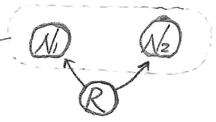
2021.12.14 Mechanistic models for competition: consumer-resource dynamics

Lotka-Volterra competition models (phenomenological : model direct impact)

$\updownarrow$ vs.

Mechanistic models : explicitly modeling limiting factors (resource , predator, etc.)

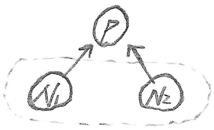
« Common resource »



no direct interactions among species, only indirect negative effects

exploitative competition

« Common predator »



apparent competition

- R^* rule
- Tilman's resource ratio hypothesis
- relative nonlinearity

連續培養系統

R^* rule

Consider 2 consumers competing for 1 resource → abiotic resource in chemostat

$$\begin{cases} \dfrac{dN_1}{dt} = e_1 a_1 R N_1 - d N_1 = g_1(R) \cdot N_1 \\ \dfrac{dN_2}{dt} = e_2 a_2 R N_2 - d N_2 = g_2(R) \cdot N_2 \\ \dfrac{dR}{dt} = d(S_0 - R) - a_1 R N_1 - a_2 R N_2 \end{cases}$$

can be m_1, m_2

can be e_1, e_2

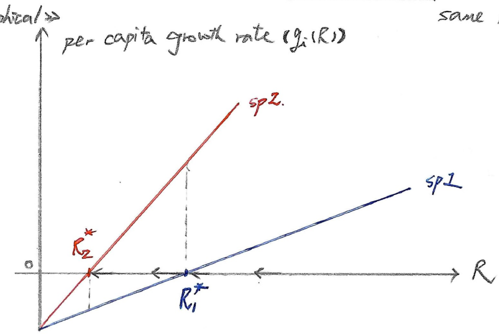
$* \; g_i(R) = e_i a_i R - d_i$

Q. can all three species coexist in the system?

At equilibrium : $g_1(R^*) = g_2(R^*) = 0$

same R^* making $g_1(R^*) = g_2(R^*) = 0$, unlikely for diff species

« Graphical »



$$R_i^* = \text{resource level when species } i \text{ stops growing} = \frac{d}{e_i a_i}$$

At R_1^*, $\frac{dN_1}{dt} = 0$ but $\frac{dN_2}{dt} > 0$, N_2 continues to consume resource until R_2^*

At R_2^*, $\frac{dN_2}{dt} = 0$ and $\frac{dN_1}{dt} < 0$, N_2 drives N_1 to exclusion

feasible when $S_0 > \frac{d}{e_1 a_1}$

« Invasion analysis »

- For $N_1 - R$ monoculture, $R_1^* = \frac{d}{e_1 a_1}$, $N_1^* = \frac{d(S_0 - R_1^*)}{a_1 R_1^*}$

$$IGR_2 = \lim_{N_2 \to 0} \frac{dN_2}{dt} \frac{1}{N_2} = e_2 a_2 R_1^* - d = d\left(\frac{e_2 a_2}{e_1 a_1} - 1\right)$$

N_2 can invade if $e_2 a_2 > e_1 a_1$

- For $N_2 - R$ monoculture, $R_2^* = \frac{d}{e_2 a_2}$, $N_2^* = \frac{d(S_0 - R_2^*)}{a_2 R_2^*}$

$$IGR_1 = \lim_{N_1 \to 0} \frac{dN_1}{dt} \frac{1}{N_1} = e_1 a_1 R_2^* - d = d\left(\frac{e_1 a_1}{e_2 a_2} - 1\right)$$

N_1 can invade if $e_1 a_1 > e_2 a_2$

→ Mutual invasibility is not possible, the two species cannot coexist

R^* rule: when multiple species are competing for a single resource, under equilibrium environment, coexistence is NOT possible. The species with the lowest R^* will win competition.

resource explicit statement of competitive exclusion

Tilman's Resource ratio hypothesis (Niche theory)

How can species coexist then? ADD ANOTHER RESOURCE (Tilman 1980, Am. Nat.)

