A metacommunity model for phytoplankton biodiversity maintenance with a seed bank and facilitative interactions

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Abstract

Seed formation is part of the reproductive cycle, leading to the accumulation of resistance stages that can withstand harsher environmental conditions for long periods of time. At the community scale, multiple species with such long-lasting life stages can be more likely to coexist thanks to seeds' buffering effect. While the implications of this process for biodiversity have been studied in terrestrial plants, seed (or cyst) banks are usually neglected in phytoplankton multispecies models, in spite of widespread empirical evidence for such cyst banks. In this study, we build a metacommunity model of interacting phytoplankton species with a cyst bank. The model is parameterized with empirically-driven growth rates functions and field-based interaction estimates (which include both facilitative and competitive interactions). Exchanges between compartments (coastal pelagic individuals, the cyst bank, and open ocean pelagic individuals) are controlled by hydrodynamical parameters to which the sensitivity of the model is assessed. We consider two models, i.e., with and without a saturating effect of the interactions on the growth rates. Our results are consistent between models, and show that a cyst bank is necessary to maintain all species in the community over 30 years. Indeed, the life histories of certain species make them more vulnerable to extinction at specific times within a year, but this process is buffered by their survival in the coastal cyst bank and re-invasion of the community. We thus highlight the possible role of coastal environments in re-seeding oceanic regions. Moreover, the cyst bank enables populations to tolerate stronger interactions within the community as well as more severe changes in the environment, such as those predicted within a climate change context. This study therefore uncovers the importance of the phytoplanktonic cyst stage for diversity maintenance, which should inspire further investigations of this life stage.

Introduction

How the high biodiversity of primary producers maintains is still an unresolved question for both experimental and theoretical ecology. Terrestrial plants and phytoplanktonic communities can

present hundreds of species relying on similar resources. Some degree of niche differentiation is generally expected (Chesson, 2000), but complex life-history structure can further increase the likelihood of coexistence (Loreau & Ebenhöh, 1994; Moll & Brown, 2008; Fujiwara *et al.*, 2011; Chu & Adler, 2015) and so does the response of life history traits to variation in the environment (Chesson & Huntly, 1988; Rees *et al.*, 2001; Huang *et al.*, 2016).

Analyses of coexistence in terrestrial plant communities sometimes take into account several life stages (e.g., Aikio *et al.*, 2002; Comita *et al.*, 2010; Chu & Adler, 2015) though many consider only a single life-stage (see, among others, Ellner, 1987; Levine & Rees, 2004; Martorell & Freckleton, 2014; Adler *et al.*, 2018). Considering at least two stages, seeds/seedlings and adults, several mechanisms that can contribute to long-term coexistence in spatially and/or temporally fluctuating environment have been uncovered (Shmida & Ellner, 1984; Chu & Adler, 2015). The storage effect, a major paradigm in the modern coexistence theory (Chesson, 2000, 2018), is one of them. It has first been defined by the presence of a long-lived life stage and temporal variation in recruitment from this stage that helps escape interspecific competition (Chesson, 1986; Cáceres, 1997; Ellner *et al.*, 2016), and has often been discussed in the presence of a seed bank (Aikio et al. 2002, Angert et al. 2009, Chu and Adler 2015). The seed stage itself contrasts with other parts of the life cycle as organisms can enter a dormant phase which allows them to sustain harsher environmental conditions for longer periods of time than later stages (Aikio *et al.*, 2002). In a meta-community model (Wisnoski *et al.*, 2019), dormancy interacts with dispersal and tends to increase local diversity in temporally fluctuating environments. These mechanisms suggest that neglecting the explicit modeling of the seed stage can alter the understanding we have of the dynamics of organisms, both at the population (Nguyen *et al.*, 2019) and community level (Manna *et al.*, 2017; Wisnoski *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, the effect of life cycles on aquatic plants communities, and more specifically that of phytoplanktonic algae, is often ignored. The classical view behind phytoplankton dynamics is that blooms (peaks in abundances that can cover several orders of magnitude) are due to seasonal variation in light, temperature and nutrients, as well as hydrodynamics processes (Reynolds 2006). In this scenario, differential responses to environmental signals ensure the coexistence of multiple species (Margalef 1978, Smayda and Reynolds 2001), assuming that vegetative cells are already present in the environment and can duplicate enough to reach high abundances. However, a complementary hypothesis suggests that resuspension and germination of phytoplanktonic resting cells, or cysts (Patrick, 1948; Marcus & Boero, 1998), is another major player. This long-standing hypothesis is supported by recent reviews (Azanza *et al.*, 2018; Ellegaard & Ribeiro, 2018) which confirm that life history strategies including dormant cysts are widespread in phytoplankton. A variety models have endeavoured to explain and predict amplitude, timing and/or spatial distribution of blooms by explicitly modeling multiple stages in the life cycle of a particular species, without interactions with other organisms

(see for example McGillicuddy et al. 2005, Yniguez et al. 2012, Hense & Beckmann 2006, Hellweger et al. 2008). Two-to-four species (Estrada *et al.*, 2010; Yamamoto *et al.*, 2002) models also exist, but they focus on explaining the dynamics of a single cyst-forming species interacting with vegetative-only groups. We have therefore no clear understanding of how the cyst stage may help maintain biodiversity in species-rich communities. We endeavour to demonstrate this here with a multispecies phytoplankton model including a cyst bank.

