

# Microbial community

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## 1 Finding solutions

We want to look at equilibria of a system of  $N_R$  resources and  $N_S$  species whose evolution is given by:

$$\begin{aligned}\dot{R}_i &= \lambda_i - \mu_i R_i - \sum_j \gamma_{ij}^T R_i S_j + \sum_j \alpha_{ij} S_j \\ \dot{S}_i &= \sum_j \sigma_{ij} \gamma_{ij} S_i R_j - \delta_i S_i\end{aligned}$$

In general, the Jacobian matrix  $J(R, S)$  is given by:

$$J(R, S) = \begin{pmatrix} -(\mu + \gamma^T S)_d & -R_d \gamma^T + \alpha \\ S_d \sigma \otimes \gamma & ((\sigma \otimes \gamma) R - \delta)_d \end{pmatrix}$$

where  $\otimes$  stands for the Hadamard product (element by element).

The equilibrium solution  $(R^*, S^*)$  are defined by the equations :

$$0 = \lambda - \mu_d R^* - R_d^* \gamma^T S^* + \alpha S^* \quad (1)$$

$$0 = S_d^* (\sigma \otimes \gamma) R^* - S_d^* \delta \quad (2)$$

Assuming we want positive solutions, i.e.,  $R^*, S^*$  are positive-valued vectors, we get an implicit solution for  $R^*$  :

$$(\sigma \otimes \gamma) R^* = \delta.$$

Note that  $\sigma \otimes \gamma$  is an  $N_S \times N_R$  matrix, while  $R^*$  is an  $N_R$  vector and  $\delta$  is an  $N_S$  vector.

Writing  $A := \sigma \otimes \gamma$ , we note that  $A_L^{-1} := (A^T A)^{-1} A^T$  allows to solve that equation explicitly :

$$A_L^{-1} A R^* = (A^T A)^{-1} A^T A R^* = 1_{N_R} R^* = R^*$$

Hence :

$$R^* = A_L^{-1} \delta$$

This implies of course the condition that  $A^T A = (\sigma \otimes \gamma)^T \sigma \otimes \gamma = (\sigma^T \otimes \gamma^T)(\sigma \otimes \gamma)$  is invertible, and hence  $N_S \geq N_R$ .

Having found an explicit solution for  $R^*$ , we can find an implicit solution for  $S^*$ :

$$(R_d^* \gamma^T - \alpha) S^* = \lambda - \mu_d R^*$$

Writing  $B := R_d^* \gamma^T - \alpha$  and using the same trick as before, we can find an explicit solution :

$$S^* = B_L^{-1}(\lambda - \mu_d R^*) = (B^T B)^{-1} B^T (\lambda - \mu_d R^*)$$

This works as long as  $B^T B$  is invertible. As  $B$  is a  $N_R \times N_S$  matrix, this implies  $N_R \geq N_S$ .

That is, it is hard to find explicit equilibria while the model parameters are given if  $N_R \neq N_S$ .

If  $N_S \neq N_R$ , we can do like the Butler paper and find the appropriate physical parameters assuming we know the equilibrium values  $R^*, S^*$ . In that case then, the Jacobian matrix at equilibrium is given by:

$$J^* := J(R^*, S^*) = \begin{pmatrix} -(\mu + \gamma^T S^*)_d & -R_d^* \gamma^T + \alpha \\ S_d^* \sigma \otimes \gamma & 0 \end{pmatrix} \quad (3)$$

## 2 The one-resource case

We take the special case  $N_R = 1$  and  $N_S$  arbitrary. Looking at the equilibrium equations (1) and (2) yields directly two solutions:

- $S_i^* = 0$  for every species and  $R^* = \frac{\lambda}{\mu}$ . That is the case where eventually every species dies out (we will call it trivial equilibrium).
- $S_i^* = 0$  for every species but one (denote it  $k$ ) and then

$$R^* = \frac{\delta_k}{\sigma_k \gamma_k} \text{ and } S_k^* = \frac{\mu R^* - \lambda}{\alpha_k - \gamma_k R^*}$$

In the one resource case, the jacobian is given by

$$J = \begin{pmatrix} -\mu - \gamma \cdot S & -\gamma^T R + \alpha \\ \sigma_i \gamma_i S_i & \delta_{ij}(\sigma_i \gamma_i R - \delta_i) \end{pmatrix} \quad (4)$$

### 2.1 The trivial equilibrium

In that case, every species dies out in the end, such that  $S_i^* = 0 \forall i = 1, \dots, N_S$ . The jacobian at equilibrium is then given by:

$$J^* = \begin{pmatrix} -\mu & -\gamma^T R^* + \alpha \\ 0 & \delta_{ij}(\sigma_i \gamma_i R^* - \delta_i) \end{pmatrix} \quad (5)$$

### 2.2 The non trivial equilibrium

In the non trivial equilibrium, one of the species survives, which gives the following jacobian at equilibrium:

$$J^* = \begin{pmatrix} -\mu - \gamma_k S_k^* & -\gamma^T R^* + \alpha \\ \delta_{ik} \sigma_i \gamma_i S_i^* & \delta_{ij}(\sigma_i \gamma_i R^* - \delta_i) \end{pmatrix}. \quad (6)$$

For instance if  $N_S = 2$  and that  $k = 2$  (ie the survivor is the last species), the Jacobian matrix would be :

$$J^* = \begin{pmatrix} -\mu - \gamma_2 S_2^* & -\gamma_1 R^* + \alpha_1 & -\gamma_2 R^* + \alpha_2 \\ 0 & \sigma_1 \gamma_1 R^* - \delta_1 & 0 \\ \sigma_2 \gamma_2 S_2^* & 0 & \sigma_2 \gamma_2 R^* - \delta_2 \end{pmatrix} = \begin{pmatrix} -\mu - \gamma_2 S_2^* & -\gamma_1 R^* + \alpha_1 & -\gamma_2 R^* + \alpha_2 \\ 0 & \sigma_1 \gamma_1 R^* - \delta_1 & 0 \\ \sigma_2 \gamma_2 S_2^* & 0 & 0 \end{pmatrix} \quad (7)$$

Note that this result is more general than the one in the paper by Butler since we accept solutions where some species simply disappear (contrarily to their assumptions when deriving the equilibria). This here changes the game since it makes the lower block of the jacobian matrix not zero anymore.

