PHYS 282
Spatiotemporal Dynamics in Biological Systems
Fall 2024

Solution of Homework #3

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1. **Relationship between the Consumer-Resource model and population dynamics model**
In class, we went over the dynamics in the chemostat. Describing the density of the organism by $\rho(t)$ and the nutrient concentration in the chemostat by $n(t)$, the CR model for the system is

$$\dot{\rho} = r(n) \cdot \rho - \mu\rho, \tag{1}$$

$$\dot{n} = \mu \cdot (n_0 - n) - r(n) \cdot \rho / Y \tag{2}$$

where $r(n) = r_0 n/(n + K)$ is the nutrient-dependent replication rate, μ is the dilution rate of the chemostat, $n_0\mu$ is the nutrient influx, and Y is the biomass yield.

In this problem, you will derive the logistic equation which describes the dynamics of the population without referencing the nutrient,

$$\dot{\rho} = \tilde{r}\rho \cdot (1 - \rho/\tilde{\rho}), \tag{3}$$

and obtain the effective replication rate $\tilde{r}$ and carrying capacity $(\rho 4)$ in terms of the chemostat parameters (μ, n) and the physiological parameters (r, K, Y). Through this exercise, you will get a feel of the occurrence of "dimension reduction" (in this case, referring to a system with two degrees of freedom, $\rho(t)$ and $n(t)$ being reduced to a single degree of freedom $\rho(t)$)

(a) *We shall work in a parameter region typical of chemostat operation, $\mu << r_0$, for which we can linearize the replication rate, taking it to be $r(n) \approx rn/K \equiv \nu n$. Using this linear form of $r(n)$, express the CR equations in terms of two dimensionless variables $u\ equiv n/n_0$and $v \equiv \rho/\rho_0$ (where $\rho_0 \equiv n_0/Y$), the dimensionless time variable, $\tau \equiv n_0\nu t$, and a dimensionless parameter, $\eta \equiv \nu/(\nu n_0)$. Sketch the two null clines and the fixed point $(u*, v*)$ for $\eta < 1$ (where a nontrivial steady state with $\rho* > 0$ exists).*

Solution

using $v \equiv \rho/\rho_0$, $u = n/n_0$, we have

$$\frac{dv}{dt} = \nu n_0 u - \mu v$$

$$\frac{du}{dt} = \mu(1-u) - \nu n_0 uv$$

Furthermore, by using $\tau = n_0\nu t$ and $\eta = \mu/(\nu n_0)$, we will have:

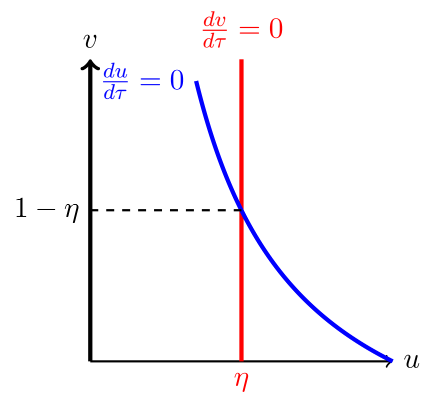
$$\frac{du}{d\tau} = \eta(1-u) - uv$$

$$\frac{dv}{d\tau} = (u-\eta)v$$

Solve for the two nullcines

$$\frac{du}{d\tau} = 0 \Rightarrow v = \frac{\eta(1-u)}{u}$$

$$\frac{dv}{d\tau} = 0 \Rightarrow u = \eta$$



The fixed point will be:

$$\frac{du}{d\tau} = 0, \frac{dv}{d\tau} = 0 \Rightarrow u^* = \eta; v^* = 1-\eta$$

(b) *Expand u, v in the vicinity of the fixed point, i.e., for $u = u^* + x$ and $v = v^* + y$. For $|x| << u^*$ and $|y| << v^*$, the equation of motion can be reduced to the following linear equation*

$$\lambda \begin{pmatrix} x \\ y \end{pmatrix} = M \begin{pmatrix} x \\ y \end{pmatrix} \tag{4}$$

where λ is the eigenvalue. Workout the form of the matrix M. From $det(M - \lambda \cdot I) = 0$ (where I is the identity matrix), solve for the two eigenvalues in term of η. In one plot, sketch how the two eigenvalues depend on η for $0 < \eta < 1$.