Phytoplankton communities in coastal environments may benefit from seed banks (hereafter called cyst banks to remain consistent with phytoplankton terminology) even more than the oceanic communities (see for example McGillicuddy *et al.*, 2005), as the distance to the sea bottom is smaller, allowing 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 dinoflagellates especially (Tester & Steidinger, 1997; Batifoulier *et al.*, 2013). Conversely, in many other bloom-forming species the nutrient-rich coastal areas might function as a reservoir for the biodiversity in the ocean, especially in the long run. Indeed, cysts are able to germinate again after dozens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy, so they can have a long-term effect on biodiversity in both oceanic and coastal environments. Therefore, we consider in this study three interlinked compartements: the coastal pelagic environment, the seed (cyst) bank, and the pelagic open ocean. The coastal pelagic environment acts as a bridge between the cyst bank and the open ocean.

Our model is parameterized from field data (growth and interaction rates), and includes biotic and abiotic constraints (e.g., particle sinking). In our analyses, we either add or remove the dormant compartment, which allows to pinpoint its contribution to coexistence. We find that the presence of cysts prevents the extinction of several species. Cyst banks also allow a community to maintain its richness even with strong disturbances of its interaction network, unless facilitative interactions completely eclipse competitive interactions. Changes in the environment, here represented by an increase in the mean temperature, can also be buffered by cysts banks. Finally, we discuss the importance of this often ignored life stage in phytoplanktonic demography and the information that would be required to further more accurate modeling of the cyst dynamics.

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 competing

populations and unfold as follow: first, populations grow or decline according to a Beverton-Holt (BH) multispecies density-dependence (eqs. 1 and 3), and then, in a second step, exchanges occur between the different compartments or patches constituting the metacommunity (eq. 4).

In this paper, individuals are phytoplanktonic cells that move between the upper layer of coastal water, its bottom layer where a cyst bank accumulates, and the ocean. Only oceanic and coastal pelagic cells are subject to BH-density dependence. Cysts are only affected by mortality m and burial due to sedimentation ζ. The different populations are field-inspired morphotypes accounting for the most frequent genera observed along the French coast (Picoche & Barraquand, 2020) and will hereafter be called taxa. Parameters and state variables are defined in Table 1.

The BH formulation of multispecies population dynamics is a Lotka-Volterra competition equivalent for discrete-time models, and is often used to represent terrestrial plant population/community dynamics. In this model, the maximum achievable growth rate is modified by both competitive and facilitative interactions, which translates into positive and negative α_{ij} coefficients respectively. We first use the classical multispecies Beverton-Holt model (model I, eq. 1). We subsequently define saturating interactions (model II, eq. 3). More specifically, in our case, the first step of the first model is written as

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

where the intrinsic growth rate $r_i(T)$ is a taxon-specific function of the temperature (see eq. 2), the interaction coefficients α_{ij} is the strength of the effect of taxon j on taxon i, and the loss term l accounts for lethal processes such a natural mortality, predation or parasitism. First estimate of interaction coefficients are inferred from a previous work on a specific coastal community with Multivariate AutoRegressive (MAR) models (**?**). How to shift from MAR- to BH-interaction matrices is described in the SI. We later calibrate this coefficient for this model, since MAR models were applied at a different timescale.

The growth rate $r_i(T)$ is a modified version of the formula by Scranton & Vasseur (2016) (eq. 2).

$$
\begin{aligned}
r_i(T) &= E(T)f_i(T) \\
\text{where } E(T) &= d \times 0.81e^{0.0631T_{\circ c}} \\
\text{and } f_i(T) &= \begin{cases}
\exp(-|T_K - T_{K,i}^{opt}|^3/b_i), & T_K \leq T_{K,i}^{opt} \\
\exp(-5|T_K - T_{K,i}^{opt}|^3/b_i), & T > T_{K,i}^{opt}
\end{cases}
\end{aligned}
\tag{2}
$$

where $r_i(T)$ can be decomposed in two parts: the taxon-independent metabolism part $E(T)$ and the

taxon-specific niche part $f_i(T)$. The metabolism part describes the maximum achievable growth rate based on Bissinger *et al.* (2008), as an update of the formula by Eppley (1972) used in Scranton & Vasseur (2016). This maximum daily growth rate is weighted by the daylength d as no growth occurs at night. The niche part $f_i(T)$ describes the decrease in growth rate due to the difference between the temperature in the environment and the taxon-specific thermal optimum $T_{K,i}^{opt}$, and is controlled by the specific thermal decay b_i which depends of the niche width. Parameterisation is detailed in the SI.

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

$$N_{t',i,c/o} = \frac{\exp(r_i(T))N_{t,i,c/o}}{1 + \sum_{j\in\mathbb{C}} \frac{a_C N_{t,j,c/o}}{H_{ij}+N_{t,j,c/o}} + \sum_{j\in\mathbb{F}} \frac{a_F N_{t,j,c/o}}{H_{ij}+N_{t,jc/o}}} - lN_{t,i,c/o} \tag{3}$$

where a_C and a_F are the maximum competition and facilitation strengths, respectively, with $\mathbb{C}$ and $\mathbb{F}$ the sets of competitors and facilitators of taxon i. We use here similar notations to Qian & Akçay (2020), but have different parameters that vary between species. Indeed, the half-saturation coefficients H_{ij} are here variable between species, since it did not make sense biologically for this quantity to be fixed (e.g., in a resource competition context, different species are expected to feel resource limitations at different concentrations of nutrients and at different number of competitors). How to use parameter estimates from model I to specify model II is described in the SI.