Without loss of generality we can put the non vanishing species at the end and hence the jacobian at equilibrium generally looks like :

$$J^* = \begin{pmatrix} -a & \mathbf{b}^T \\ \mathbf{c} & D \end{pmatrix} \quad (8)$$

where:

- $a = \mu + \gamma_{N_S} S_{N_S}^*$  is a positive number.
- $\mathbf{b}$  is a  $N_S$  vector defined by  $b_i = -\gamma_i R^* + \alpha_i$ .
- $\mathbf{c}$  is a vector who is mostly zero. More explicitly,  $c_i = \delta_{iN_S} \sigma_i \gamma_i S_i^*$ .
- $D$  is a  $N_S \times N_S$  diagonal matrix. Explicitly,

$$D = \text{diag}(\sigma_1 \gamma_1 R^* - \delta_1, \dots, \sigma_{N_S-1} \gamma_{N_S-1} R^* - \delta_{N_S-1}, 0)$$

## 2.3 Stability of the non trivial equilibrium

We now seek the solution to the equation  $\det(J^* - \lambda) = 0$  (there is a bit of confusion here, since until the eigenspectrum is fully written down,  $\lambda$  refers to the eigenvalues and not the  $\lambda$  of the model). Explicitly, it is:

$$\det \begin{pmatrix} -a - \lambda & \mathbf{b}^T \\ \mathbf{c} & D - \lambda \end{pmatrix} = 0 \quad (9)$$

Assuming that  $\lambda \neq -a$ , this can be rewritten as:

$$(-\lambda - a) \det(D - \lambda - \mathbf{c}(-\lambda - a)^{-1} \mathbf{b}^T) = 0 \iff \det(D - \lambda - \mathbf{c}(-\lambda - a)^{-1} \mathbf{b}^T) = 0 \quad (10)$$

Assuming a finite  $\lambda$  this is equivalent to:

$$\det((-\lambda - a)(D - \lambda) - \mathbf{c} \mathbf{b}^T) = \det(\lambda^2 + (a - D)\lambda - (aD + \mathbf{c} \mathbf{b}^T)) = 0. \quad (11)$$

Using the famous equality  $\det M = \exp \text{Tr} \ln M$ , Eq.(11) can be written as

$$\text{Tr}(\ln(\lambda^2 + (a - D)\lambda - (aD + \mathbf{c} \mathbf{b}^T))) = -\infty. \quad (12)$$

Explicitly:

$$\sum_{i=1}^{N_S} \ln(\lambda^2 + (a - D_i)\lambda - (aD + \mathbf{c} \mathbf{b}^T)_i) = -\infty \quad (13)$$

$$\implies \ln \left( \prod_{i=1}^{N_S} \lambda^2 + (a - D_i)\lambda - (aD + \mathbf{c} \mathbf{b}^T)_i \right) = -\infty \quad (14)$$

$$\implies \prod_{i=1}^{N_S} (\lambda^2 + (a - D_i)\lambda - (aD + \mathbf{c} \mathbf{b}^T)_i) = 0 \quad (15)$$

$$\implies (\lambda^2 + a\lambda - c_{N_S} b_{N_S}) \prod_{i=1}^{N_S-1} (\lambda^2 + (a - D_i)\lambda - aD_i) = 0 \quad (16)$$

$$\implies \left( \lambda - \frac{a}{2} \left( \sqrt{1 + \frac{4c_{N_S} b_{N_S}}{a^2}} - 1 \right) \right) \left( \lambda + \frac{a}{2} \left( \sqrt{1 + \frac{4c_{N_S} b_{N_S}}{a^2}} + 1 \right) \right) \prod_{i=1}^{N_S-1} (\lambda - D_i) = 0 \quad (17)$$

So the spectrum of the Jacobian is given by the  $N_S + 1$  values:

$$\sigma(J^*) = \{\sigma_i \gamma_i R^* - \delta_i, i = 1, \dots, N_S - 1\} \cup \left\{ \frac{a}{2} \left( \sqrt{1 + \frac{4c_{N_S} b_{N_S}}{a^2}} - 1 \right), -\frac{a}{2} \left( \sqrt{1 + \frac{4c_{N_S} b_{N_S}}{a^2}} + 1 \right) \right\} \quad (18)$$

With the full spectrum in hand, we can now define a stability condition : we say the equilibrium is stable when every eigenvalue has a negative real part. This implies first of all :

$$\frac{4c_{N_S} b_{N_S}}{a^2} < 0 \iff c_{N_S} b_{N_S} < 0 \iff b_{N_S} < 0 \iff R^* = \frac{\delta_{N_S}}{\sigma_{N_S} \gamma_{N_S}} > \frac{\alpha_{N_S}}{\gamma_{N_S}} \quad (19)$$

It also implies

$$\sigma_i \gamma_i R^* - \delta_i < 0 \quad \forall i = 1, \dots, N_S - 1 \iff R^* = \frac{\delta_{N_S}}{\sigma_{N_S} \gamma_{N_S}} < \min_{i \in \{1, \dots, N_S - 1\}} \left( \frac{\delta_i}{\sigma_i \gamma_i} \right) \quad (20)$$

Hence we must have

$$\boxed{\frac{\alpha_{N_S}}{\gamma_{N_S}} < R^* < \min_{i \in \{1, \dots, N_S - 1\}} \left( \frac{\delta_i}{\sigma_i \gamma_i} \right)} \quad (21)$$

for the equilibrium to be stable.