2 resources: R_a & R_b

a_{ij} = consumption of species i on resource j

$$\frac{dN_1}{dt} = e_1 a_{1a} R_a N_1 + e_1 a_{1b} R_b N_1 - dN_1$$

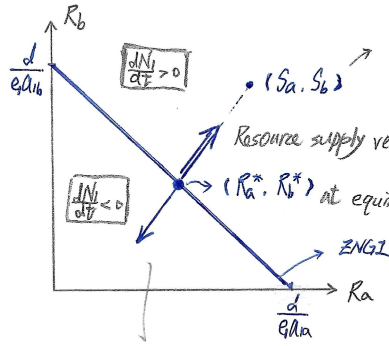
$$\frac{dN_2}{dt} = e_2 a_{2a} R_a N_2 + e_2 a_{2b} R_b N_2 - dN_2$$

$$\frac{dR_a}{dt} = d(S_a - R_a) - a_{1a} R_a N_1 - a_{2a} R_a N_2$$

$$\frac{dR_b}{dt} = d(S_b - R_b) - a_{1b} R_b N_1 - a_{2b} R_b N_2$$

• We're going to talk about the biological intuition behind the (complex) mathematical analysis ...

◎ Visualize dynamics on R_a–R_b state space



Resource supply point (resource equilibrium when no consumer)

Resource supply vector : $\begin{bmatrix} d(S_a - R_a) \\ d(S_b - R_b) \end{bmatrix} = \vec{U}$

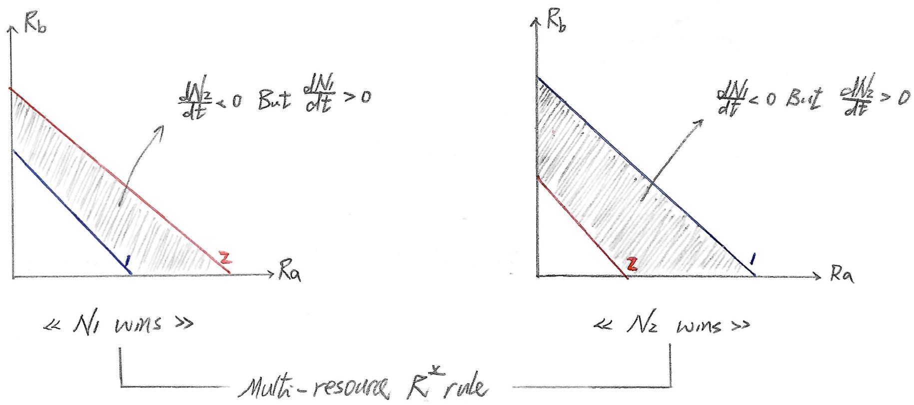
(R_a^*, R_b^*) at equilibrium, consumption vector = supply vector and crosses ZNGIs (assimilation = death)

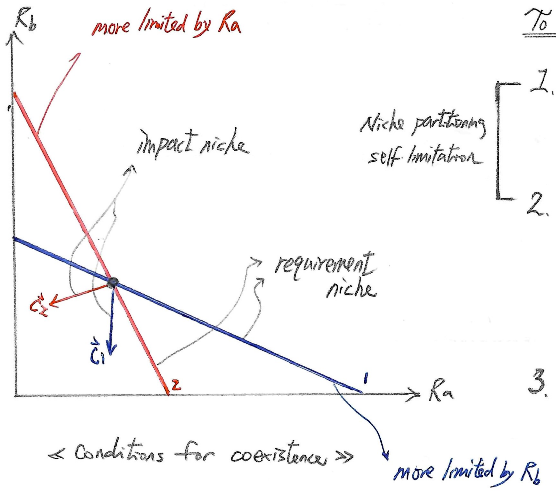
ZNGI for N_1 : $e a_{1a} R_a + e a_{1b} R_b - d = 0$

consumption vector (from resource dynamics) : $\begin{bmatrix} a_{1a} R_a N_1 \\ a_{1b} R_b N_1 \end{bmatrix} = \vec{C_1}$

◎ Limiting resource : the resource whos decrease leads to largest decrease in consumer performance

◎ Combine 2 species ZNGI





To coexist:

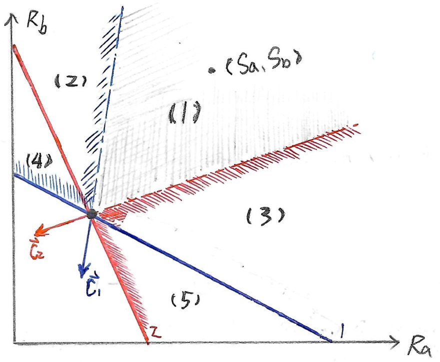
Niche partitioning / self-limitation
1. ZNGIs must intersect, tradeoff in resource requirements (which resource is limiting)
2. Each species must consume more (have larger impact on) the resource that it finds most limiting
3. The resource supply ratio has to be intermediate (bounded by the inverse of consumption vectors)

at coexistence equilibrium, condition 3 for stable coexistence:

$$\underbrace{\begin{bmatrix} d(S_a - R_a^*) \\ d(S_b - R_b^*) \end{bmatrix}}_{\vec{U}} - \underbrace{\begin{bmatrix} a_{1a} R_a^* N_1^* \\ a_{1b} R_b^* N_1^* \end{bmatrix}}_{\vec{C_1}} - \underbrace{\begin{bmatrix} a_{2a} R_a^* N_2^* \\ a_{2b} R_b^* N_2^* \end{bmatrix}}_{\vec{C_2}} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$$

$$\Rightarrow d \begin{bmatrix} S_a - R_a^* \\ S_b - R_b^* \end{bmatrix} = N_1^* \begin{bmatrix} a_{1a} R_a^* \\ a_{1b} R_b^* \end{bmatrix} + N_2^* \begin{bmatrix} a_{2a} R_a^* \\ a_{2b} R_b^* \end{bmatrix}$$

equal magnitude, opposite directions



(1) N_1, N_2 coexist

(2) N_1 outcompete N_2

(3) N_2 outcompete N_1

(4) N_2 cannot even survive

(5) N_1 cannot even survive

@ A mechanistic view of coexistence (intra > inter [stabilization]): each species consumes more of the resource that it finds most limiting. If the opposite is true, you get priority effect.

Relative nonlinearity

Is it never possible to coexist on one resource? IN FLUCTUATING ENVIRONMENT

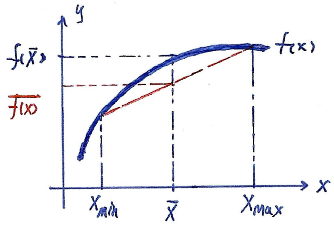
(Armstrong & McGehee 1980, Am.Nat.)

How to get the system fluctuate? → Logistic growing resource + Nonlinear functional response

$$\begin{cases} \dfrac{dN_1}{dt} = e_1 a_1 R N_1 - d N_1 \\ \dfrac{dN_2}{dt} = e_2 \left(\dfrac{a_2 R}{K_2 + R} \right) N_2 - d N_2 \quad (= g_2(R) \cdot N_2) \\ \dfrac{dR}{dt} = rR\left(1 - \dfrac{R}{K}\right) - a_1 R N_1 - \dfrac{a_2 R}{K_2 + R} \cdot N_2 \end{cases}$$

◎ A fact about cycles in Rosenzweig – MacArthur model ($N_2 - R$ system)

※ Jensen's inequality : mean of function vs. function of the mean



for concave-down functions : $\overline{f(x)} < f(\bar{x})$

the opposite is true for convex-up functions

1. Along a fluctuation cycle (from $0 \sim \tau$) : $\overline{g_2(R)} < g_2(\bar{R})$, with $\bar{R} = \frac{1}{\tau}\int_0^\tau R(t)dt$

2. Along the stable limit cycle : $\overline{g_2(R)} = \frac{1}{\tau}\int_0^\tau g(R(t))dt = \frac{1}{\tau}\int_0^\tau \frac{1}{N_2}\frac{dN_2}{dt} \cdot dt$

