Consumer resources model

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1 Establishing the model

We want to write down a consumers-resources model (CRM) which describes the coupled evolution between N_S different species of biomass (denoted S_i with $i = 1, \dots, N_S$) and the N_R resources they feed off (denoted R_ν with $\nu = 1, \dots, N_R$).

The coupled evolution of the set of variables $\{R_\nu, S_i\}$ is given by:

$$\begin{cases} \dfrac{dR_\mu}{dt} = l_\mu - m_\mu R_\mu - \displaystyle\sum_j \gamma_{j\mu} R_\mu S_j + \sum_j \alpha_{\mu j} S_j & (1) \\ \dfrac{dS_i}{dt} = \displaystyle\sum_\nu \sigma_{i\nu}\gamma_{i\nu} R_\nu S_i - d_i S_i - \sum_\nu \tau_{\nu i} S_i & (2) \end{cases}$$

The temporal evolution of a resource R_μ is essentially driven by the following processes:

- Constant input from an outsider experimenter : this corresponds to the constant $+l_\mu$ term,
- Natural diffusion/deterioration at rate m_μ : this corresponds to the $-m_\mu R_\mu$ term,
- Consumption by the biomass species S_j at a rate $\gamma_{j\mu}$. In total this corresponds to the Lotka-Volterra style term [**insert ref**] $-\sum_j \gamma_{j\mu} R_\nu S_j$,
- Production coming from the species S_j at a rate $\alpha_{\mu j}$: $+\sum_j \alpha_{\mu j} S_j$. This is essentially what makes this model different from traditional CRMs [**insert ref**].

On the other hand, biomass of species S_i changes because of the following processes [**insert figure**]:

- Consumption of resource R_ν at a rate $\gamma_{i\nu}$. Only a fraction $\sigma_{i\nu}$ of this is allocated to biomass growth : $+\sum_\nu \sigma_{i\nu}\gamma_{i\nu} R_\nu S_i$.
- Cell death/diffusion at rate d_i : this is the $-d_i S_i$ term.
- Release of resource R_ν at rate $\tau_{\nu i}$ (this is the syntrophic interaction). In total $-\sum_\nu \tau_{\nu i} S_i$.

We will mostly focus on the case where no resource coming from syntrophy is lost, *i.e.* $\tau_{\mu i} = \alpha_{\mu i}$.

2 Equilibria of the model and their stability

We are interested in studying the stability of the equilibrium points of our model Eqs.(1)-(2). We say that $\{R^*_\mu, S^*_j\}$ are *equilibria* of our model if they are fixed points of it, that means if the following equations are fulfilled :

$$\begin{cases} 0 = l_\mu - m_\mu R^*_\mu - \sum_j \gamma_{j\mu} R^*_\mu S^*_j + \sum_j \alpha_{\mu j} S^*_j & (3) \\ 0 = \sum_\nu \sigma_{i\nu}\gamma_{i\nu} R^*_\nu S^*_i - d_i S^*_i - \sum_\nu \tau_{\nu i} S^*_i & (4) \end{cases}$$

As said above, our main goal is to study the stability of such equilibria. There are however different notions of stability that we need to introduce.

2.1 Linear stability

We can define in general the *jacobian* J of our system as the jacobian matrix of its temporal evolution (1)-(2):

$$J \equiv \begin{pmatrix} \frac{\partial \dot{R}_\mu}{\partial R_\nu} & \frac{\partial \dot{R}_\mu}{\partial S_j} \\ \frac{\partial \dot{S}_i}{\partial R_\nu} & \frac{\partial \dot{S}_i}{\partial S_j} \end{pmatrix} = \begin{pmatrix} \left(-m_\mu - \sum_j \gamma_{j\mu} S_j\right)\delta_{\mu\nu} & -\gamma_{j\mu} R_\mu + \alpha_{\mu j} \\ \sigma_{i\nu}\gamma_{i\nu} S_i & \left(\sum_\nu \sigma_{i\nu}\gamma_{i\nu} R_\nu - d_i - \sum_\nu \tau_{\nu i}\right)\delta_{ij} \end{pmatrix}, \quad (5)$$

where δ is the Kronecker delta symbol.

We can then define for a given equilibrium point $\{R^*_\mu, S^*_i\}$ the *jacobian at equilibrium* J^* as the jacobian of said equilibrium.