Let's now assume  $\lambda = -a$  and see if Eq.(9) still holds. If we assume  $\lambda = -a$ , then Eq.(9) becomes :

$$\det \begin{pmatrix} 0 & \mathbf{b}^T \\ \mathbf{c} & D + a \end{pmatrix} = 0 \quad (22)$$

Keeping in mind that the only non-zero entry in  $\mathbf{c}$  is the last one, thanks to the Laplace expansion of the determinant, this equation becomes:

$$\det \begin{pmatrix} \mathbf{b}^T \\ \tilde{D} \end{pmatrix} = \det \begin{pmatrix} b_1 & \dots & b_{N_S} \\ \tilde{D}_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \tilde{D}_{N_S-1} \end{pmatrix} = 0, \quad (23)$$

where  $\tilde{D}$  is a  $(N_S - 1) \times (N_S - 1)$  diagonal matrix whose entries are given by  $\tilde{D}_i = \sigma_i \gamma_i R^* - \delta_i + a$ . Eq.(23) can be further simplified using again Laplace expansion:

$$b_1 \det \begin{pmatrix} 0 & \dots & \dots & 0 \\ \tilde{D}_2 & \ddots & & \\ & \ddots & \ddots & \\ & & \tilde{D}_{N_S-1} & 0 \end{pmatrix} - \tilde{D}_1 \det \begin{pmatrix} b_2 & \dots & b_{N_S} \\ \tilde{D}_2 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \tilde{D}_{N_S-1} \end{pmatrix} = 0 \quad (24)$$

Since the first term of this is clearly zero, we see that :

$$\det \begin{pmatrix} b_1 & \dots & b_{N_S} \\ \tilde{D}_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \tilde{D}_{N_S-1} \end{pmatrix} = 0 \iff \tilde{D}_1 \det \begin{pmatrix} b_2 & \dots & b_{N_S} \\ \tilde{D}_2 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \tilde{D}_{N_S-1} \end{pmatrix} = 0 \quad (25)$$

By a recursive reasoning we conclude that

$$\det \begin{pmatrix} \mathbf{b}^T \\ \tilde{D} \end{pmatrix} = 0 \iff \prod_{i=1}^{N_S-1} \tilde{D}_i = 0 \quad (26)$$

And hence  $-a$  is part of the eigenspectrum if and only if one of the  $D_i$  ( $i = 1, \dots, N_S - 1$ ) is equal to  $-a$ .

### 3 The general case

We now consider the most general case with  $N_R$  resources and  $N_S$  species. We assume we found a positive equilibrium, i.e. the Jacobian is of the form of Eq.(3). We rewrite it in the following way :

$$J^* = \begin{pmatrix} -D & \Gamma \\ \beta & Z \end{pmatrix} \quad (27)$$

with

- $D = (\mu + \gamma^T S^*)_a$ , i.e.  $D$  is a diagonal  $N_R \times N_R$  matrix with strictly positive elements.
- $\Gamma = \alpha - R_d^* \gamma^T$  is a  $N_R \times N_S$  matrix whose entries do not have a well defined sign.
- $\beta = S_d^* \sigma \otimes \gamma$  is  $N_S \times N_R$  matrix with non negative entries
- $Z$  is a  $N_S \times N_S$  matrix. In our problem, it is essentially zero. However we extend it to the general case where  $Z_{ij}$  is arbitrary.

We seek a solution to the problem  $\det(J^* - \lambda) = 0$ . Explicitly :

$$\det \begin{pmatrix} -D - \lambda & \Gamma \\ \beta & Z - \lambda \end{pmatrix} = 0 \quad (28)$$

We now assume that  $\det(-D - \lambda) \neq 0$ . Using the properties of block matrices, this implies:

$$\det(-D - \lambda) \det(Z - \lambda - \beta(-D - \lambda)^{-1} \Gamma) = 0 \iff \det(Z - \lambda + \beta(D + \lambda)^{-1} \Gamma) = 0 \quad (29)$$

That means that the equation we are interested in is :

$$\det(A(\lambda) - \lambda) = 0 \quad (30)$$

with  $A(\lambda) = Z + \beta(D + \lambda)^{-1} \Gamma$ . Note then that component wise,

$$A_{ij} = Z_{ij} + \sum_{k,l} \beta_{ik} (D + \lambda)_{kl}^{-1} \Gamma_{lj} = Z_{ij} + \sum_{k,l} \beta_{ik} \delta_{kl} \frac{1}{D_k + \lambda} \Gamma_{lj} = Z_{ij} + \sum_k \frac{\beta_{ik} \Gamma_{kj}}{D_k + \lambda} \quad (31)$$

The solution is sadly not trivial at all. We will now explore special cases where a solution can be easily found.

