

# Notes on ecosystems stability

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## 1 Super quadratic self-regulation

Consider the case as in the draft but with production

$$P(n_i) = rn_i - rn_i^l/K^l \quad (\text{super-regulated}), \quad (1)$$

with  $l \geq 2$ , recovering the logistic case for  $l = 2$ . Following the same notation and calculation as in the draft we have, in this case, the following community matrix

$$C = -DA - \frac{(l-1)r}{K^l} D^{l-1}. \quad (2)$$

In this case we have that instabilities sets in if

$$\sum_i \frac{1}{|\mu - (l-1)r(n_i^*)^{l-2}/K^{l-2}|^2} \geq 1/\sigma^2, \quad (3)$$

which correctly recover the logistic case for  $l = 2$ . The stability condition for  $l > 2$  can be approximated by

$$\sigma \leq (l-1)\sqrt{S}\mu r/K^l, \quad (4)$$

where we used the fact that

$$(n_i^*)^{l-2} = \sum_j A_{ij} n_j^*/n_i^* - r/n_i^* = \mathcal{O}(\mu S). \quad (5)$$

## 2 General

Consider the production function

$$P(n_i) = r(n_i^k - n_i^l/K^{l-k}) \quad (\text{general}), \quad (6)$$

with  $k \leq 1$ ,  $l \geq 2$  and the carrying capacity  $K$  either finite or infinite. We recover the logistic case for  $k = 1$  and  $l = 2$ , the sublinear case for  $l = 2$  and  $K \rightarrow \infty$  and the super-regulated case for  $k = 1$ . The community matrix reads

$$C = -DA - (1-k)rD^{k-1} - \frac{(l-1)r}{K^{l-k}} D^{l-1}, \quad (7)$$

therefore the system becomes unstable if

$$\sum_i \frac{1}{|\mu - (1-k)r(n_i^*)^{k-2} - (l-1)r(n_i^*)^{l-2}/K^{l-k}|^2} \geq 1/\sigma^2. \quad (8)$$

It seems less straightforward to find an approximate stability condition in terms of  $S$  in this case. The fact that we have

$$r(n_i^*)^{k-2} - r(n_i^*)^{l-2}/K^{l-k} = \sum_j A_{ij} n_j^*/n_i^* = \mathcal{O}(\mu S), \quad (9)$$

could be maybe used but the terms appear with weights in the equation for stability. I will explore further.

### 3 More general

Consider the system of  $S$  species

$$\frac{dn_i}{dt} = P(n_i) - n_i \sum_{j \neq i} A_{ij} n_j, \quad (10)$$

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 distributed with mean  $\mu$  and standard deviation  $\sigma$ . The community matrix reads in this case

$$C = -D(n^*)A - D(P(n^*)/n^* - P'(n^*)), \quad (11)$$

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

We have instability when

$$\sum_i \frac{1}{|\mu - P(n_i^*)/(n_i^*)^2 + P'(n_i^*)/n_i^*|^2} \geq 1/\sigma^2. \quad (12)$$

### 4 Sublinear production across a gradient

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.

#### 4.1 Single population

Let's focus on a single population example to clarify the ideas. Consider a production function of the form

$$P(n) = rn^k, \quad (13)$$

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

$$Q(n) = sn^l. \quad (14)$$

The evolution equation for the population is

$$\frac{dn}{dt} = P(n) - Q(n) = rn^k - sn^l, \quad (15)$$

which reduces to logistic growth for  $k = 1$  and  $l = 2$ . The equilibrium is given by

$$n^* = \left(\frac{r}{s}\right)^{1/(l-k)}, \quad (16)$$

and the stability condition is given by

$$\left. \frac{d[P(n) - Q(n)]}{dn} \right|_{n=n^*} < 0, \quad (17)$$

which leads, after some calculations, to the condition

$$k < l, \quad (18)$$

independent from  $r$  and  $s$ .

It possible to appreciate from Eq. (16) that  $k > l$ , 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  $P(n^*) = s(n^*)^l$  as can be noted by Eq. (16) for  $r$  and then substituting it in the defining Eq. (13) 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, consistently with what is proposed in the 2015 paper. I discuss anyway why  $r$  is preferable to be changed instead of  $s$  elsewhere. Figure 1 shows an example with specific parameters.

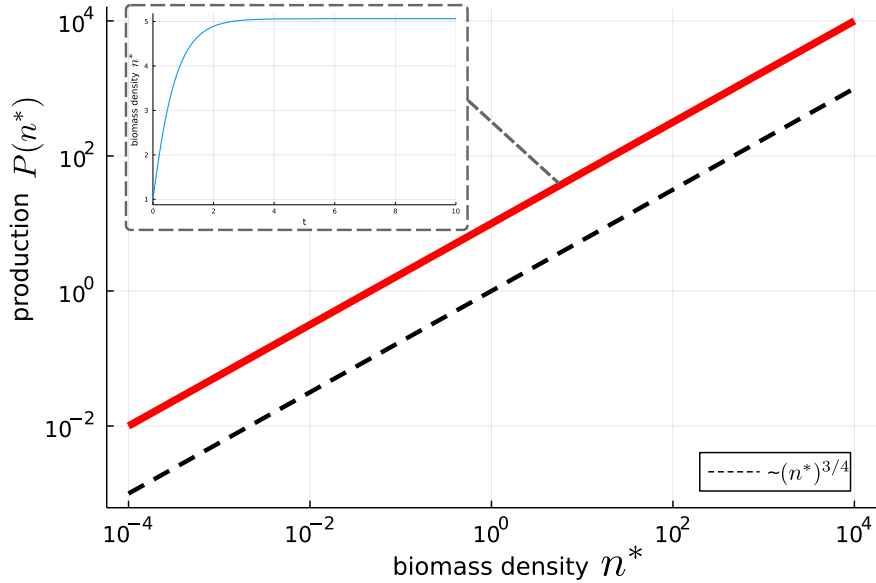


Figure 1: Production versus biomass density for  $r \in [1, 100]$ ,  $s = 10$ ,  $k = 1/2$  and  $l = 3/4$ . In the inset the equilibration process for  $r = 10$ .

In summary, for an environmental change that amount to a change in  $r$ , the production across a biomass gradient scales as  $(n^*)^l$ . In order for the stationary solution to be stable an exponent  $k < l$  for the dynamical production is needed. Therefore, in order to have sublinear  $P(n^*)$  across a biomass gradient, we need  $k < l < 1$ .