Notes on ecosystems stability

Onofrio Mazzarisi

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1 $\alpha\beta\gamma$ -model

Consider a competitive community of S species defined by the following dynamics for the population densities

$$\frac{dn_i}{dt} = n_i^{\alpha} - n_i^{\beta} \sum_j A_{ij} n_j^{\gamma} \,, \tag{1}$$

where the sum runs from j=1 to j=S and the off-diagonal elements of A are extracted from a distribution with mean $\mu>0$ and standard deviation σ while $A_{ii}=1/K, \, \forall i, \, K$ being the (uniform) carrying capacity. (To be more precise $K^{1/(\beta+\gamma-\alpha)}$ is the carrying capacity). If the equilibrium is feasible it formally reads

$$(n_i^*)^{\alpha-\beta} = \sum_j A_{ij} (n_j^*)^{\gamma} . \tag{2}$$

The element of the jacobian for $j \neq i$ read

$$J_{ij} = -\gamma n_i^{\beta} A_{ij} n_i^{\gamma} \,, \tag{3}$$

while the diagonal components read

$$J_{ii} = \alpha n_i^{\alpha - 1} - \beta n_i^{\beta - 1} \sum_{j \neq i} A_{ij} n_j^{\gamma} - (\beta + \gamma) A_{ii} n_i^{\beta + \gamma}.$$

$$\tag{4}$$

1.1 Uniform case

In the case of uniform interactions ($\sigma = 0$) the species population are all equal and the equilibrium reads

$$n^* = \left[\mu(S-1) + \frac{1}{K}\right]^{1/(\alpha-\beta-\gamma)}.$$
 (5)

The jacobian evaluated at equilibrium is

$$J_{ij}\Big|_{n=n^*} = -\gamma \mu(n^*)^{\beta+\gamma-1}, \qquad (6)$$

$$J_{ii}\Big|_{n=n^*} = \alpha(n^*)^{\alpha-1} - \beta(n^*)^{\beta+\gamma-1}\mu(S-1) - \frac{(\beta+\gamma)}{K}(n^*)^{\beta+\gamma-1}.$$
 (7)

The maximum eigenvalue λ_{\max} is S-1 degenerate and reads formally

$$\lambda_{\max} = J_{ii} \Big|_{n=n^*} - J_{ij} \Big|_{n=n^*}. \tag{8}$$

The stability condition

$$\lambda_{\max} = \alpha (n^*)^{\alpha - 1} - (n^*)^{\beta + \gamma - 1} \left[\beta \mu (S - 1) + \frac{(\beta + \gamma)}{K} - \gamma \mu \right] < 0,$$
 (9)

can be written as

$$\alpha(n^*)^{\alpha-\beta-\gamma} - \left[\beta\mu(S-1) + \frac{(\beta+\gamma)}{K} - \gamma\mu\right] < 0, \tag{10}$$

which, using the expression for n^* and after some manipulations reads

$$(S-1)(\beta-\alpha) > \frac{K\mu\gamma + \alpha - \beta - \gamma}{K\mu}.$$
 (11)

We have then three possibilities:

$$S > 1 + \frac{K\mu\gamma + \alpha - \beta - \gamma}{K\mu(\beta - \alpha)} \qquad \text{if} \quad \beta/\alpha > 1, \qquad (12)$$

$$S < 1 + \frac{K\mu\gamma + \alpha - \beta - \gamma}{K\mu(\beta - \alpha)} \qquad \text{if} \quad \beta/\alpha < 1, \qquad (13)$$

$$S < 1 + \frac{K\mu\gamma + \alpha - \beta - \gamma}{K\mu(\beta - \alpha)} \qquad \text{if} \quad \beta/\alpha < 1, \tag{13}$$

$$\mu < \frac{1}{K} \qquad \qquad \text{if} \quad \beta/\alpha = 1. \tag{14}$$

A series of comments is in order.

- Depending on β/α we have two regimes: one in which increasing S enhances stability $(\beta/\alpha > 1)$ and one in which it hinders stability $(\beta/\alpha < 1)$. Notably this is independent from γ , indicating that only the interplay between the density dependence of the contribution of a species to the interactions and the density dependence of its production term that is (qualitatively) relevant; and not the form of the contribution of the competitors to the interactions.
- The critical case $(\beta/\alpha = 1)$ not only recovers the usual GLV result but generalize it, indeed it does not depend on γ which cancels out.
- For $K \to \infty$ and $\beta = 1$ we recover the result

$$S = 1 + \frac{1}{1 - \alpha} \,, \tag{15}$$

once again independently on γ .