Look at when this could be approximated as  $A_{ij} = \delta_{ij} f_{ij}(\lambda)$  or taylor expand around small  $\lambda$

### 3.1 Solvable cases

**Each species eats its own resource** We consider the case of a system with  $N_S = N_R$  and each species eats one resource, that it does not share with anyone. Without loss of generality we can say that species  $S_i$  feeds from resource  $R_i$ . We also take  $\alpha_{ij}$  lower triangular, which biologically means that species  $S_i$  releases biomass in resources  $R_j$  with  $j > i$  (i.e.  $S_1$  releases to  $R_1, \dots, R_{N_R}$ ,  $S_2$  to  $R_2, \dots, R_{N_R}$  and so on). Mathematically, these conditions translate to

$$\alpha_{ij} = 0 \text{ if } i < j \text{ and } \gamma_{ij} = \delta_{ij}\gamma_{ii} \quad (32)$$

With such definitions, we see clearly that  $\beta$  is diagonal while  $\Gamma$  is lower triangular, which means that if we choose  $Z$  to be lower triangular,  $A(\lambda)$  is also lower triangular, meaning that Eq.(30) is easily solvable :

$$\det(A(\lambda) - \lambda) = 0 \iff \prod_i^{N_S} (A_{ii}(\lambda) - \lambda) = 0 \iff \prod_i^{N_S} \left( Z_{ii} + \frac{\beta_{ii}\Gamma_{ii}}{D_i + \lambda} - \lambda \right) = 0. \quad (33)$$

This gives  $N_S$  equations characterizing  $\lambda$  :

$$Z_{ii} + \frac{\beta_{ii}\Gamma_{ii}}{D_i + \lambda} - \lambda = 0 \quad (34)$$

$$\iff \lambda^2 + (D_i - Z_{ii})\lambda - (\beta_{ii}\Gamma_{ii} + Z_{ii}D_i) = 0 \quad (35)$$

$$\iff \lambda = \frac{Z_{ii} - D_i \pm \sqrt{(D_i + Z_{ii})^2 + 4\beta_{ii}\Gamma_{ii}}}{2}. \quad (36)$$

This means the full spectrum of  $N_S + N_R = 2N_S$  eigenvalues is given by :

$$\sigma(J^*) = \left\{ \frac{Z_{ii} - D_i + \sqrt{(D_i + Z_{ii})^2 + 4\beta_{ii}\Gamma_{ii}}}{2}, \frac{Z_{ii} - D_i - \sqrt{(D_i + Z_{ii})^2 + 4\beta_{ii}\Gamma_{ii}}}{2} \text{ with } i = 1, \dots, N_S \right\} \quad (37)$$

A stability condition on the equilibrium is then directly found :

$$\max_{i=1, \dots, N_S} \Re \left( Z_{ii} - D_i + \sqrt{(D_i + Z_{ii})^2 + 4\beta_{ii}\Gamma_{ii}} \right) < 0. \quad (38)$$

We assume that the index  $k$  is the one giving the maximum value of  $\Re \left( Z_{ii} - D_i + \sqrt{(D_i + Z_{ii})^2 + 4\beta_{ii}\Gamma_{ii}} \right)$ .

We also assume  $Z_{kk} = 0$ . Then we know the system is unstable if :

$$-D_k + \Re \left( \sqrt{D_k^2 + 4\beta_{kk}\Gamma_{kk}} \right) > 0 \quad (39)$$

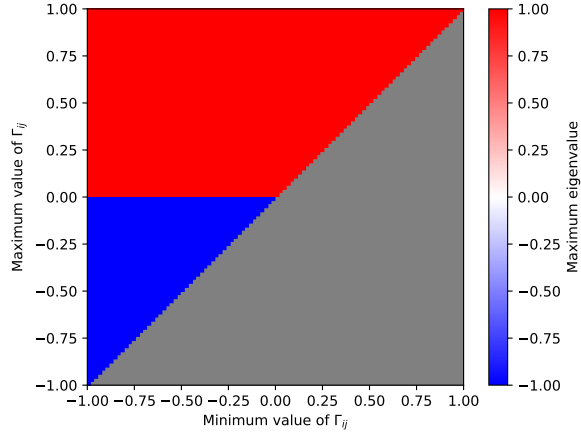
This is achieved if and only if:

$$\Gamma_{kk} > 0 \quad (40)$$

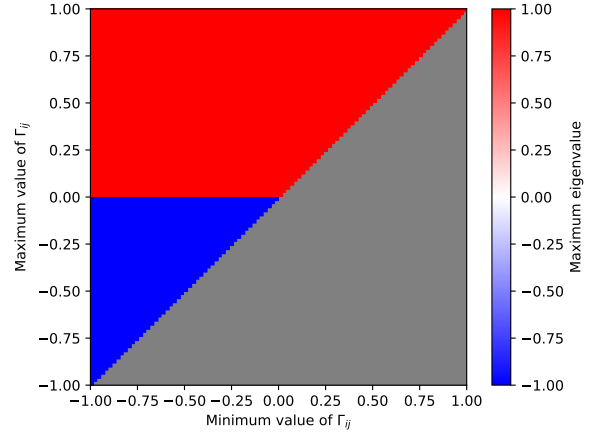
Hence we clearly see that the stability condition Eq.(38) is:

$$\text{The system is dynamically stable} \iff \Gamma \text{ has non positive entries.} \quad (41)$$

Comparison between Fig.1 and Fig.2 tends to show that when  $\Gamma$  is fully negative, the system is fully stable, as expected. The slight deviation in the mean is because of the number of random variables picked : even if the upper boundary of the interval is positive, the matrix may contain only negative elements. That zone should disappear as  $N_R$  increases and we pick more random variables (i.e. more chances of picking a positive one), which is indeed what we observe in Fig.2