After growth and mortality happen, exchanges take place between the three compartments during the second step of the model (eq. 4).

$$\begin{cases} N_{t+1,i,c} &= (1 - s_i - e)N_{t',i,c} + \gamma N_{t',i,b} + eN_{t',i,o} \\ N_{t+1,i,o} &= (1 - s_i - e)N_{t',i,o} + eN_{t',i,c} \\ N_{t+1,i,b} &= (1 - \gamma)N_{t',i,b} + s_i N_{t',i,c} \end{cases} \tag{4}$$

Param	Name	Value (unit)	Status
$N_{t,i,c/o/b}$	Abundance of taxon i at time t in the coast (c) or ocean (o), or in the coastal benthos (b)	NA (Number of cells)	Dynamic
$T_{K/°C}$	Temperature	NA ($K/°C$)	Dynamic
$r_i(T)$	Growth rate of taxon i	NA	Dynamic
b_i	Thermal decay	Field-based, taxon-specific (K^3)	Calibrated
T_i^{opt}	Optimal temperature for taxon i	Field-based, taxon-specific (K)	Calibrated
d	Daylength	0.5 (%)	Fixed
$\alpha_{ij,c/o}$	Interaction strength of taxon j on i in model I	Field-based, taxon-specific (Cells^{-1})	Calibrated
k_{c2o}	Ocean/Coast interaction strength ratio in model I	1.5	Fixed
a_C/a_F	Maximum competitive/facilitative interaction strength in model II	Field-based, taxon-specific (NA)	Calibrated
H_{ij}	Half-saturation for the interaction strength of taxon j on i in model II	Field-based, taxon-specific (Cells)	Calibrated
s_i	Sinking rate of taxon i	$\{0.1; \mathbf{0.3}; 0.5\}\beta(0.55, 1.25)$	Fixed
e	Exchange rate between ocean and coast	0.4; 0 in scenario	Scenario
l	Loss rate of vegetative phytoplanktonic cells	0.04; 0.1; $\mathbf{0.2}$	Fixed
m	Cyst mortality rate	$\approx 10^{-4}/\mathbf{10^{-5}}; 1-\zeta$ in scenario	Scenario
ζ	Cyst burial rate	$10^{-3}, \mathbf{10^{-2}}, 10^{-1}$	Fixed
γ	Germination × Resuspension rate	$10^{-3}, \mathbf{10^{-2}}, 10^{-1} \times 10^{-5}, 10^{-3}, \mathbf{10^{-1}}$	Fixed

Table 1: Definition of main state variables and parameters of the models. Calibrated parameters are either directly estimated on data for this study or parameters for which initial estimates exist, but are improved through calibration. Fixed values or distributions are estimated from the literature and references are given in the main text. When a range of values is given, the bold numbers indicate the reference values while the others are used to test the sensitivity of the model. Scenario parameters are the parameters which are used to build ecological scenarii.

Each compartment (ocean, coast, seed bank) contains 10^3 cells at the beginning of the simulation, and is run for 30 years with a daily time step. We mimick the temperature input as a noisy sinusoidal signal with the same mean and variance as the empirical data set described below.

Parameterisation

Parameters values

Loss rate   The loss rate of vegetative cells can be attributed to natural mortality, predation or parasitism. This rate is quite variable in the literature: the model of Scranton & Vasseur (2016) considered a rate around 0.04 day^{-1} while a review by Sarthou *et al.* (2005) indicates a grazing rate of the standing stock between 0.2 and 1.8 day^{-1} and an autolysis rate around between 0.005 and 0.24 day^{-1} (in the absence of nutrients, or because of viral charge). A maximum value of 0.2 is fixed for the model.

Sinking rate   Phytoplanktonic particles have a higher density than water and cannot swim to prevent sinking (although they are able to regulate their buoyancy, Reynolds 2006). Sinking is mostly affected by hydrodynamics, but at the species-level, size, shape, density-regulation and colony-formation capabilities are key determinants of the particle floatation. In this model, the sinking rate of each taxon is drawn from a beta distribution with a mean value of 9%, and a maximum around 30%, that is $s \backsim 0.3\beta(0.55, 1.25)$ (see Fig. SXX), adapted from observations by Passow (1991) and Wiedmann *et al.* (2016).

Exchange rate The exchange rate between the ocean and the coast depends on the shape and location of the coast (estuary, cape, ...). At our calibration site (see section SXX), the renewal time ranges 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 burial by sedimentation ζ. Mortality values range between 10^{-5} and 10^{-4} per day (more details on the approximation of mortality rates from McQuoid *et al.* (2002) are given in the SI). However, cyst burial by sedimentation might be a prevailing phenomenum in driving phytoplanktonic dynamics. Once cysts have been buried, they are not accessible for resuspension even if they could have germinated from 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 and varies here between 0.001 and 0.1 per day.

Germination/resuspension Germination and resuspension are both needed for cyst to get back to the water column ($\gamma = $ resuspension$\times$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

In addition to phenology parameters whose estimation process is described in the SI, the 49 non-null interactions that form the community matrix of the model are calibrated on field-data. These interactions are computed from previous models (**?**, see SI for details on the equations) but need to be adjusted to take into account the differences in structure and time-step between studies.