Solution

The Jacobian matrix is:

$$J = \begin{pmatrix} \frac{\partial}{\partial u}(\frac{du}{d\tau}) & \frac{\partial}{\partial v}(\frac{du}{d\tau}) \\ \frac{\partial}{\partial u}(\frac{dv}{d\tau}) & \frac{\partial}{\partial v}(\frac{dv}{d\tau}) \end{pmatrix} = \begin{pmatrix} -\eta - v & -u \\ v & u - \eta \end{pmatrix} \tag{5}$$

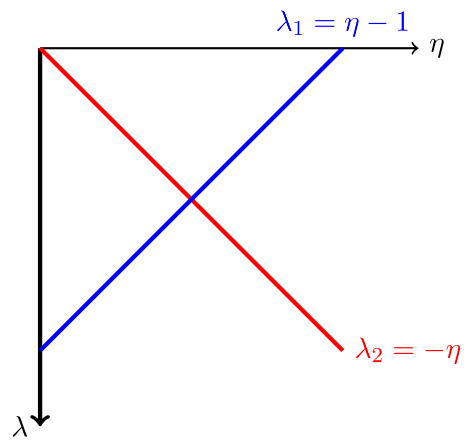
at fixed point $u^* = \eta$, $v^* = 1 - \eta$,

$$M = \begin{pmatrix} -1 & -\eta \\ 1-\eta & 0 \end{pmatrix} \tag{6}$$

From $det(M - \lambda \cdot I) = 0$, we have:

$$det(M - \lambda I) = \lambda^2 + \lambda + \eta(1-\eta) = 0$$

$$\Rightarrow \lambda_1 = \eta - 1, \lambda_2 = -\eta$$



(c) *The more negative eigenvalue (denoted as λ_{fast}) describes the decay rate of the fast mode and the less negative eigenvalue (denoted as $\lambda_(slow)$) describes the decay rate of the slow mode. For $\eta > 0.5$, what is the expression for $\lambda_{slow}(\eta)$? To find the slow mode itself, use $\lambda_{slow}(\eta)$? in the linear equation (4) to obtain an equation relating $x(t)$ and $y(t)$; this equation describes the slow mode. To see what this slow-mode means, re-express the equation for the slow mode in terms of $u(t)$ and $v(t)$, using the expressions for the fixed point $u^*(\eta)$ and $v^*(\eta)$. Sketch the slow-mode in (u, v) space along with the fixed point and the null clines. Next re-express the slow-mode for $u(t)$ and $v(t)$ in terms of the original variables $n(t)$ and $\rho(t)$. Can you interpret the meaning of the slow mode now?*

Solution

for $\eta > 0.5$, $-\eta$ is more negative, so the decay rate of the slow mode will be:

$$\lambda_{slow}(\eta) = \eta - 1$$

Then use equation 4:

$$(\eta - 1)\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -1 & -\eta \\ 1-\eta & 0 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \tag{7}$$

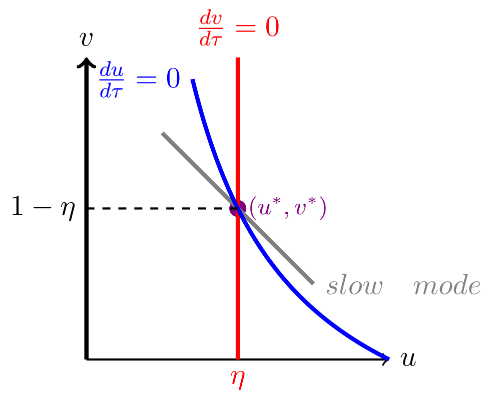
$$\Rightarrow x + y = 0$$

This equation describe the slow mode. let's reexpress the slow mode in terms of $u(t)$ and $v(t)$:

$$u + v - 1 = 0$$

and in terms of $\rho(t)$ and $n(t)$ (by using $v \equiv \rho/\rho_0$, $u = n/n_0$):

$$\rho = \rho_0(1 - \frac{n}{n_0})$$



The slow mode evolves along a straight line that reflects the conservation of the normalized total mass, which is the sum of biomass and nutrients.