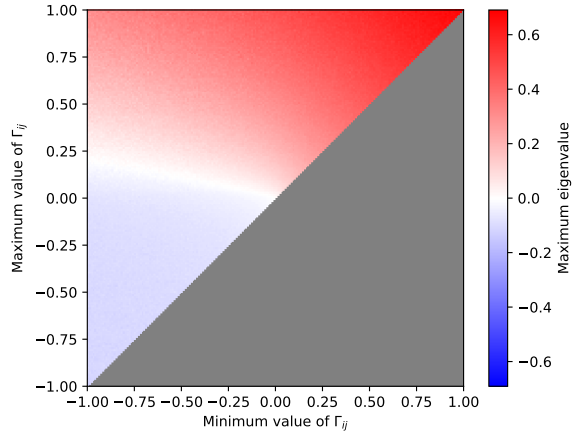


(a)  $N_R = 3$

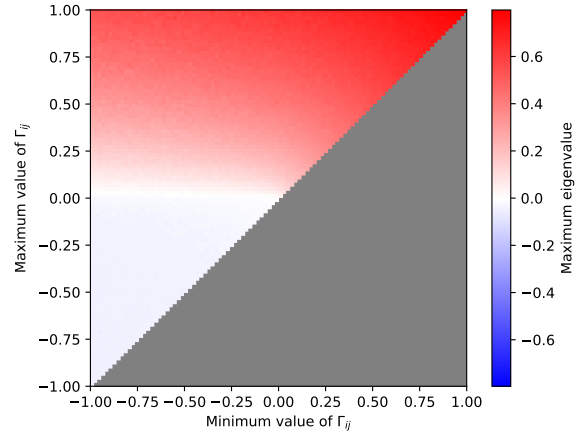


(b)  $N_R = 8$

Figure 1: Sign of the maximal maximum eigenvalue picked over 300 simulations for each point, according to parameters describing the distribution of the entries of the triangular  $\Gamma$  matrix. More specifically each non-zero entry is picked uniformly over the given interval. We clearly observe a transition from stable to unstable systems.



(a)  $N_R = 3$



(b)  $N_R = 8$

Figure 2: Average maximum eigenvalue (over 300 simulations for each point) according to parameters describing the distribution of the entries of the triangular  $\Gamma$  matrix. More specifically each non-zero entry is picked uniformly over the given interval. We clearly observe a transition from stable to unstable systems.

## 4 The minimization approach

Another way to look at the problem is to try to map it to an optimization problem (i.e. find some kind of energy that the ecosystem would minimize at equilibrium). We try to follow the idea of [3], i.e. the conditions for an Ecologically Stable State (ESS)  $\mathbf{R}^*$  ( $\alpha$  is the index for the resources) to exist with species  $S_i$  are given by :

- Steady environment :  $h_\alpha(\mathbf{R}^*) + \sum_i S_i q_{i\alpha}(\mathbf{R}^*) = 0$
- Non-invasibility :  $g_i(\mathbf{R}^*) \leq 0$
- Feasible populations :  $S_i \geq 0$
- Steady populations :  $S_i g_i(\mathbf{R}^*) = 0$

The idea is that if

$$\mathbf{q}_i = -\nabla g_i(\mathbf{R}) \text{ and } \mathbf{h} = -\nabla f(\mathbf{R}) \quad (42)$$

for some function  $f$ , then the problem is equivalent to minimizing  $f(\mathbf{R})$  under the constraints  $g_i(\mathbf{R}) \leq 0$ . Let  $\mathbf{R}_0$  be the value the environment takes at an equilibrium when there are no species. Because  $f$  is defined up to a constant, we may choose  $f(\mathbf{R}_0) = 0$ . Then the quantity minimized at an ESS will simply be  $d(\mathbf{R}, \mathbf{R}_0) := f(\mathbf{R})$  (a quantity called the environmental perturbation). [3] explicitly builds this quantity for some ecological models, but not the one we consider. This is what we will attempt to do now.

### 4.1 Full model

Our full model is characterized by the equations:

$$\dot{R}_\alpha = \lambda_\alpha - \mu_\alpha R_\alpha - \sum_i S_i \gamma_{i\alpha} R_\alpha + \sum_i S_i \alpha_{\alpha i} \quad (43)$$

$$\dot{S}_i = \left( \sum_\alpha \sigma_{i\alpha} \gamma_{i\alpha} R_\alpha - \delta_i \right) S_i \quad (44)$$

Setting the LHS of the above equations gives the steady state equations. From the second equation, we see:

$$g_i(\mathbf{R}) = \sum_\alpha \sigma_{i\alpha} \gamma_{i\alpha} R_\alpha - \delta_i. \quad (45)$$

Hence

$$\partial_\alpha g_i(\mathbf{R}) = \sigma_{i\alpha} \gamma_{i\alpha}. \quad (46)$$

On the other hand, Eq.(43) gives us the steady environment equations:

$$0 = -\mu_\alpha (R_\alpha - R_\alpha^0) - \sum_i S_i (\gamma_{i\alpha} R_\alpha - \alpha_{\alpha i}) \quad (47)$$

Now the idea would be to cast (47) into the form:

$$0 = h_\alpha(\mathbf{R}) - \sum_i S_i \partial_\alpha g_i(\mathbf{R}). \quad (48)$$



This is however highly non trivial. Indeed, we can rewrite Eq.(47)

$$0 = -\mu_\alpha(R_\alpha - R_\alpha^0) - \sum_i S_i \frac{\gamma_{i\alpha} R_\alpha - \alpha_{\alpha i}}{\partial_\alpha g_i} \partial_\alpha g_i = -\mu_\alpha(R_\alpha - R_\alpha^0) - \sum_i S_i Q_{i\alpha}(R_\alpha) \partial_\alpha g_i(\mathbf{R}) \quad (49)$$

The fact that  $Q_{i\alpha}(R_\alpha)$  also depends on  $i$  sadly does not allow us to treat it the same way as was done in [3] (This is essentially what is written for the "species-dependent biomass value" in Table 1 of [3]).

