Sinking rate** Phytoplanktonic particles have a higher density than water and cannot swim to prevent sinking (although see Reynolds (2006) for a discussion on the settling of phytoplanktonic cells compared to inorganic particles). Sinking is mostly affected by hydrodynamics, but at the species-level, size, shape and colony-formation capacity are key determinants of the particle floatation. In this model, the sinking rate of each species is drawn from a beta distribution with a mean value of 9%, and a maximum around 30%, that is  $s \sim 0.3\beta(0.55, 1.25)$  (see Fig. S??)

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<sup>1</sup>This was way too low and led to blooms during autumn and winter. Basically added 5

## Exchange rate

The exchange rate between the ocean and the coast depends on the shape and location of the estuary. In Marennes-Oléron and more specifically in Auger, the renewal time is very short, between 1 and 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily rate between 40 and 100 %.

**Cyst mortality and burial** Cyst loss is the result of cyst mortality  $m$  and inaccessibility  $\zeta$  because of burial by sedimentation. Mortality values range between  $10^{-5}$  and  $10^{-4}$  (more details on the approximation of mortality rates from McQuoid *et al.* (2002) are given in SI). However, cyst burial by sedimentation<sup>2</sup> might be a prevailing phenomenon in driving phytoplanktonic dynamics. Once cysts have been buried, they are not accessible for resuspension even if they could have germinated if put in an accessible location. Burial depends on the hydrodynamics of the site, but also on biotic processes (i.e., bioturbation) and anthropogenic disturbances such as fishing or leisure activities (e.g., jet skiing). This parameter is thus heavily dependent on the environmental context we wish to describe and varies here between 0.01 and 0.3

**Germination/resuspension** Germination and resuspension are both needed for cyst to get back to the water column ( $\gamma = \text{resuspension} \times \text{germination}$ ). Following McQuoid *et al.* (2002) and Agrawal (2009), we assume a temperature threshold: germination is triggered by temperatures going above 15°C. As actual rates of germination are not easily deduced from the literature, a set of credible values are tested (1%, 0.1%, 0.01%). Similarly, resuspension values are seldom computed for phytoplanktonic cells, but models for other particles such as sediments can be used. In this paper, we explore values between  $10^{-5}$  (stratified water column) to 0.1 (highly mixed environment).

## Parameter calibration

**Sensitivity analysis** As mentioned above, several parameters are site-specific and the effect of a change in parameter values needs to be evaluated. The sinking, resuspension/germination and burial rates are the parameters to evaluate. The range of probable values for each parameter, and more specifically the set of values to be tested, is given in Table 1. The main diagnostics are the final mean abundance, amplitude and timing of the bloom (peak in abundance) for each genus.

For each combination of values, the diagnostics are performed on the last year of the simulation and the variability of these diagnostics with respect to each parameter is determined, as well as the best fit to real data.

## Scenarios

Maintenance of biodiversity by exchanges between compartments can be gauged with two main scenarios.

1. modifying the storage of cysts in seed bank (by setting seed mortality/burial to 1)
2. changing the exchanges between the coast and the ocean ( $e=0$ )

Final richness and average abundance/biomass productivity (approximated by the final total abundances, to create a link with ecosystem functions) can be diagnostics.

We can make 2 a-priori ecological hypotheses. First, removing the seed bank would increase the sensitivity to competition, i.e. decrease the maximum sustainable interspecific competition strength, and decrease the resilience of the community confronted to changes in the environment. (Fig. 1). Under high competition, variability in final

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<sup>2</sup>Any idea for a better way to call it than burial?

richness may increase because exclusion is more likely, especially without a seed bank. This is also true for higher temperatures.