(d) *Over long time scales (after the fast mode has settled down), the two dynamical variables $n(t)$ and $\rho(t)$ collapses onto the slow mode, such that the slow mode equation becomes a constraint, and the system is effectively that of a single variable. Use this constraint to express $n(t)$ in term of $\rho(t)$, and substitute the resulting expression for $n(t)$ into Eq. (1) to obtain an effective equation for $\rho(t)$. Show that it is of the logistic form Eq. (3) and find the two parameters of the logistic equation, $\tilde{r}$ and $\tilde{\rho}$ in terms of the original parameters of the system.*

Solution

Use the contraint in (c) to express $n(t)$ in term of $\rho(t)$:

$$\rho = \rho_0(1 - \frac{n}{n_0}) \Rightarrow n = n_0(1 - \frac{\rho}{\rho_0})$$

Then we can substitute the resulting expression for $n(t)$ into Eq. (1):

$$\dot{\rho} = \nu n \rho - \mu \rho = \rho(-\mu + \nu n_0(1 - \frac{\rho}{\rho_0})) = (\nu n_0 - \mu)\rho(1 - \frac{\nu n_0}{\rho_0(\nu n_0 - \mu)}\rho)$$

By using $\eta \equiv \mu/\nu n_0$,

$$\dot{\rho} = \nu n_o(1 - \eta)\rho(1 - \frac{\rho}{\rho_0(1 - \eta)})$$

comparing with $\dot{\rho} = \tilde{r}\rho \cdot (1 - \rho/\tilde{\rho})$, we have

$$\tilde{r} = \nu n_0(1 - \eta), \tilde{\rho} = \rho_0(1 - \eta)$$

(e) *Comment on the range of η for which derivation of the logistic equation (part(d)) breaks down. Given that large the separation of the two time scales (λ_{fast} and λ_{slow}), the better is the derivation, what range of η is the chemostat system best approximated by the logistic equation? What are the values of $\tilde{r}$ and $\tilde{\rho}$ in this limit? Can you come up with a general explanation for why the logistic equation is a good approximation of chemostat dynamics in this limit?*

the separation of the two time scales (λ_{fast} and λ_{slow}) is:

$$\lambda_{slow} - \lambda_{fast} = \eta - 1 - (-\eta) = 2\eta - 1$$

The system can be approximated by logistic equation when the separation is maximized. The range of η is: $\eta \to 1$. In this limit, $\tilde{r} = \nu n_0(1-\eta)$ and $\tilde{\rho} = \rho_0(1-\eta)$ are small. The significant separation between fast and slow dynamics ensures that the system can be treated as reaching a quasi-steady state quickly (fast mode), followed by gradual changes (slow mode), which satisfies by the constraint $\rho = \rho_0(1 - \frac{n}{n_0})$. The cost is the long relaxation time: $t_r \propto \frac{1}{\lambda_{slow}} = \frac{1}{1-\eta}$

2. **Competition for nutrient**
Two species described by densities $\rho_1(t)$ and $\rho_2(t)$ grow on the same nutrient source, of concentration $n(t)$. Suppose the growth rate of species i is given by the Monod growth law, $r_i(n) = r_{i,0} \cdot n/(n + K_i)$, the death rate is given by μ_i, and the nutrient influx is j_0. Find a criterion on the physiological parameters $(r_{i,0}, K_i, \mu_i)$ in order for species i to survive in the steady state.