We will furthermore say that a given equilibrium is *linearly stable* if its jacobian J^* is not positive definite, *i.e.* if the largest eigenvalue of J^* has a non positive real part.

Note that if we are interested only in positive valued equilibria (*i.e.* $S^*_i > 0 \ \forall i$), then Eq.(4) is equivalent to :

$$\sum_\nu \sigma_{i\nu}\gamma_{i\nu} R^*_\nu - d_i - \sum_\nu \tau_{\nu i} = 0, \quad (6)$$

which means that the lower right block of the jacobian in Eq.(5) will be zero. Hence at equilibrium the jacobian J^* will have the following block form:

$$J^* = \begin{pmatrix} -\Delta & \Gamma \\ \mathrm{B} & 0 \end{pmatrix}, \quad (7)$$

where

- $\Delta_{\mu\nu} = \mathrm{diag}(m_\mu + \sum_j \gamma_{j\mu} S^*_j)$ is a positive $N_R \times N_R$ diagonal matrix,
- $\Gamma_{\mu j} = -\gamma_{j\mu} R^*_\mu + \alpha_{\mu j}$ is a $N_R \times N_S$ matrix which does not have entries with a definite sign.
- $\mathrm{B}_{i\nu} = \sigma_{i\nu}\gamma_{i\nu} R^*_\nu$ is a $N_S \times N_R$ matrix with positive entries.

2.2 Dynamical stability

Once we established that a system is linearly stable [**Check if the following is true**], we may quantify *how stable* it is. One way of doing this is studying its dynamical stability [**Insert ref**]. The idea is to take an equilibrium point $\{R^*_\mu, S^*_i\}$ and perturb the abundance of the species and resources at that point :

$$R^*_\mu \to R(t_0) \equiv R^*_\mu \left(1 + \Delta_D \nu_\mu\right), \tag{8}$$

$$S^*_i \to S(t_0) \equiv S^*_i \left(1 + \Delta_D \nu_i\right), \tag{9}$$

where the $\nu_{\mu,i}$ are random numbers drawn from a uniform distribution between -1 and +1, t_0 is the time where the previously at equilibrium system is perturbed and $\Delta_D \in [-1, 1]$ is a fixed number quantifying the magnitude of the perturbation.

2.3 Structural stability

3 Building the model numerically

We want to be able to build feasible models numerically, *i.e.* we would like to generate a set of constant numbers $\{l_\nu, m_\nu, R^*_\nu, S^*_j, \gamma_{j\nu}, \alpha_{\nu j}, \sigma_{j\nu}, \tau_{j\nu}\}$ such that the equilibria equations Eq.(3) and (4) are fulfilled.

3.1 Algorithmic procedure

We hereby detail the procedure used to numerically build feasible systems. It goes like this:

1. We first draw randomly R^*_ν and S^*_i as a uniform distribution of mean equal to the corresponding metaparameter, *i.e.* :

$$\sum_\nu R^*_\nu = N_R R_0 \text{ and } \sum_i S^*_i = N_S S_0. \tag{10}$$

2. The efficiency matrix $\sigma_{i\nu}$ is then drawn similarly, on a uniform distribution such that σ_0 is the average of the matrix :

$$\sum_{i,\nu} \sigma_{i\nu} = N_S N_R \sigma_0. \tag{11}$$

3. We build gamma using the desired *food matrix* F. F is a binary matrix given by the user (in the `configuration.in` file) and is defined as the adjacency matrix of the consumption network (*i.e.* it tells which species eats which resource). We then build γ with the same network structure as F (*i.e.* both matrices have the same zero elements). The consumption rates are then randomly drawn from a uniform distribution and γ is rescaled such that γ_0 represents the average consumption rate of the system :

$$\sum_{i,\nu} \gamma_{i\nu} = N_S N_R \gamma_0. \tag{12}$$

4. We then need to build $\alpha_{\nu i}$. This is the tricky part of the algorithm because there are constraints on α, for instance energy conservation/dissipation Eq.(14). The general strategy is to assume that the metaparameters are chosen in a way that those constraints will practically always be satisfied (see above). We can then build α from a random uniform distribution such that:

$$\sum_{i,\nu} \alpha_{\nu i} = N_S N_R \alpha_0. \tag{13}$$

   If for some reason the algorithm fails to build a feasible system this way after a given number of attempts, the $\alpha_{\nu i}$ are drawn by the algorithm and the initial α_0 is rescaled accordingly.