The calibration procedure consisted in lauching 1000 simulations, each characterized by a specific set of interaction coefficients. More precisely, for each simulation, each interaction coefficient (α_{ij} in model I, H_{ij} in model II) has the same probability of keeping its value, being increased or decreased by 10%, or being halved or doubled. The abundances of the coastal compartment are then extracted over the last 2 years of the simulation and compared to observations to compute the following summary statistics:

- average abundance $f_1 = \sqrt{\frac{1}{S}\sum_i^S \left(\bar{N}_{i,obs} - \bar{N}_{i,sim}\right)^2}$ where S is the number of taxa and $\bar{N}_i$ is the logarithm of the mean abundance of taxon i

- amplitude of the cycles $f_2 = \sqrt{\frac{1}{S} \sum_i^S \left[(\max(N_{i,obs}) - \min(N_{i,obs})) - (\max(N_{i,sim}) - \min(N_{i,sim})) \right]^2}$ where N_i is the logarithm of the abundance of taxon i.

- period of the bloom. The year is divided in 3 periods, i.e. summer, winter and the spring/autumn group (as taxa blooming in these periods can appear in either or both seasons). We give a score of 0 if the taxon blooms in the same period as its observed counterpart and 1 otherwise.

Simulations with taxon extinction (i.e., taxon is absent for more than 6 month in a compartment) are discarded. Models are ranked according to their performance for each summary statistic and the set of interactions with the best rank for each summary statistics is kept throughout the rest of the simulations.

Sensitivity analysis Certain parameters, which were evaluated from the literature, may be site- or model- specific, or vary over one order of magnitude, e.g. rates of sinking s, resuspension/germination γ, cyst mortality m and burial ζ, as well as the loss rate l. The dependence between variation in values and outputs of present models needs to be investigated before drawing conclusions for specific ecological scenarii. The set of tested values for each parameter is given in Table 1. Variations in average abundances and amplitudes at the community- and taxon levels for the last 2 years of simulations are the major model diagnostics.

Empirical dataset used for calibration

The modeled community is inspired by previously analysed field data REPHY, 2017; Picoche & Barraquand, 2020. We use time series of phytoplanktonic abundances that have been monitored biweekly for 21 years in the Marennes-Oléron Bay, on the French Atlantic Coast (Picoche & Barraquand, 2020). The Auger sampling site is characterized by a high phytoplanktonic biodiversity, even by its region standard, sustained by the joint influences of the Atlantic Ocean and terrestrial inputs from the Seudre River, with a possible high contribution of the benthic community (Guarini *et al.*, 2004). We aim to approximate the population dynamics of the 11 most abundant and most frequent groups of genera, or taxa, focusing on the amplitude of fluctuations and their timing (phenology). The estimation of the parameters characterizing each taxon (T_i^{opt} and b_i), is described in the SI. The interactions between model taxa have already been inferred from abundance fluctuations (Picoche & Barraquand, 2020). The community matrix is characterized by a phylogeny-based modular structure which differentiates between centric and pennate diatom and dinoflagellates, a high level of facilitative interactions ($\approx 70\%$) and a strong self-regulation.

Scenarii

The effect of the cyst bank on biodiversity and community dynamics can be evaluated through the response to disturbance with and without the cyst compartment. We evaluated two main disturbances:

1. interaction strength variation

2. temperature change, either in mean value or variability

In the first scenario, interaction strengths were multiplied or divided by a factor ranging between 1 and 10. In order to differentiate the effects of facilitative and competitive interactions on coexistence, only one type of interactions was subject to this change. For each value of the multiplicative factor, we therefore ran 4 simulations for each growth model: one where positive (respectively, negative) interactions were multiplied by the factor and one where positive (respectively, negative) interactions were divided by the same factor.

In the second scenario, five different climate change cases were assessed. In the first three, the average temperature was increased by 2, 5, or 7°C. In the next two, keeping the reference average temperature, the total variance of the temperature, including seasonality and noise, was either decreased or increased by 25%. To acknowledge the stochasticity induced by the noise, the model was ran with five different time signals in each case.

In both scenarios, simulations were ran for 30 years for both growth models, with and without a cyst compartment, and only the last 2 years were considered.