Solution
The equations of the system are:

$$\dot{\rho}_1 = \rho_1 \left(r_{1,0} \frac{n}{n + K_1} - \mu_1 \right) \qquad \dot{\rho}_2 = \rho_2 \left(r_{2,0} \frac{n}{n + K_2} - \mu_2 \right) \qquad \dot{n} = j_0 - \frac{\rho_1 r_1}{Y_1} - \frac{\rho_2 r_2}{Y_2}$$

Suppose species 1 survives, and species 2 goes to extinction. From the equation for ρ_1 at steady state we have:

$$\dot{\rho}_1 = \rho_1^* \left(r_{1,0} \frac{n_1^*}{n_1^* + K_1} - \mu_1 \right) = 0 \quad \stackrel{\rho_1^* > 0}{\Rightarrow} \quad r_{1,0} \frac{n_1^*}{n_1^* + K_1} = \mu_1 \quad \Rightarrow$$

$$\Rightarrow \quad \frac{r_{1,0}}{\mu_1} = 1 + \frac{K_1}{n_1^*} \quad \Rightarrow \quad \frac{1}{n_1^*} = \frac{1}{K_1} \left(\frac{r_{1,0}}{\mu_1} - 1 \right)$$

Where n_1^* is the steady-state resource concentration when only species 1 is present.
Similarly, if we assume that species 2 survives and species 1 goes to extinction we have:

$$\frac{1}{n_2^*} = \frac{1}{K_2} \left(\frac{r_{2,0}}{\mu_2} - 1 \right)$$

where again n_2^* is the steady-state resource concentration when only species 2 is present.

Now, let's consider the case where species species 1 survives and species 2 is going to extinction. In this case when $n = n_1^*$ we need $\dot{\rho}_2(n_1^*) < 0$ (the population of species 2 will always decrease until $\rho_2^* = 0$). Therefore:

$$\dot{\rho}_2 = \rho_2 \left(r_{2,0} \frac{n_1^*}{n_1^* + K_2} - \mu_2 \right) < 0 \;\Rightarrow\; r_{2,0} \frac{n_1^*}{n_1^* + K_2} < \mu_2 \;\Rightarrow\; \frac{r_2, 0}{\mu_2} < 1 + \frac{K_2}{n_1^*} \;\Rightarrow$$

$$\Rightarrow\; \frac{r_{2,0}}{\mu_2} - 1 < \frac{K_2}{K_1} \left(\frac{r_{1,0}}{\mu_1} - 1 \right) \;\Rightarrow\; \boldsymbol{\frac{1}{K_2} \left(\frac{r_{2,0}}{\mu_2} - 1 \right) < \frac{1}{K_1} \left(\frac{r_{1,0}}{\mu_1} - 1 \right)}$$

This condition can be rewritten as:

$$\frac{1}{K_2} \left(\frac{r_{2,0}}{\mu_2} - 1 \right) < \frac{1}{K_1} \left(\frac{r_{1,0}}{\mu_1} - 1 \right) \;\Rightarrow\; \frac{1}{n_2^*} < \frac{1}{n_1^*} \;\Rightarrow\; n_1^* < n_2^*$$

Therefore, species 1 survives if $n_1^* < n_2^*$. By symmetry, species 2 will survive when $n_2^* < n_1^*$. In general, if we have N species in this system the only one that will survive is the species with the lowest value of n_i^*. The ecological meaning of this condition is that the species that will outcompete all the others is the one that uses the resource most efficiently, because it is the species that leaves the lowest steady-state concentration of resource in the environment, thus making it harder for other species to keep up with its own growth.

3. **MacArthur's model of resource competition**

MacArthur's model applied to 2-species (of densities ρ_1, ρ_2) and 2 nutrients (of concentrations n_A, n_B) is

$$\dot{\rho}_1 = (v_{1A} n_A + v_{1B} n_B) \cdot \rho_1 - \mu_1 \rho_1 \tag{8}$$

$$\dot{\rho}_2 = (v_{2A} n_A + v_{2B} n_B) \cdot \rho_2 - \mu_2 \rho_2 \tag{9}$$

$$\dot{n}_A = \gamma_A n_A \cdot \left(1 - \frac{n_A}{K_A} \right) - (v_{1A} \rho_1 + v_{2A} \rho_2) n_A \tag{10}$$

$$\dot{n}_B = \gamma_B n_B \cdot \left(1 - \frac{n_B}{K_B} \right) - (v_{1B} \rho_1 + v_{2B} \rho_2) n_B \tag{11}$$

where $v_{i\alpha}$ is the consumption matrix indicating the uptake preference of species i for nutrient α, μ_i is the death rate of species i, and γ_α is the generation rate, K_α is the concentration scale of nutrient α in the habitat. (The yield factor has been omitted.)