## 4.2 Models that work this way

However, what we can do is look at Eq.(47) and see what models give rise to such an equation. More precisely, Eq.(47) can be recast in :

$$0 = -\mu_\alpha(R_\alpha - R_\alpha^0) - \sum_i S_i (\gamma_{i\alpha} R_\alpha^{-n+1} - \alpha_{\alpha i} R_\alpha^{-n}) R_\alpha^n \quad (50)$$

i.e. (if  $R_\alpha \neq 0$ ) :

$$0 = h_\alpha^n(\mathbf{R}) - \sum_i S_i \partial_\alpha \tilde{g}_i^n(\mathbf{R}) \text{ with } h_\alpha^n = -\mu_\alpha (R_\alpha^{-n+1} - R_\alpha^0 R_\alpha^{-n}) \text{ and } \partial_\alpha \tilde{g}_i^n = \gamma_{i\alpha} R_\alpha^{-n+1} - \alpha_{\alpha i} R_\alpha^{-n} \quad (51)$$

For  $n \neq 1, 2$ , this gives rise to :

$$f_n(\mathbf{R}) = \sum_\alpha \left[ \mu_\alpha R_\alpha^{-n+1} \left( \frac{R_\alpha^0}{n-1} - \frac{R_\alpha}{n-2} \right) + \frac{\mu_\alpha (R_\alpha^0)^{-n+2}}{(n-1)(n-2)} \right] \quad (52)$$

$$\tilde{g}_i^n = - \sum_\alpha \left( \frac{\gamma_{i\alpha}}{n-2} R_\alpha^{-n+2} - \frac{\alpha_{\alpha i}}{n-1} R_\alpha^{-n+1} \right) - \delta_i \quad (53)$$

These are the equations we get when we study the models:

$$\dot{R}_\alpha = \lambda_\alpha - \mu_\alpha R_\alpha - \sum_i S_i \gamma_{i\alpha} R_\alpha + \sum_i S_i \alpha_{\alpha i} \quad (54)$$

$$\dot{S}_i = \sum_\alpha \frac{\gamma_{i\alpha}}{2-n} R_\alpha^{-n+2} S_i - \sum_\alpha \frac{\alpha_{\alpha i}}{1-n} R_\alpha^{-n+1} S_i - \delta_i S_i \quad (55)$$

To get something that makes sense biologically, we need  $n < 2$  (since  $\gamma_{i\alpha}$  represents the food consumption rate : you want your species to grow as they eat food). If we want to interpret the second term of Eq.(55) as some sort of cost of releasing byproducts for the species, we need  $n < 1$ . That is, overall we need  $n < 1$  for this model to make sense.

### 4.2.1 $n = 1$ case

For  $n = 1$ , we have:

$$h_\alpha^1 = -\mu_\alpha + \mu_\alpha \frac{R_\alpha^0}{R_\alpha} \text{ and } \partial_\alpha \tilde{g}_i^1 = \gamma_{i\alpha} - \frac{\alpha_{\alpha i}}{R_\alpha} \quad (56)$$

That implies

$$f_1(\mathbf{R}) = \sum_\alpha \mu_\alpha \left[ (R_\alpha - R_\alpha^0) - R_\alpha^0 \ln \left( \frac{R_\alpha}{R_\alpha^0} \right) \right] \quad (57)$$

$$\tilde{g}_i^1 = \sum_{\alpha} (\gamma_{i\alpha} R_{\alpha} - \alpha_{\alpha i} \ln(R_{\alpha}) - \delta_i) \quad (58)$$

Those are the equations arising from the model :

$$\dot{R}_{\alpha} = \lambda_{\alpha} - \mu_{\alpha} R_{\alpha} - \sum_i S_i \gamma_{i\alpha} R_{\alpha} + \sum_i S_i \alpha_{\alpha i} \quad (59)$$

$$\dot{S}_i = \sum_{\alpha} \gamma_{i\alpha} R_{\alpha} S_i - \delta_i S_i - \sum_{\alpha} \alpha_{\alpha i} \ln(R_{\alpha}) S_i \quad (60)$$

This is surprisingly close to our original model. There are two differences though:

- We assume a 100% efficacy consumption from the species :  $\sigma_{i\alpha} = 1$ .
- Creating biomass is now not free anymore : it has now a logarithmic cost. This might be a way of modelling some kind of energy conservation, I think. It has however a huge default : if resources are low ( $R_{\alpha} < 1$ ),  $\ln(R_{\alpha}) < 0$  which gives the opposite effect to what we want. However that might be workable with because a huge  $S_i$  will then imply a large  $R_{\alpha}$  (through the byproduct term), which will then give the expected behaviour and will reduce the unbiological impact of that phenomenon. Quick simulations tend to show that stable equilibria for that system exist.

Look at in which conditions  $\alpha\gamma - \gamma(D + \lambda)^{-1}\gamma^T$  is negative definite (contradiction argument to say that  $\lambda > 0$  implies bounds on  $\alpha_{ij}$ ). Also use Sebastian's condition on energy conservation to have a bound on  $\alpha$  for biological systems. Do simulations for systems with restriction that the parameters must be positive. Look at when clever way to see if matrix is positive definite or not.