Results

Phytoplankton dynamics

The classical Beverton-Holt (model I) and saturating interaction (model II) formulations both reproduced the main characteristics of phytoplanktonic dynamics. They produced one or two blooms during the year, with a range of abundances covering several orders of magnitude, with the right timing of these blooms. At the Auger site that was used for calibration, abundances increase in spring and can last over part of summer, or start a new bloom in autumn, which is what we obtained in the models. Annual mean abundance of the various taxa was also well reproduced. That said, in some cases abundances could be lower than expected and the variation in abundances due to seasonality was underestimated (Fig. 1). In all cases, saturating interactions led to higher abundances than mass-action interactions throughout the year (Fig. SXXX).
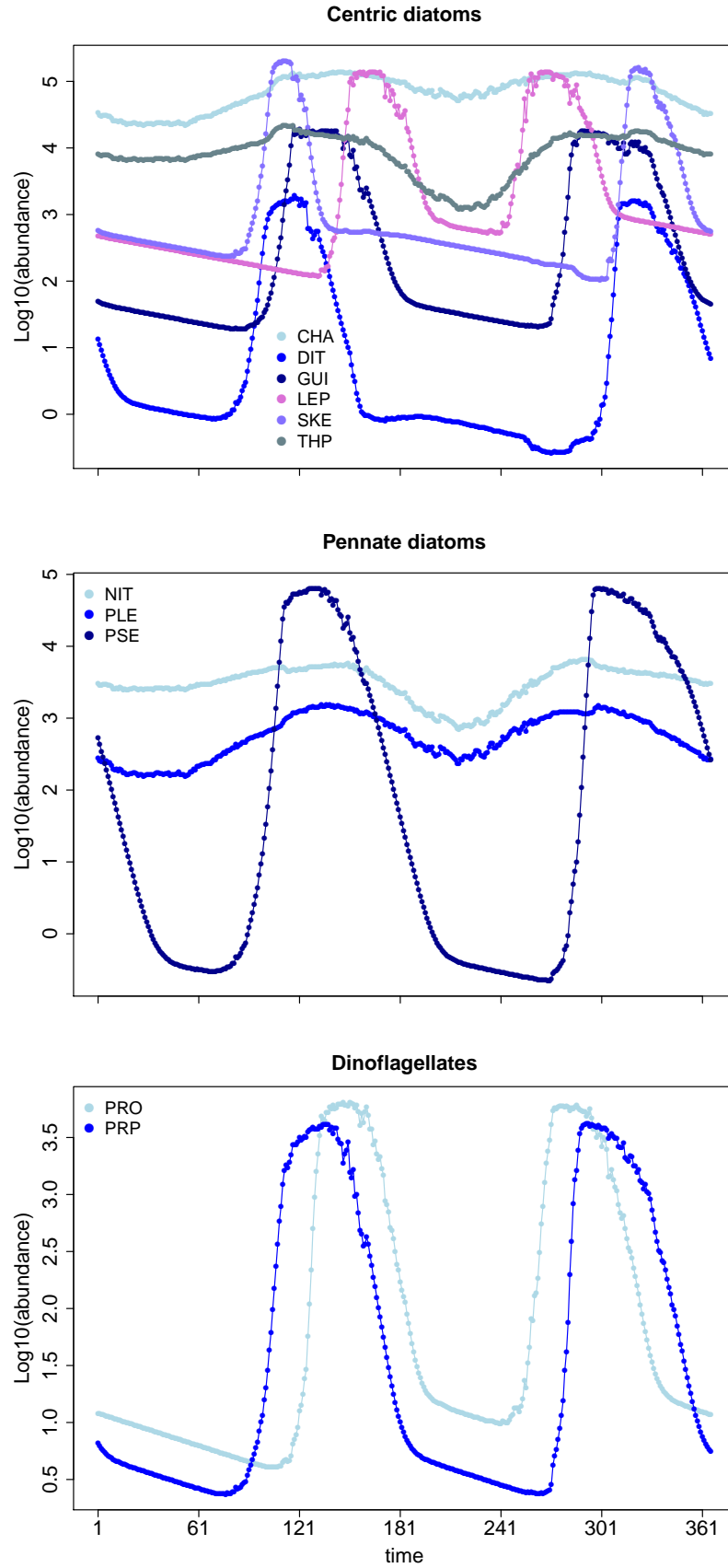
Figure 1: Simulated phytoplankton dynamics for a year in model I. Each panel corresponds to a cluster of interactions.

Sensitivity to uncalibrated parameters

Total phytoplankton dynamics were not strongly affected by changes in the parameter values (Fig. 2). As values varied in a plausible range, the average change in abundance on the coast between the reference simulation and the sensitivity simulations varied between -4.6 and 1.9% for model I and between -4.2 and 1.1% for model II, with similar deviations (same sign and magnitude) in the two models. The only parameter that led to a substantially different results between the two models was the resuspension parameter (leading to a different value of the parameter γ in Eq. 4) which, when decreased, led to an increase in abundance of approximately 1.9% in model I while it was only 0.9% in model II. In the two models, the decrease in mortality rate of vegetative cells m had the more impact of the final average abundance, leading to an increase in abundances. The exchange rate between the ocean and the coast had much less effect on the coastal average abundance.

On the other hand, the decimal logarithm of the maximum to minimum ratio of abundance (i.e., the order of magnitude of the range of abundances for each taxa) was more affected by changes in parameters and could vary by -39.4 to 18.6% in model I, and between -41.2% and 23% in model II. Results were qualitatively the same in the two models, with a decrease in cyst burial being the main driver of the decrease in amplitude, and a decrease in resuspension leading to an increase in amplitude.

In three cases (cyst burial rate set to 0.1, resuspension to 10^{-5} or the exchange rate set to 0), the final richness of the community decreased from 11 to 4. Extant taxa were the same in all simulations (CHA, THP, NIT, PSE). In a specific case (resuspension set to 0.001), a taxon periodically disappeared from the ocean, to be subsequently re-seeded by the coastal population.