5. We build $\tau_{\nu i}$. It usually is equal to $\alpha_{\nu i}$ or 0.

6. With all of these parameters drawn, we can solve Eq.(4) for the species death rate d_i (with the caveat that $d_i > 0$, this is one of the constraints on τ and hence α).

7. Finally, we solve Eq.(3) for l_ν and m_ν imposing the constraint $l_\nu, m_\nu > 0$. In practice this means one of them is drawn randomly (in the code, l_ν comes from an exponential distribution) with constraints (in the code the minimum value of l_ν) such that both l_ν and m_ν are positive.

4 Conditions on the model parameters

Impose energy/dissipation constraint :

$$\sum_\nu (1-\sigma_{i\nu})\,\gamma_{i\nu} R^*_\nu \geqslant \sum_\nu \alpha_{\nu i} \tag{14}$$

4.1 Impose energy constraint with metaparameters

The idea is to find metaparameters such that the energy dissipation constraint is automatically satisfied (which eases building the system numerically). This is easily done by finding the minimum of the LHS and maximum of RHS of Eq.(14). Indeed :

$$\sum_\nu (1-\sigma_{i\nu})\,\gamma_{i\nu} R^*_\nu \geqslant (1-\widehat{\sigma})\breve{\gamma}\breve{R^*}, \tag{15}$$

where $\breve{}$ denotes the minimum value of the random variable and $\widehat{}$ its maximum value. On the other hand,

$$\sum_\nu \alpha_{\nu i} \leqslant \widehat{\alpha} N_R. \tag{16}$$

This means that if we take metaparameters such that

$$\widehat{\alpha} N_R < (1-\widehat{\sigma})\breve{\gamma}\breve{R^*}, \tag{17}$$

then Eq.(14) is automatically followed.

Because of the way we choose our variables we have for every random variable in the problem,

$$\breve{X} = (1-\epsilon)\langle X\rangle \text{ and } \widehat{X} = (1+\epsilon)\langle X\rangle \tag{18}$$

where $\langle X\rangle$ denotes the mean of X. This means Eq.(17) is equivalent to, in terms of metaparameters:

$$\alpha_0 < \frac{(1-\epsilon)^2}{1+\epsilon}\,(1-(1+\epsilon)\,\sigma_0)\,\frac{\gamma_0 R_0}{N_R}. \tag{19}$$

In the $\epsilon \ll 1$ limit, this is equivalent to:

$$\alpha_0 < (1-3\epsilon)\,(1-(1+\epsilon)\sigma_0)\,\frac{\gamma_0 R_0}{N_R}. \tag{20}$$

4.2 Positivity of the parameters

Feasability means at least that every physical parameter defined here must be positive. In particular, this implies:

$$d_i > 0 \implies \sum_\mu \sigma_{i\mu}\gamma_{i\mu}R^*_\mu > \sum_\mu \tau_{\mu i} \tag{21}$$

If $\tau_{i\mu} = 0$. this is trivially satisfied because $\sigma_{i\mu}$, $\gamma_{i\mu}$ and R^*_μ have all been drawn positive. However if $\tau_{\mu i} = \alpha_{\mu i}$ this is not always the case and we have to get parameters satisfying :

$$\sum_\mu \sigma_{i\mu}\gamma_{i\mu}R^*_\mu > \sum_\mu \alpha_{\mu i} \ \forall i. \tag{22}$$

We can try to estimate the value of some metaparameters that would satisfy this. We have :

$$\sum_\mu \sigma_{i\mu}\gamma_{i\mu}R^*_\mu \geqslant \breve{\sigma}\breve{\gamma}\widetilde{R^*}. \tag{23}$$

Using this boundary and Eq.(17), we know that $d_i > 0$ if

$$\widehat{\alpha}N_R \leqslant \breve{\sigma}\breve{\gamma}\widetilde{R^*}, \tag{24}$$

i.e.

$$\alpha_0 < \frac{(1-\epsilon)^3}{1+\epsilon}\frac{\sigma_0\gamma_0 R_0}{N_R}, \tag{25}$$

or in the $\epsilon \ll 1$ limit :

$$\alpha_0 < (1-4\epsilon)\frac{\sigma_0\gamma_0 R_0}{N_R}. \tag{26}$$

Similarly we must have a positive death rate for the resources, *i.e.* :

$$m_\nu = \frac{l_\nu - \sum_j \gamma_{j\nu}R^*_\nu S^*_j + \sum_j \alpha_{\nu j}S^*_j}{R^*_\nu} > 0. \tag{27}$$