## 5 Energy dissipation

As Sebastian wrote, we must take into account energy dissipation. Biologically, this means that a species  $j$  cannot produce more of the resource  $i$  than it consumes at equilibrium :

$$\alpha_{ij} S_j^* < \gamma_{ij}^T R_i^* S_j^* \iff \alpha_{ij} - \gamma_{ij}^T R_i^* < 0 \quad (61)$$

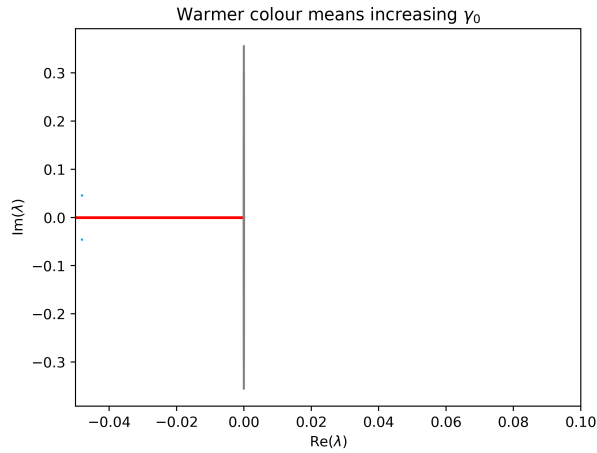
This means that the matrix  $\alpha - R_d^* \gamma^T$  has negative entries, giving the result:

In biologically relevant situations, the matrix  $\Gamma$  has negative entries.

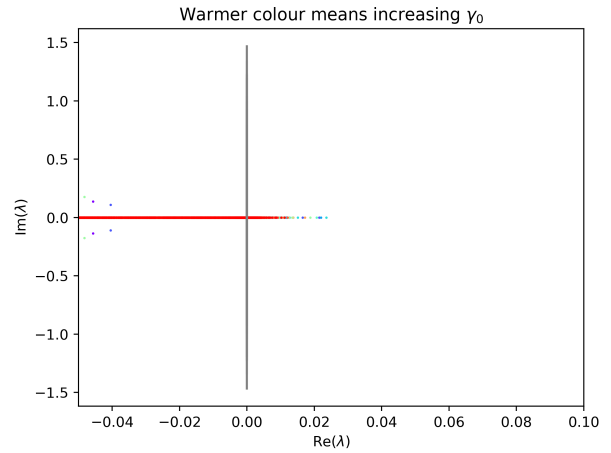
(62)

## 6 The effect of species consumption efficiency

A difference between our model and the one developed by Butler and O'Dwyer [1] is the consumption efficiency of the resource  $j$  by species  $i$   $\sigma_{ij}$ . While at first sight it may seem like a simple coefficient added to the problem this is not exactly the case. Indeed the computation made in [1] to prove the stability of a purely competitive (no syntrophy) system relied on the fact that the consumption efficiency could be factored out, i.e.  $\sigma \otimes \gamma = \epsilon \gamma$  where  $\epsilon$  is a positive scalar constant. Hence we expect that by introducing heterogeneity in  $\sigma$ , a purely competitive system will not always be at equilibrium. This is indeed what is observed numerically (Fig.3). Fig.4 shows the effects on the eigenspectrum of adding heterogeneity.

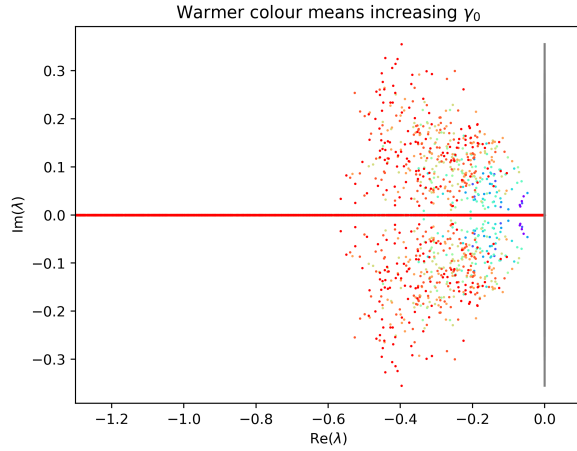


(a) With a homogenous  $\sigma$ .

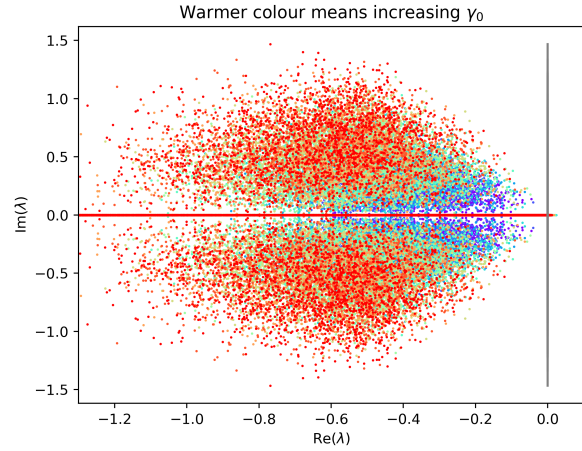


(b) With a heterogeneous  $\sigma$ .

Figure 3: Close up of the eigenspectrum distribution of the jacobian at a feasible equilibrium where the  $\gamma_{ij}$  have been picked normally (mean  $\gamma_0$ , small variance) for the same number of simulations. We see that with a homogeneous  $\sigma$ , dynamical stability is ensured as no positive eigenvalues are observed, as was shown in [1]. Introducing heterogeneity in  $\sigma$  however seems to always lead to some instability as positive eigenvalues are found.



(a) With a homogenous  $\sigma$ .



(b) With a heterogeneous  $\sigma$ .

Figure 4: Full eigenspectrum distribution of the jacobian at a feasible equilibrium where the  $\gamma_{ij}$  have been picked normally (mean  $\gamma_0$ , small variance) for the same number of simulations. Adding heterogeneity seems to lower the multiplicity of the eigenvalues (as we observe more distinct points for the same total number of non distinct eigenvalues). Note also that increasing  $\gamma_0$ , i.e. make the species eat more, seems to lower the mean eigenvalue.

## 7 Diagonal dominance

A math theorem (derived directly Gershgorin circle theorem [2]) states that a symmetric diagonally dominant matrix is positive semi-definite. Let  $M$  be a symmetric matrix which is also diagonally dominant, i.e.,

$$|M_{ii}| > \sum_{j \neq i} |M_{ij}|, \forall i, \quad (63)$$

then  $M$  is positive semi-definite.

