## Steps

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

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

| 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) |
| $\zeta$ | cyst burial | {0.01 ; 0.1 ; 0.3} (NA) |
| $\gamma$ | 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 parametes has been assessed. In the "Value (unit)" column, V indicates a state variable while (NA) indicates that the parameter is dimensionless.

## Saturating interactions

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

There are both competitive ($\alpha_{ij}$>0) and facilitative ($\alpha_{ij}$<0) interactions, which means that the denominator $1+\sum_j \alpha_{ij}N_{t,j,c}$ can be very close to 0, or negative, thus leading to unrealistic growth rate values. Ignoring possible overyielding, we should have $\sum \alpha_{ij}N_{t,j,c} \geq 0$, 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. I did not find direct formulations of such feature in a Beverton-Holt growth model. My only idea is loosely based on the Unique Interaction Model of Qian and Akçay (2020) who however use a continuous-time, linear model. I only added a saturating competition in addition to saturating facilitation:

$$
N_{t+h,i,c} = \frac{e^{r_i(T)}N_{t,i,c}}{1+\sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_{ij}N_{t,j,c}}{H_C+N_{t,j,c}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_{ij}N_{t,j,c}}{H_F+N_{t,j,c}}} - lN_{t,i,c}
$$

where $\mathbb{C}$ and $\mathbb{F}$ are the sets of competitive and facilitative interactions.

## Jacobian ($\alpha = \alpha_{ij}$)

We can try and start with a simplified version of the model, without the loss term.

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

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

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

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

$$\frac{\partial X_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i}\frac{\partial N_i}{\partial n_i} = \frac{\partial X_i}{\partial N_i} e^{n_i}$$

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

$$\frac{\partial u_i}{\partial N_j} = \partial \frac{\alpha_{ij}N_j}{H_{\bullet} + N_j}\frac{1}{\partial N_j} = \frac{a_{ij}(H_{\bullet} + N_j) - a_{ij}N_j}{(H_{\bullet} + N_j)2} = \frac{a_{ij}}{(H_{\bullet} + N_j)^2}$$

Therefore,

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

If we have $b_{ij}$ the MAR coefficients:

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

## Alternative ($H = H_{ij}$)

According to FB:

$$N_{t+1,i} = \frac{e^{r_i}N_{t,i}}{1 + \sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_C N_{t,j}}{H_{ij}+N_{t,j}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_M N_{t,j}}{H_{ij}+N_{t,j}}}$$

How to choose $\alpha_C$ et $\alpha_M$?

$$\alpha_C, \alpha_M \text{ so that } \forall t, 1 + \sum_{j/\alpha_{ij}\in\mathbb{C}} \frac{\alpha_C N_{t,j}}{H_{ij} + N_{t,j}} + \sum_{j/\alpha_{ij}\in\mathbb{F}} \frac{\alpha_M N_{t,j}}{H_{ij} + N_{t,j}} > \exp(r_{i,max}(T))$$

To compute $\alpha_C$, compute $b_{i.,max} = -\sum_{j,j\neq i} |b_{ij}|N_j$ and translate into $\alpha_C$ (with classical BH formula ? or with saturating interactions (see equations above) ? With LV model? Using $\overline{N_j}$, $N_{j,max}$?) (or should we first compute $\alpha_{ij}$ and then $\alpha_C = \sum_{j,j\neq i} |\alpha_{ij}|N_j$[1]

And use $H_{ij} = \frac{\alpha_C}{\alpha_{ij}}$ ?

Note from CP:

- I don't think dimensions match.
- Wouldn't $\sum \frac{\alpha_C N_{j,max}}{H_{ij}+N_{j,max}} >> \sum_{\in\mathbb{F}} \frac{\alpha_M N_{j,max}}{H_{ij}+N_{j,max}}$ be enough?

[1] I'd rather do this one as the formula is non-linear and I fear that we distort the value if we first compute $b_{i.,max}$