Being the specification of γ mostly irrelevant, for symmetry reason it is probably sensible to consider models with $\gamma = \beta$, leaving the potential asymmetry of the competitive interaction between two species to the coefficient A_{ij} .

Non-uniform case

2 On sublinear production

Observations point towards a sublinear production scaling with respect to the population biomass density. This observations may refer to dynamical production or to the equilibrium production observed across a biomass gradient.

Here we discuss how dynamical sublinear production does not generally leads to sublinear production across a biomass gradient. Nonetheless, although not sufficient, it might be necessary for (or at least functional to) sublinear scaling across a biomass gradient.

2.1 Single population

Let us focus on a single population example to calrify the ideas. Consider a production function of the form

$$P(n) = rn^{\alpha} \,, \tag{16}$$

where n is the biomass density of the population, $\alpha \leq 1$ specify the intensity of sublinear dynamical scaling (linear when $\alpha = 1$) and r is the parameter that allows to move across a biomass gradient. Consider then a loss term of the form

$$L(n) = sn^{\beta}. \tag{17}$$

The evolution equaiton for the population is

$$\frac{dn}{dt} = P(n) - L(n) = rn^{\alpha} - sn^{\beta}, \qquad (18)$$

which reduces to logistic growth for $\alpha = 1$ and $\beta = 2$. The equilibrium is given by

$$n^* = \left(\frac{r}{s}\right)^{1/(\beta - \alpha)},\tag{19}$$

and the stability condition is given by

$$\left. \frac{d\left[P(n) - L(n) \right]}{dn} \right|_{n=n^*} < 0, \tag{20}$$

which leads, after some calculations, to the condition

$$\alpha < \beta$$
, (21)

independent from r and s.

It possible to appreciate from Eq. (19) that $\alpha > \beta$, apart from making the equilibrium unstable, implies that the stationary population decreases for increasing r, which is biologically unreasonable.

The equilibrium production scales, at varying growth rate r, as $P(n^*) = s(n^*)^{\beta}$ as can be noted by Eq. (19) for r and then substituting it in the defining Eq. (16) or simply by considering the dynamical equation at stationarity. Notice that, if s is varied instead, the exponent of dynamical and across-biomass-gradient production coincide. Figure 1 shows an example with specific parameters.

In summary, for an environmental change that amount to a change in r, the production across a biomass gradient scales as $(n^*)^{\beta}$. In order for the stationary solution to be stable an exponent $\alpha < \beta$ for the dynamical production is needed. Therefore, in order to have sublinear $P(n^*)$ across a biomass gradient, we need $\alpha < \beta < 1$. If the increment of the equilibrium biomass density is due to decreasing s, equilibrium and dynamical production scale in the same way and in order to have sublinear $P(n^*)$ we need $\alpha < 1$ with $\alpha < \beta$ for stability but no constraint on β . Either way we need $\alpha < 1$.

2.2 Competitive community

Consider the $\alpha\beta\gamma$ -model

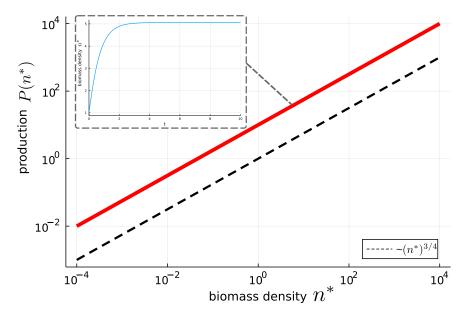


Figure 1: Production versus biomass density in single population descirbed in Eq. (18) for $r \in [1, 100]$, s = 10, $\alpha = 1/2$ and $\beta = 3/4$. In the inset the equilibration process for r = 10.

3 $(\sigma\sqrt{S}, \mu S)$ plane

4 General production with GLV interactions

Consider the system of S species

$$\frac{dn_i}{dt} = P(n_i) - n_i \sum_{j \neq i} A_{ij} n_j , \qquad (22)$$

where the summation runs over all the species and we leave the production function generic and A is a matrix with zero diagonal and off-diagonal elements gaussianly ditrubuted with mean μ and standard deviation σ . The community matrix reads in this case

$$C = -D(n^*)A - D(P(n^*)/n^* - P'(n^*)), \qquad (23)$$

where the notation D(x) stands for a diagonal matrix filled with the components of the vector x and $P(n^*) = (P(n_1^*), ..., P(n_S^*))$ and $P'(n^*) = (dP(n_1^*)/dn_1^*, ..., dP(n_S^*)/dn_S^*)$.

We have instability when

$$\sum_{i} \frac{1}{|\mu - P(n_i^*)/(n_i^*)^2 + P'(n_i^*)/n_i^*|^2} \ge 1/\sigma^2.$$
 (24)