With all parameters, except the sinking rate, an increase in abundance was linked with a decrease in amplitude
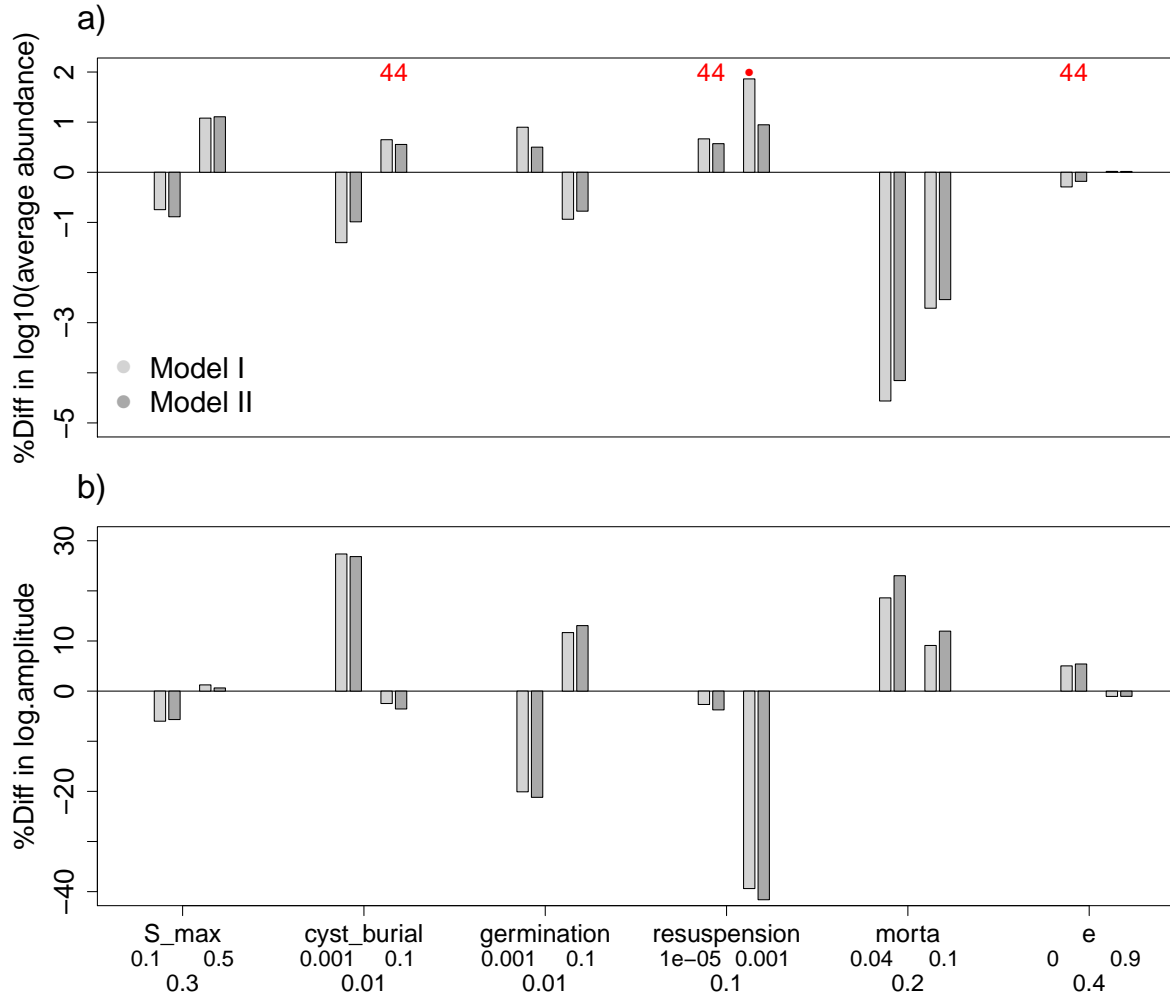
Figure 2: Sensitivity of the model to variation in parameters, measured as the difference between the reference simulation and the simulation with a change in parameter. The two metrics used were the average decimal log abundance (a) and the decimal logarithm of the ratio between maximum and minimum abundance (b) of the coastal phytoplanktonic community. Values used in the sensitivity analysis are in the second row of the x-axis while values used in the reference simulation are shown in the third row. Note that the reference value is not necessarily inside the range of values used in the sensitivity analysis (e.g. mortality rates in the sensitivity analysis are both below the value used in other simulations). Numbers in red are the final number of taxa and dots correspond to simulations in which at least one taxon reached 0 at one point but did not disappear.

Scenarios

Two scenarios were designed to test the buffering effect of the cyst bank against disruption. In both cases, it consisted in removing the cyst bank by setting cyst mortality to 100% per day Without disturbing the system otherwise, this led to a decrease in taxon richness from 11 to 4 taxa at the end of the simulation. Taking into account the extinct taxa, the geometric mean abundance of the community was around 10^{-2} while it was around 10^3 with a cyst bank. The average abundance of extant taxa only was around 30 without a cyst bank.

Biotic effects

Our first hypothesis was that the absence of the cyst bank would cause the community to be more affected by higher competition. Counter-intuitively, our results (Fig. 3) showed that an increase in competition only had negative effect with model I and for high competition values (6 times the reference ones at least), shifting from 4 taxa to 3 taxa in the oceanic compartment of a community without cyst bank while it did not affect the richness of a community with a cyst bank. On the contrary, a decrease in competition (from a factor 0.5 and lower) or an increase in facilitation (starting from a factor 2 and higher) led to much smaller communities in model II, sometimes with a total competitive exclusion. Richness was lowest when competition was divided by 6 or when facilitation was multiplied by 8 in model II. The same pattern (richness stability with model I, sensitivity to a decrease in competition or an increase in facilitation with model II) was observed in a community with a cyst bank, but for larger disturbances. Competition indeed had to be at least divided by 6 or facilitation, to be multiplied by 7 for richness to decrease to 9 taxa.