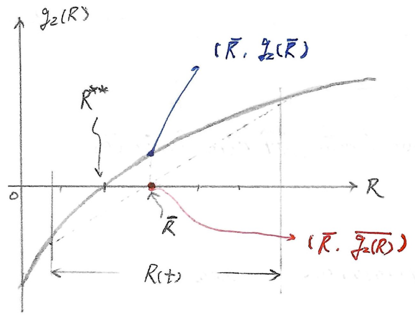
$$= \frac{1}{\tau}\left[\ln N_2(t) \Big|_0^\tau \right] = 0$$

$\ln N_2(\tau) = \ln N_2(0)$

$\rightarrow$ $g_2(R^{**}) = \overline{g_2(R)} = 0 < g_2(\bar{R})$

since $g_2(R)$ is an increasing function , $\bar{R} > R^{**}$

$\Rightarrow$ in a fluctuating environment , for a species with concave-down per capita growth rate, the resource level required to maintain zero growth in higher than that required in a stable environment (i.e. fluctuation hurts species w/ concave functions)

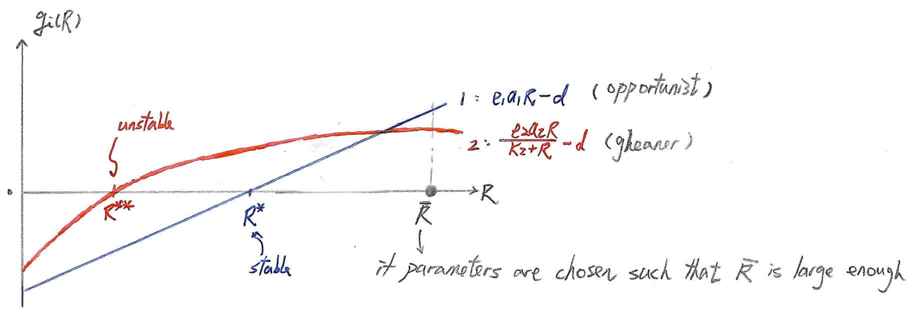


◎ Back to Armstrong – Mcgehee

1. Consider a system with $N_1 - R$, this system can reach stable equilibrium $R^* = \frac{d}{e_1 a_1}$, $N_1^* = \frac{r}{a_1}\left(1 - \frac{d}{e_1 a_1 K}\right)$, Note this equilibrium is stable

2. N_2 can invade if its R-star , $R^{**} = \frac{dK_2}{e_2 a_2 - d}$, is less than R^* (i.e. $R^{**} < R^*$)

e.g.



3. In Rosenzweig–MacArthur, R^{**} can be either stable or unstable. If K is small, R^{**} is stable then N_2 outcompetes N_1. If K is large cycles emerge, with $\bar{R} > R^{**}$. N_1 can invade if its "average per capita growth rate along the cycle" is positive (i.e. imagine multiple invasion attempts throughout the cycle).

$$\text{average IGR}_1 = \frac{1}{\tau}\int_0^\tau \frac{1}{N_1}\frac{dN_1}{dt}\,dt = \frac{1}{\tau}\int_0^\tau \left(e_1a_1R(t) - d\right)dt$$

$$= e_1a_1 \cdot \left[\frac{1}{\tau}\int_0^\tau R(t)dt\right] - \frac{1}{\tau}dt\Big|_0^\tau = e_1a_1\cdot\bar{R} - d > 0$$

$\Rightarrow$ N_1 can invade if $\bar{R} > R^*$, therefore coexistence is possible if $\underline{R^{**} < R^* < \bar{R}}$

another is "storage effect"

This is one type of "fluctuation-dependent coexistence" called "Relative nonlinearity" that emerge via logistic growth resource + consumers with different degree of nonlinearity. Coexistence is therefore possible if the single limiting factor fluctuates

probably common..

① nonlinear functional responses are common

② fluctuations are common and coexistence is not limited to fixed points (usefulness of invasion growth rate)

③ A form of stabilization (harm conspecifics more than harm heterospecifics) the concave-down species (N_2) is harmed by fluctuations but creates cycles that benefits the other species (N_1), whereas the more-linear species losses in a stable environment but dampes cycles