

Notes on ecosystems stability

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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

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

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 and for dimensional consistency we could study instead, e.g., the population density normalized over a density threshold \tilde{n}_i , $x_i = (n_i/\tilde{n}_i)$. We consider, without loss of generality for the results that follows, $\tilde{n}_i = 1 \forall i$ and stick with the notation n_i . If the equilibrium is feasible it formally reads

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

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

$$J_{ij} = -\gamma n_i^\beta A_{ij} n_j^\gamma, \quad (3)$$

while the diagonal components read

$$J_{ii} = \alpha n_i^{\alpha-1} - \beta n_i^{\beta-1} \sum_{j \neq i} A_{ij} n_j^\gamma - (\beta + \gamma) A_{ii} n_i^{\beta+\gamma}. \quad (4)$$

1.1 Dynamic May / anti-May bound, uniform interaction limit

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

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

The jacobian evaluated at equilibrium is

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

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

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

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

The stability condition

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

can be written as

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

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

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

We have then three possibilities:

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

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

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

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 $K \rightarrow \infty$ and $\beta = 1 = \gamma$ we recover the result

$$S = 1 + \frac{1}{1-\alpha} . \quad (15)$$

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} .

One can therefore identify two different regimes (we could dub them *May* and *anti-May*) characterized by the dynamical response of the population with respect to their density encoded in the exponents α and β , respectively associated to production and losses. The GLV case $\alpha = \beta$ is right in the middle for uniform interactions ($\sigma \rightarrow 0$) and falls into the May regime otherwise ($\sigma \neq 0$).

2 Cavity solution

In order to better relate to the data from observations let us consider the dynamics of the biomass densities b_i for S species. The dynamics is completely described by

$$\frac{db_i}{dt} = r_i b_i \left(\frac{b_i}{\tilde{b}} \right)^{\alpha-1} - b_i \sum_{j \neq i} A_{ij} b_j, \quad (16)$$

where the entries of the interaction matrix A_{ij} have the dimensions of inverse time times inverse mass and are randomly distributed with average μ and standard deviation σ , the r_i are growth rates with the dimensions of inverse time extracted from a distribution $P(r)$ and the biomass density scale \tilde{b} is assumed, due to physiological and ecological arguments, to be a species independent constant.

Cavity trick

The cavity solution is the random variable b^* given by

$$b^* = \left(\frac{\mu S \langle b^* \rangle + \sigma \sqrt{S} \eta}{r \tilde{b}^{1-\alpha}} \right)^{1/(\alpha-1)}, \quad (17)$$

where represent $\langle b^* \rangle$ is the equilibrium average biomass density and η have zero mean and variance $\langle (b^*)^2 \rangle$. The equilibrium probability distribution function for b^* , $P(b^*)$, can be obtained through the pushforward of the distribution of η and r

$$P(b^*) = \frac{(1-\alpha)|b^*|^{\alpha-2}}{\sqrt{2\pi\sigma^2 S \langle (b^*)^2 \rangle}} \int_0^\infty dr \, r P(r) \exp \left\{ -\frac{[(b^*)^{\alpha-1} - \mu S \langle b^* \rangle / r]^2}{2\sigma^2 S \langle (b^*)^2 \rangle / r^2} \right\}, \quad (18)$$

where we set without loss of generality $\tilde{b} = 1$ and the fraction of survival species ϕ and the first two moment have to be self-consistently computed

$$\phi = \int_0^\infty db^* \, P(b^*), \quad (19)$$

$$\langle b^* \rangle = \frac{1}{\phi} \int_0^\infty db^* \, b^* P(b^*), \quad (20)$$

$$\langle (b^*)^2 \rangle = \frac{1}{\phi} \int_0^\infty db^* \, (b^*)^2 P(b^*). \quad (21)$$

Notice that the integrals for the first and the second moment have to be properly regularized, Their value is cut-off independent up to a certain value which the depend on the parameters and then diverges. If the value of density up to which they are cut-off independent is so big that is unphysical or unbiological then one can stop before and extract the values of the moments. See also, e.g., Ref. [1] for the analysis of a similar situation in the context of consumer-resource dynamics

In the case of a unique r for every species in the community, i.e. $P(\tilde{r}) = \delta(r - \tilde{r})$ the distribution reads

$$P(b^*) = \frac{(1-\alpha)|b^*|^{\alpha-2}}{\sqrt{2\pi\sigma^2 S \langle (b^*)^2 \rangle / r^2}} \exp \left\{ -\frac{[(b^*)^{\alpha-1} - \mu S \langle b^* \rangle / r]^2}{2\sigma^2 S \langle (b^*)^2 \rangle / r^2} \right\}. \quad (22)$$

2.1 Dynamical mean field theory

In order to obtain information about the dynamics of the distributions of the biomass densities of the community, following, e.g., Ref. [2] we can derive from Eq. (16), for large S , a dynamical mean field theory which provide us a stochastic differential equation describing statistically the entire ensemble of species thourg the evolution of the representative random variable b

$$\frac{db}{dt} = rb \left(\frac{b}{\bar{b}} \right)^{\alpha-1} - b \left(\mu S \langle b \rangle_t + \sigma \sqrt{S} \eta_t \right), \quad (23)$$

where $\langle b \rangle_t = \langle b(t) \rangle$ is the average at time t of the random variable b and η is a gaussian variable with zero mean and correlation given by $\langle b(t)b(s) \rangle$; these first and second moment have to be computed self-consistently at each time. At equilibrium the cavity solution is recovered.

