

Steps

$$\begin{cases} N_{t+h,i,c} &= \frac{e^{r_i(T)} N_{t,i,c}}{1 + \sum_j \alpha_{ij} N_{t,j,c}} - l N_{t,i,c} \\ N_{t+h,i,o} &= \frac{e^{r_i(T)} N_{t,i,o}}{1 + k_{c2o} \sum_j \alpha_{ij} N_{t,j,o}} - l N_{t,i,o} \\ N_{t+h,i,b} &= N_{t,i,b} (1 - m - \zeta) \end{cases} \quad (1)$$

$$\begin{cases} N_{t+1,i,c} &= N_{t+h,i,c} (1 - s_i - e) + \gamma N_{t+h,i,b} + e N_{t+h,i,o} \\ N_{t+1,i,o} &= N_{t+h,i,o} (1 - s_i - e) + e N_{t+h,i,c} \\ N_{t+1,i,b} &= N_{t+h,i,b} (1 - \gamma) + s_i N_{t+h,i,c} \end{cases} \quad (2)$$

Param	Name	Value (unit)
$N_{t,i,c/o/b}$	Abundances of species i at time t (coast, ocean, benthos)	NA (Number of cells)
T	temperature	NA (K)
$r_i(T)$	maximum growth rate of species i	NA (NA)
$\alpha_{ij,c/o}$	interaction strength of species j on i	Adapted from Picoche&Barraquand 2020 (NA)
k_{c2o}	conversion coefficient from coastal to oceanic interactions	1.5 [arbitrary] (NA)
s_i	sinking rate of species i	$\{0.1; 0.3; 0.5\} \beta(0.55, 1.25)$ (NA)
e	exchange rate between ocean and coast	$\{0.4; 0.6; 1\}$ (NA)
l	loss of vegetative phytoplankton (predation, mortality...)	0.04 (NA)
m	cyst mortality	$\approx 10^{-4}/10^{-5}$ (NA)
ζ	cyst burial	$\{0.01; 0.1; 0.3\}$ (NA)
γ	germination \times resuspension rate of species	$\{0.1; 0.01; 0.001\} * \{10^{-5}, 0.1\}$ (NA)

Table 1: Definition of main state variables 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 parameters has been assessed. In the “Value (unit)” column, V indicates a state variable while (NA) indicates that the parameter is dimensionless.

Saturating interactions

$$N_{t+dt,i,c} = \frac{e^{r_i(T)} N_{t,i,c}}{1 + \sum_j \alpha_{ij} N_{t,j,c}} - l N_{t,i,c} \quad (3)$$

For the sake of simplicity, we hereafter ignore the loss term and concentrate on the growth rate/interaction part, and drop the compartment name ($N_{t+h,i,c} \rightarrow N_{t+h,i}$) as the functioning of the oceanic compartment reproduces the coastal one, only with stronger (competitive only?) interactions.

There are both competitive ($\alpha_{ij} > 0$) and facilitative ($\alpha_{ij} < 0$) interactions, which means that the denominator $1 + \sum_j \alpha_{ij} N_{t,j}$ can be very close to 0, or negative, thus leading to unrealistic growth rate values. Ignoring possible overyielding, we should have $\sum \alpha_{ij} N_{t,j} \geq 0$, as $e^{r_i(T)}$ is considered a maximum growth rate in ideal conditions.

For now, coefficients are directly adapted from the MAR model (exact equivalence).

We consider saturating interactions, for both competition and facilitation. There are two ways to consider interaction differences between species.

$$N_{t+dt,i} = \frac{e^{r_i(T)} N_{t,i}}{1 + \sum_{j/\alpha_{ij} \in \mathbb{C}} \frac{a_{ij} N_{t,j}}{H_C + N_{t,j}} + \sum_{j/\alpha_{ij} \in \mathbb{F}} \frac{a_{ij} N_{t,j}}{H_F + N_{t,j}}} \quad (4)$$

where coefficients a_{ij} are the maximum interaction strength of species j on species i (the interaction strengths when the abundance of the competitor/facilitator tends towards infinity), H_C and H_F are the half-saturation constants corresponding to competitive and mutualistic interactions respectively, \mathbb{C} and \mathbb{F} are the sets of competitive and facilitative interactions.

OR

$$N_{t+dt,i} = \frac{e^{r_i(T)} N_{t,i}}{1 + \sum_{j/a \in \mathbb{C}} \frac{a_C N_{t,j}}{H_{ij} + N_{t,j}} + \sum_{j/a \in \mathbb{F}} \frac{a_M N_{t,j}}{H_{ij} + N_{t,j}}} \quad (5)$$

where coefficients a_C and a_F are the maximum interaction strength for competition and facilitation respectively, H_{ij} coefficients are the abundance of species j to reach half of the maximum effect in the interaction of j on i , and \mathbb{C} and \mathbb{F} are the sets of competitive and facilitative interactions. Variations in H_{ij} can be attributed to the limiting resource (light can saturate more rapidly than nutrients, especially in a coastal environment where they are supposed to be plentiful, which would lead to a smaller H_{ij} in the case of light).