This means we have to impose parameters that verify:

$$l_\nu + \sum_j \alpha_{\nu j}S^*_j > \sum_j \gamma_{j\nu}R^*_\nu S^*_j. \tag{28}$$

We can do a reasoning similar to before, *i.e.* find a lower boundary for the LHS and an upper boundary for the RHS. We have

$$l_\nu + \sum_j \alpha_{\nu j}S^*_j \geqslant \breve{l} + \breve{\alpha}\widetilde{S^*} \tag{29}$$

and

$$\sum_j \gamma_{j\nu}R^*_\nu S^*_j \leqslant N_S\widehat{\gamma}\widehat{R^*}\widehat{S^*}. \tag{30}$$

Hence if we get parameters satisfying

$$\breve{l} + \breve{\alpha}\widetilde{S^*} > N_S\widehat{\gamma}\widehat{R^*}\widehat{S^*}, \tag{31}$$

then Eq.(27) will be immediately satisfied. In terms of metaparameters this is equivalent to:

$$\alpha_0 > \frac{N_S \gamma_0 R_0 S_0 (1+\epsilon)^3 - l_0(1-\epsilon)}{S_0(1-\epsilon)^2}. \tag{32}$$

In the $\epsilon \ll 1$ limit this is equivalent to:

$$\alpha_0 > (1+5\epsilon)\, N_S \gamma_0 R_0 - (1+\epsilon)\, \frac{l_0}{S_0}. \tag{33}$$

(Interesting, if l_0/S_0 is large enough, *i.e.* "there is enough food for everyone" then this condition is irrelevant).

4.3 Combining conditions

If we combine both upperbounds we get a restriction on the metaparameters:

$$\alpha_0 < \min\left(\frac{(1-\epsilon)^2}{1+\epsilon} \left(1 - (1+\epsilon)\,\sigma_0\right) \frac{\gamma_0 R_0}{N_R}, \frac{(1-\epsilon)^3}{1+\epsilon} \frac{\sigma_0 \gamma_0 R_0}{N_R} \right). \tag{34}$$

We of course also get a restriction on the lowerbound of α_0 through Eq.(33):

$$\alpha_0 > \frac{N_S \gamma_0 R_0 S_0 (1+\epsilon)^3 - l_0(1-\epsilon)}{S_0(1-\epsilon)^2}. \tag{35}$$

To get an idea on the order of magnitude of α_0 (which will be our order parameter if $\gamma_0 = 1$), we have for $N_R = 25$, $\sigma_0 = 0.2$, $R_0 = 1$ and $\epsilon = 0.1$:

$$\alpha_0 < 5.3 \times 10^{-3}. \tag{36}$$

So what we see in Eq.(34) is that α_0 has an upper bound which is dictated either by energy conservation or system feasability. What relations do the metaparameters have to fulfill in these two different regimes?

Suppose that the limiting factor is system feasability. That means:

$$\begin{aligned} &\frac{(1-\epsilon)^3}{1+\epsilon} \frac{\sigma_0 \gamma_0 R_0}{N_R} \leqslant \frac{(1-\epsilon)^2}{1+\epsilon} \left(1 - (1+\epsilon)\,\sigma_0\right) \frac{\gamma_0 R_0}{N_R} \\ &\iff (1-\epsilon)\sigma_0 \leqslant 1 - (1+\epsilon)\sigma_0 \\ &\iff \sigma_0 \leqslant \frac{1}{2} \end{aligned} \tag{37}$$

This means if $\sigma_0 \leqslant \frac{1}{2}$, the limiting factor will be system feasability while if $\sigma_0 \geqslant \frac{1}{2}$, it will be energy conservation.

γ_0	σ_0	α_0	R_0	S_0	l_0
1	1	0	300	1	11091
	0.75	0			
		0.5			
	0.5	0			
		0.5			
		1			
	0.25	0			
		0.5			
		1			
		1.5			

Table 1: Parameters used for the simulations

5 Numerical simulations

We run a bunch of simulations with the following metaparemeters. We made sure that these are compatible with the bounds on α_0 Eqs.(33)-(34).