The geometric mean abundance was also affected by such biotic changes. The order of magnitude of the average abundance without a cyst bank varied between a -1.4 and -2.8 with model I and between -1.3 and -3.3 with model II, while it was between 34.4 and 1.4 for model I and between 0.7 and 3.3 for model II with a cyst bank. It should be noted that model I was able to produce much higher abundances when competition was low, which can be related to the presence of a hard threshold on the amplifying effect of the interactions on the growth rate.
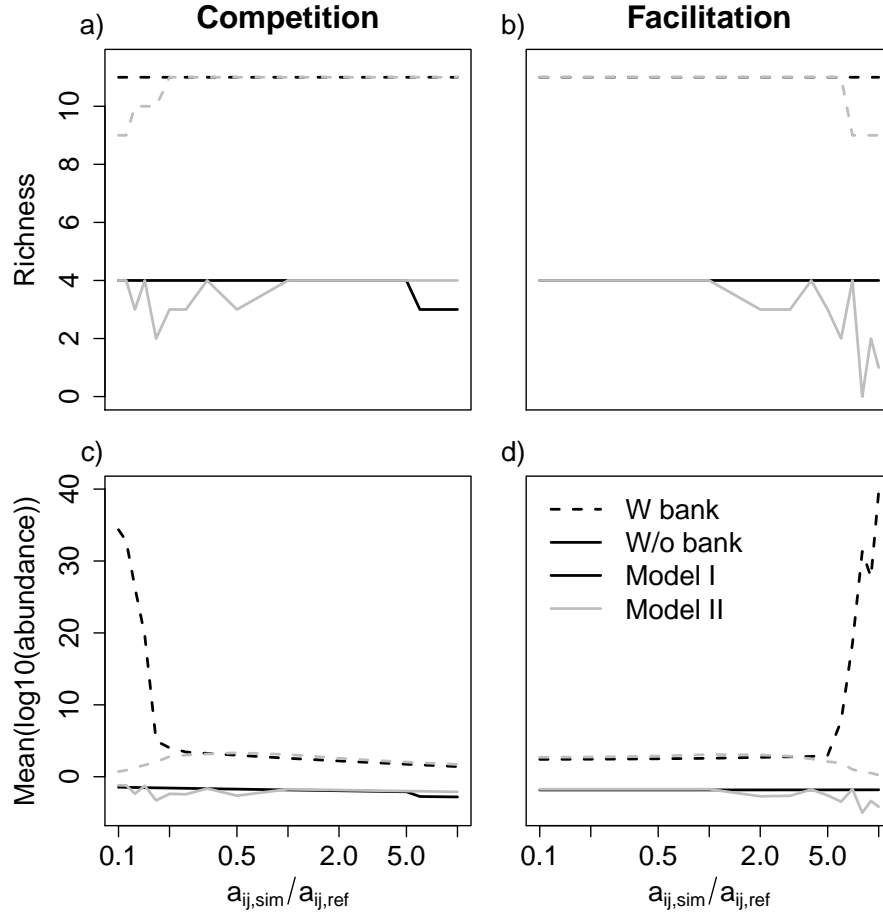
Figure 3: Variation in the total number of taxa still present in the ocean at the end of the simulation (richness) and the geometric mean abundance, including extinct taxa, with (dashed line) and without (solid line) a seed bank, as a function of the strength of competition and facilitation with a classical Beverton-Holt (black lines) or a saturating interaction (grey lines) formulation. The x-axis shows the factor by which each interaction was multiplied (note the logarithmic scale)

Taxa which disappear were always the same and were characterized by a lower minimum abundance, a higher amplitude and a small niche (Fig. 4). In contrast, their interactions were not qualitatively different from the other taxa.
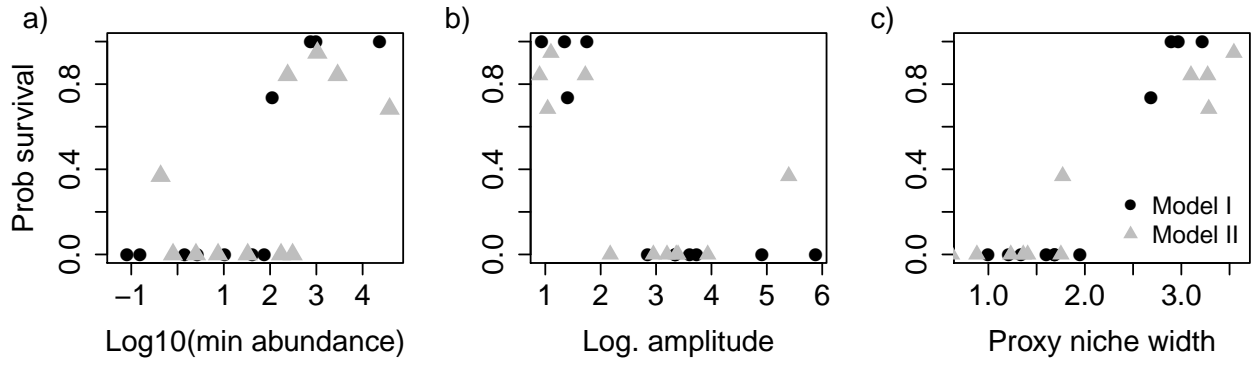
Figure 4: Probability of survival of taxa when competition increases, as a function of their dynamics characteristics (min abundance, logarithm of amplitude and niche width) in the reference parameter set .

Abiotic effects Our second hypothesis was that the absence of a cyst bank would reduce the ability of a community to buffer changes in the environment, here represented by variation in the temperature. As can be seen on Fig. 5, this was true for both models, as the communities without a cyst bank could not maintain their richness with an increase in temperature above 2°C, as opposed to communities with a cyst bank, which could only be affected by a 7°C increase (scenario SSP5 8.5). In all cases however, the total abundances were not strongly affected. Indeed, the total abundance of a community is driven by a small number of numerically dominant taxa, which did not disappear. High total abundances tended to correspond to the abundance of only one or two taxa. Model II consistenly led to higher abundances, as was already the case in the reference simulations.