Jacobian

We use the notation from eq. 4, but the derivation of the Jacobian is the same for both eq. 4 and 5.

$$N_{t+1,i} = \frac{e^{r_i} N_{t,i}}{1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_{t,j}}{H_C + N_{t,j}} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_{t,j}}{H_F + N_{t,j}}} \quad (6)$$

Let's have $n_{t,i} = \log(N_{t,i})$.

$$n_{t+1,i,c} = r_i + n_{t,i} - \log\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_{t,j}}{H_C + N_{t,j}} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_{t,j}}{H_F + N_{t,j}}\right) \quad (7)$$

We assume that there is an equilibrium for $N_i = e^{n_i}$ (we just remove the time subscript) and we have $X_i = \log\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_j}{H_C + N_j} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_j}{H_F + N_j}\right)$. We want to compute $\frac{\partial X_i}{\partial n_i}$ and $\frac{\partial X_i}{\partial n_j}$.

$$\frac{\partial X_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i} \frac{\partial N_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i} e^{n_i} \quad (8)$$

Let's take it step by step: $X_i = \log(u(N_i))$ and $u(N_i) = 1 + \sum_j \frac{f_i(N_j)}{g_i(N_j)}$ where $g_i(N_j)$ can be either $H_C + N_j$ or $H_F + N_j$. The sum on j can be simplified by the derivation:

$$\frac{\partial u_i}{\partial N_j} = \partial \frac{a_{ij} N_j}{H_i + N_j} \frac{1}{\partial N_j} = \frac{a_{ij}(H_i + N_j) - a_{ij} N_j}{(H_i + N_j)^2} = \frac{a_{ij} H_i}{(H_i + N_j)^2} \quad (9)$$

Therefore,

$$\frac{\partial X_i}{\partial n_j} = \frac{a_{ij} H_i}{(H_i + N_i)^2} \frac{N_j}{\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_j}{H_C + N_j} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_j}{H_F + N_j}\right)} \quad (10)$$

If we have b_{ij} the MAR coefficients:

$$\begin{cases} b_{ii} - 1 = \frac{a_{ii} H_C}{(H_C + N_i)^2} \frac{N_i}{\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_j}{H_C + N_j} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_j}{H_F + N_j}\right)} \\ b_{ij, i \neq j} = \begin{cases} \frac{a_{ij} H_C}{(H_C + N_j)^2} \frac{N_j}{\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_j}{H_C + N_j} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_j}{H_F + N_j}\right)} & \forall a_{ij} \in \mathbb{C} \\ \frac{a_{ij} H_F}{(H_F + N_j)^2} \frac{N_j}{\left(1 + \sum_{j/a_{ij} \in \mathbb{C}} \frac{a_{ij} N_j}{H_C + N_j} + \sum_{j/a_{ij} \in \mathbb{F}} \frac{a_{ij} N_j}{H_F + N_j}\right)} & \forall a_{ij} \in \mathbb{F} \end{cases} \end{cases} \quad (11)$$

In both formula, it is clear that the model has no unique solutions for all coefficients. Either a or H need to be fixed beforehand. In addition to this constraint, the formula in eq. 11 might be too complex (cannot be linearized) to help parameterize either H_{ij} or a_{ij} . Values at limit abundance can be used to approximate these parameters.

When abundances tend to infinite, the interaction coefficient tends to a_{ij} , which gives no information on the half-saturation coefficient. However, it would be surprising that populations can reach their maximum abundances in field conditions, and therefore their maximum competition strengths. In the absence of any information on the species-specific shape of the interaction

On the contrary, at low density (far from saturation), the system can be modeled by a non-saturating function (eq. 3). Taking the tangent of the function at this point, H_{ij} can be approximated by $\frac{a_C}{\alpha_{ij}}$. In this case, a proxy of the maximum competition strength a_C could be $\sum |\alpha_{ij}| N_{j,max}$.

Steps

- Compute α_{ij} from eq. 3 (i.e. from the derivation of Beverton-Holt and relationship with MAR interaction coefficients b_{ij})
- Compute a_C from α_{ij} as $\sum |\alpha_{ij}| N_{j,max}$
- Compute $H_{ij} = \frac{a_C}{\alpha_{ij}}$
- Optional: the tangent of the saturating function at low density might be well-above the final type-II response. In this case, multiplying α_{ij} by 2 or 3 might be necessary to get closer to actual data.
- Question: how to compute a_F ? If overyielding is out of question (however, see Shurin et al. 2014 where it was observed but not frequent), $1 + \sum_{j/\alpha_{ij} \in \mathbb{C}} \frac{a_C N_{j,max}}{H_{ij} + N_{j,max}} + \sum_{j/\alpha_{ij} \in \mathbb{F}} \frac{a_F N_{j,max}}{H_{ij} + N_{j,max}} < \exp(r_{i,max})$. Otherwise, a factor can be applied. Instead of $\exp(r_{i,max})$, $O_y \exp(r_{i,max})$ with O_y a overyielding factor (max 1.1 from Shurin et al. 2014).