3 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.

3.1 Single population

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

$$P(n) = rn^\alpha, \quad (24)$$

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

$$L(n) = sn^\beta. \quad (25)$$

The evolution equaiton for the population is

$$\frac{dn}{dt} = P(n) - L(n) = rn^\alpha - sn^\beta, \quad (26)$$

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

$$n^* = \left(\frac{r}{s} \right)^{1/(\beta-\alpha)}, \quad (27)$$

and the stability condition is given by

$$\left. \frac{d[P(n) - L(n)]}{dn} \right|_{n=n^*} < 0, \quad (28)$$

which leads, after some calculations, to the condition

$$\alpha < \beta, \quad (29)$$

independent from r and s .

It possible to appreciate from Eq. (27) 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. (27) for r and then substituting it in the defining Eq. (24) 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.

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 $\alpha < 1$.

3.2 Competitive community

With the help of the cavity solution we can extend the analysis above to the case of a competitive community.

4 Model construction and connection with data on productivity

Our model is informed by macroecological observations of biomass density production across major groups. In particular, we assume that the observations refers to the equilibrium production (see Sec. (3)). We define our model in the following way

$$\frac{db_i}{dt} = \underbrace{r_i b_i \left(\frac{b_i}{\tilde{b}_i} \right)^{k-1}}_{\text{Production}} - \overbrace{z_i b_i \sum_{j \neq i} A_{ij} b_j}^{\text{Losses}}, \quad (30)$$

where $\alpha < 1$ specify the intensity of sublinear dynamical scaling, the entries of the interaction matrix A_{ij} are randomly distributed with average μ and standard deviation σ , the r_i are growth rates extracted from a distribution $P(r)$, the biomass density scale \tilde{b}_i are in principle species dependent and we explicitly write a mortality rate z_i in the losses with the dimension of an inverse time. This is useful because we want to relate the characteristic time scale of the dynamics a species (captured by the rates r_i and z_i) to its mass which we call m_i . For the sake of clarity let us summarize the dimensionality of the several terms involved in the model

$$[b_i] = [\tilde{b}_i] = \frac{\text{mass}}{\text{area}}, \quad [r_i] = [z_i] = \frac{1}{\text{time}}, \quad [A_{ij}] = \frac{\text{area}}{\text{mass}}. \quad (31)$$

We want to encapsulate physiological properties in the rates r_i , z_i , and potentially \tilde{b}_i and the ecological variability in the elements of the interaction matrix A_{ij} . The density biomass scale \tilde{b}_i set the value at which the per capita growth rate is r_i . We also want to connect this quantity to the maximum per capita growth rate for a given species, we can therefore consider \tilde{b}_i also as the minimal biomass density for a given species at which it is able to reproduce therefore we impose that there is no growth for $b_i < \tilde{b}_i$, but other choices of subminimal reproduction do not change qualitatively the result of the paper. Next we connect the model with the body-mass m_i of a

species. The time scale of the problem are assumed/observed to scale with the body-mass with an exponent $-1/4$, i.e. $r_i \sim m_i^{-1/4}$ and $z_i \sim m_i^{-1/4}$. The population density scale for a given species is defined $\tilde{n}_i := \tilde{b}_i/m_i$, Its inverse can be interpreted as the minimal area within which an individual of a certain species has to find another in order to be able to reproduce on average in its lifetime, if the area covered by an individual scales like m_i , then we can roughly consider $\tilde{b}_i \simeq \tilde{b} \forall i$, i.e. species independent. We could also use an ecological argument to justify this, indeed the observed biomass densities across major group have a mass independent lower bound (within two or three order of magnitude compared with the astronomical difference of nearly 20 order of magnitude in body-mass).

5 Macroecological laws

Intro ...

5.1 Species abundance distribution

5.2 Mean-variance scaling

5.3 Size-density scaling

5.4 Size-spectrum scaling

6 Stability in parameter space

7 Simulations

References

- [1] Wenping Cui, Robert Marsland Iii, and Pankaj Mehta. Effect of Resource Dynamics on Species Packing in Diverse Ecosystems. *Physical Review Letters*, 125, 2020.
- [2] F. Roy, G. Biroli, G. Bunin, and C. Cammarota. Numerical implementation of dynamical mean field theory for disordered systems: application to the Lotka–Volterra model of ecosystems. *Journal of Physics A: Mathematical and Theoretical*, 52(48):484001, nov 2019.