The variance of the temperature did not affect richness nor total abundance of communities with and without a cyst bank.
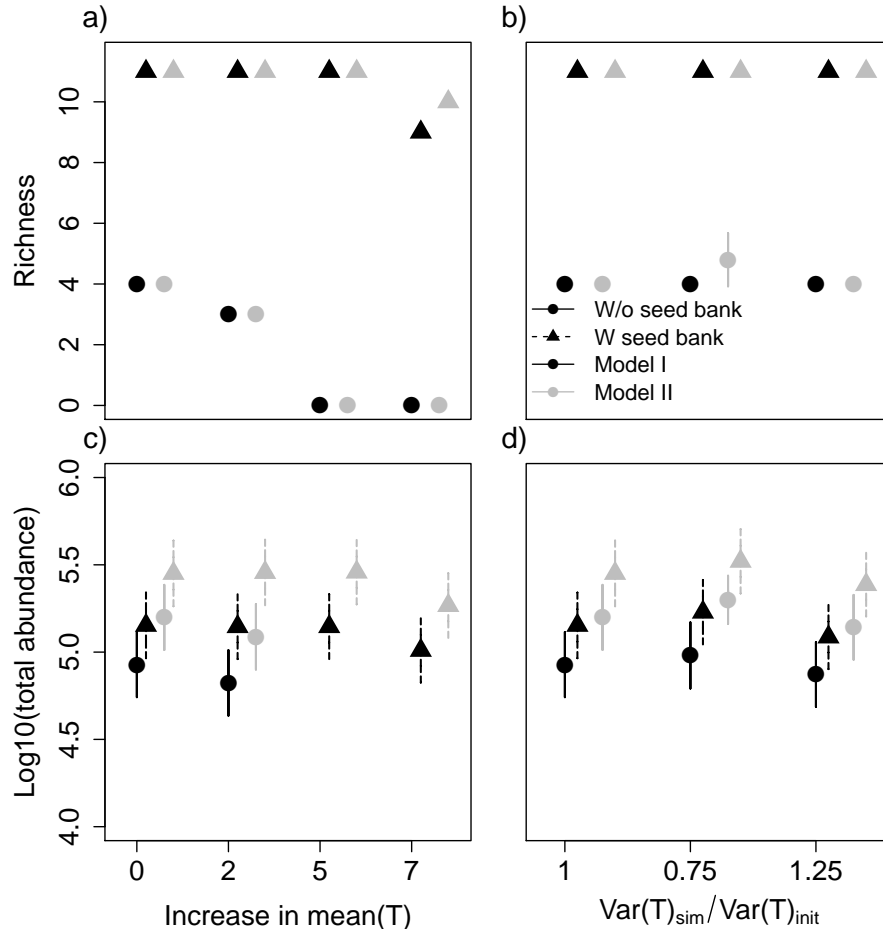
Figure 5: Variation in richness and total abundance with and without a cyst bank as a function of the mean and variance of the temperature with a classical Beverton-Holt (left) or a saturating interaction (right) formulation.

Discussion

Using a meta-community model which accounts for movements between the ocean and the coast, as well as movements between the top and the bottom of the coastal water column, we were able to show that a specific life stage, the cyst stage, can help maintain biodiversity in different marine compartments. Using literature-derived and field-calibrated parameters, we modeled the behaviour of phytoplanktonic communities with and without a cyst bank. Biodiversity decreased drastically in the absence of a cyst bank, and so did the total abundance of the community. Moreover, when faced with a biotic or abiotic perturbation, communities that could divert part of their population to a dormant stage were less prone to species loss and could maintain their biomass through the years. These results were consistent for the two interaction models that we considered, with and without saturation in interaction strengths.

Our assessment of cyst bank effects is somehow contingent upon how realistic is our modelling of

community dynamics. Our model parameters were partly based on calibration of a specific field abundance dataset, which allowed us to represent realistic biotic interactions between phytoplanktonic taxa and phenology, and partly based on literature-derived estimates. The range of values found in the literature for certain parameters demonstrated both the variability of the environment and phytoplanktonic reactions, and the uncertainty one can have when measuring certain processes. Hydrodynamics features are highly site-dependent and sometimes poorly defined: cyst burial and resuspension, for instance, are functions of the shape of the coastal site and its interface with the ocean, as well as stochastic phenomena, such as gusts of wind, bioturbation or anthropogenic disturbances. On the other hand, taxon specificities such as shape, buoyancy regulation capacity or cyst formation rate can influence the rate of contribution to the seed bank (which could be approximated by the variation in sinking rate in our model). Our model proved quite resilient to variations in these parameters, which makes our conclusions qualitatively reliable.

Effect of interactions on the model : setting of a threshold in model I, saturating interaction effect, positive interaction effect more destabilizing (+ justify it, as it does exist in nature?).

Seed bank buffering effect in terrestrial plant literature for interation and environment: The capacity of a seed bank to buffer disadvantageous environments to maintain population over time is a staple in terrestrial plant literature [[refS]]. Both empirical [[ref]] and theoretical [[ref]] evidence show that investing part of the biomass of a population in stages that will spread their growth over periods longer than the usual life cycle of the organisms is a successful strategy to maintain over time. This is the basis of bet-hedging

What this adds to phytoplanktonic studies (a few words on models already existing, such as Dalelio and Hinners?).

What needs to be explored now (specific cyst formation and regulation, parameters regulating the dynamics of the cyst bank itself -burial and resuspension, for instance)

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