As a matrix  $M$  is positive (semi?)-definite  $\iff$  its symmetric part  $\tilde{M} = \frac{M+M^T}{2}$  is positive (semi?)-definite, we conclude that a matrix  $M$  is positive definite if its symmetrical part is diagonally dominant.

More precisely, let  $M$  be a matrix with positive entries. From above we know that it is positive definite if

$$2M_{ii} > \sum_{j \neq i} (M_{ij} + M_{ji}) \quad \forall i \quad (64)$$

But if  $M$  is positive definite,  $-A$  is negative definite. This allows to formulate the implications for  $A = -M$ :

$$2M_{ii} > \sum_{j \neq i} (M_{ij} + M_{ji}) \quad \forall i \iff 2A_{ii} < \sum_{j \neq i} (A_{ij} + A_{ji}) \quad \forall i \quad (65)$$

$$\implies M \text{ is positive definite} \iff A \text{ is negative definite} \quad (66)$$

In conclusion:

For a matrix  $A$  with negative entries :  $2A_{ii} < \sum_{j \neq i} (A_{ij} + A_{ji}) \quad \forall i \implies A \text{ is negative definite}$

(67)

### 7.1 Diagonal dominance for our model

Using the result of Eq.(67) we may try to find sufficient conditions on the system parameters to achieve stability.

**Claim :** If the symmetric part of  $\beta\Gamma$  (denoted  $\widetilde{\beta\Gamma}$ ) is strongly diagonally dominant, i.e. if it satisfies :

$$\left| \widetilde{\beta\Gamma}_{ii} \right| > \frac{\max(D_k)}{\min(D_k)} \sum_{j \neq i} \left| \widetilde{\beta\Gamma}_{ij} \right| \quad \forall i$$

then the system is dynamically stable.

**Proof :** We know the system is dynamically unstable if there exists a  $\lambda \geq 0$  satisfying Eq.(30). We are going to assume that such a  $\lambda$  exists and we will prove it leads to a contradiction in this regime.

First of all, let's look at what the strong diagonal dominance condition implies. We have,  $\forall i$  :

$$\begin{aligned}
& \left| \widetilde{\beta\Gamma}_{ii} \right| > \frac{\max(D_k)}{\min(D_k)} \sum_{j \neq i} \left| \widetilde{\beta\Gamma}_{ij} \right| \\
& \iff 2 \sum_k \beta_{ik} |\Gamma_{ki}| > \frac{\max(D_k)}{\min(D_k)} \sum_{j \neq i} \sum_k (\beta_{ik} |\Gamma_{kj}| + \beta_{jk} |\Gamma_{ki}|) \\
& \implies 2 \sum_k \beta_{ik} |\Gamma_{ki}| > \frac{\max(D_k) + \lambda}{\min(D_k) + \lambda} \sum_{j \neq i} \sum_k (\beta_{ik} |\Gamma_{kj}| + \beta_{jk} |\Gamma_{ki}|) \\
& \iff 2 \sum_k \frac{\beta_{ik} |\Gamma_{ki}|}{\max(D_k) + \lambda} > \sum_{j \neq i} \sum_k \frac{\beta_{ik} |\Gamma_{kj}| + \beta_{jk} |\Gamma_{ki}|}{\min(D_k) + \lambda} \\
& \implies 2 \sum_k \frac{\beta_{ik} |\Gamma_{ki}|}{D_k + \lambda} > \sum_{j \neq i} \sum_k \frac{\beta_{ik} |\Gamma_{kj}| + \beta_{jk} |\Gamma_{ki}|}{D_k + \lambda} \\
& \iff 2 \sum_k \frac{\beta_{ik} \Gamma_{ki}}{D_k + \lambda} < \sum_{j \neq i} \sum_k \frac{\beta_{ik} \Gamma_{kj} + \beta_{jk} \Gamma_{ki}}{D_k + \lambda} \\
& \iff 2A_{ii} < \sum_{j \neq i} (A_{ij} + A_{ji})
\end{aligned}$$

where we used that:

$$\frac{\max(D_k)}{\min(D_k)} \geq \frac{\max(D_k) + \lambda}{\min(D_k) + \lambda} \quad \forall \lambda \geq 0 \quad (68)$$

and also

$$\sum_k \frac{a_k}{\min(b_k)} \geq \sum_k \frac{a_k}{b_k} \geq \sum_k \frac{a_k}{\max(b_k)} \text{ for a positive set of } a_k, b_k \quad (69)$$

and finally that the  $\Gamma_{ij}$  are negative in biologically relevant systems.

But  $\lambda \geq 0$  implies that  $A_{ij}$  has negative entries. According to Eq.(67) this means  $A$  is negative definite. As  $A$  is negative definite, Eq.(30) implies that  $\lambda$  is negative and hence the contradiction.

This proves that  $\lambda < 0$  and that the system is dynamically stable.

QED.

## References

- [1] Stacey Butler and James P. O'Dwyer. "Stability criteria for complex microbial communities". In: *Nature Communications* 9.1 (2018), p. 2970. DOI: 10.1038/s41467-018-05308-z. URL: <https://doi.org/10.1038/s41467-018-05308-z>.
- [2] S Gervsgorin. "Über die Abgrenzung der Eigenwerte einer Matrix". In: (Jan. 1931), pp. 749–754.
- [3] III Marsland Robert, Wenping Cui, and Pankaj Mehta. "The Minimum Environmental Perturbation Principle: A New Perspective on Niche Theory". In: *arXiv e-prints*, arXiv:1901.09673 (Jan. 2019), arXiv:1901.09673. arXiv: 1901.09673 [q-bio.PE].