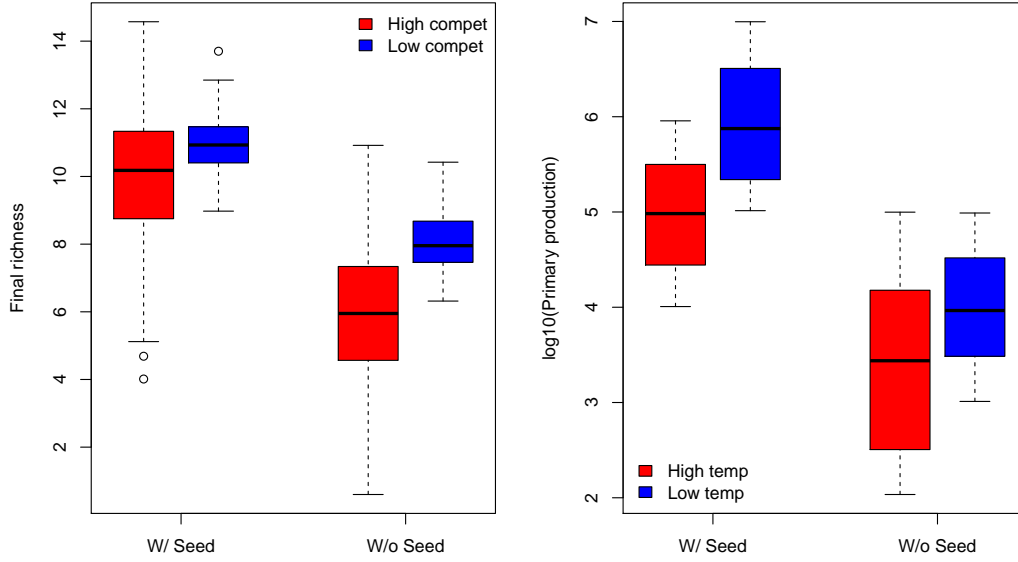


Figure 1: Expected changes in the model outputs in the ocean. Left panel, final richness with and without seed bank, with high (red) and low (blue) interspecific competition. Right panel, final primary productivity with and without seed-bank, with a high (red) and low (blue) mean temperature.

Second, by reducing the exchange with the ocean might end up depleting the ocean biomass and richness as it loses species by sinking but cannot regain them thanks to coastal production fueled by a seed bank. Fig. 2 gives a more precise view of the possible interactions of seed mortality and exchange between the coast and the ocean.

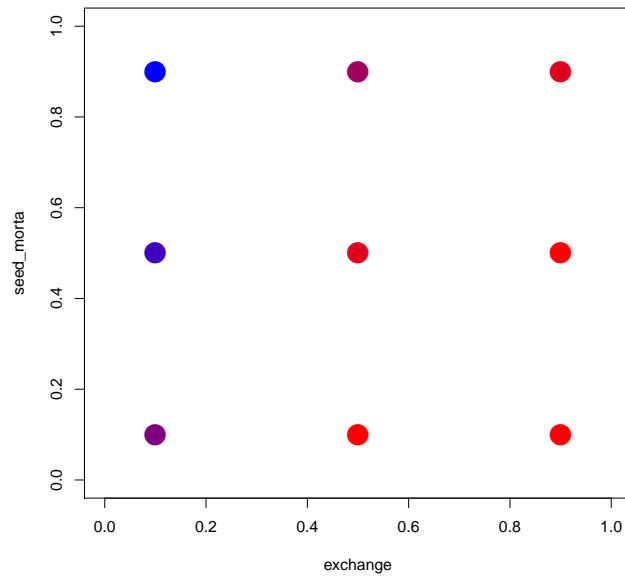


Figure 2: Expected changes in community richness in the ocean for different values of seed mortality/burial (=access to the seed compartment) and exchange with the ocean. Point color indicates final richness in the ocean, from low (blue) to high (red).

## Results

### Phytoplankton dynamics

There are still issues in the calibration of the model: abundances can be lower than expected and the variation in abundances due to seasonality is, for now, underestimated (Fig. 3).

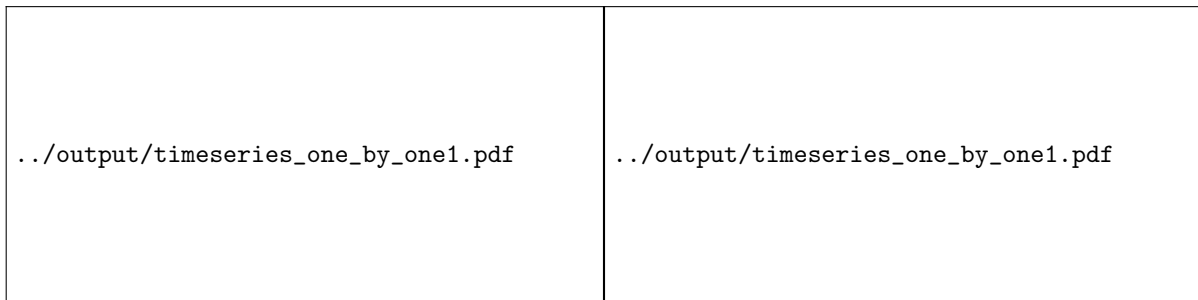


Figure 3: Examples of phytoplankton dynamics (*Chaetoceros* on the left, *Skeletonema* on the right). The solid black line is the observed average abundance of the species.

### Parameter effect

Find a way to represent the variation in total abundances in the models (Fig. 2) (mostly bar plots?)

### Scenarios

### Discussion

## References

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