(a) *Assume the existence of a non-trivial steady state with n_A^*, n_B^*, ρ_1^*, ρ_2^* all being non-zero. From $\dot{\rho}_1/\rho_i = 0$ in Eqs.* **(??)** *and* **(??)***, show that in the limit the death rate $\mu_i \to 0$, the steady state concentrations $n_\alpha \to 0$. Using this result in Eqs.* **(??)** *and* **(??)***, show that $\dot{n}_\alpha / n_\alpha = 0$ lead to the following equation for the steady state densities*

$$\begin{pmatrix} v_{1A} & v_{2A} \\ v_{1B} & v_{2B} \end{pmatrix} \cdot \begin{pmatrix} \rho_1 \\ \rho_2 \end{pmatrix} = \begin{pmatrix} \gamma_A \\ \gamma_B \end{pmatrix}$$

Solution

From Eqs. **(??)** and **(??)** at steady state we have:

$$\begin{cases} \mu_1 = v_{1A} n_A^* + v_{1B} n_B^* \\ \mu_2 = v_{2A} n_A^* + v_{2B} n_B^* \end{cases} \Rightarrow \quad n_A^* = \frac{\mu_1 v_{2B} - \mu_2 v_{1B}}{v_{1A} v_{2B} - v_{1B} v_{2A}} \qquad n_B^* = \frac{\mu_1 v_{2A} - \mu_2 v_{1A}}{v_{1B} v_{2A} - v_{1A} v_{2B}}$$

Therefore, we will have $n^*_\alpha \to 0$ if $\mu_i \to 0$.

From Eqs. (**??**) and (**??**) at steady state we have:

$$\begin{cases} \gamma_A(1 - n^*_A/K_A) = v_{1A}\rho^*_1 + v_{2A}\rho^*_2 \\ \gamma_B(1 - n^*_B/K_B) = v_{1B}\rho^*_1 + v_{2B}\rho^*_2 \end{cases}$$

and in the limit $n^*_\alpha \to 0$ this reduces to:

$$\begin{cases} \gamma_A = v_{1A}\rho^*_1 + v_{2A}\rho^*_2 \\ \gamma_B = v_{1B}\rho^*_1 + v_{2B}\rho^*_2 \end{cases} \quad \Rightarrow \quad \begin{pmatrix} v_{1A} & v_{2A} \\ v_{1B} & v_{2B} \end{pmatrix} \cdot \begin{pmatrix} \rho^*_1 \\ \rho^*_2 \end{pmatrix} = \begin{pmatrix} \gamma_A \\ \gamma_B \end{pmatrix}$$

(b) *Write down the solution of the above matrix equation for ρ^*_1 and ρ^*_2. Show that the feasibility condition, i.e., $\rho^*_1 > 0$ and $\rho^*_2 > 0$, can be written as two conditions between the environmental parameters γ_A, γ_B, and $m_i \equiv v_{iB}/v_{iA}$, which describes the nutrient preference of species i. Plot the "ecological phase diagram" in the space (γ_A, γ_B), marking clearly the region of coexistence, and the region of dominance/extinction.*

Solution

By simply solving the linear system:

$$\begin{cases} \gamma_A = v_{1A}\rho^*_1 + v_{2A}\rho^*_2 \\ \gamma_B = v_{1B}\rho^*_1 + v_{2B}\rho^*_2 \end{cases} \quad \Rightarrow \quad \rho^*_1 = \frac{v_{2B}\gamma_A - v_{2A}\gamma_B}{v_{1A}v_{2B} - v_{1B}v_{2A}} \qquad \rho^*_2 = \frac{v_{1B}\gamma_A - v_{1A}\gamma_B}{v_{1B}v_{2A} - v_{1A}v_{2B}}$$

Therefore, we have $\rho^*_1 > 0$ when:

$$\begin{cases} v_{2B}\gamma_A > v_{2A}\gamma_B \\ v_{1A}v_{2B} > v_{1B}v_{2A} \end{cases} \quad \text{or} \quad \begin{cases} v_{2B}\gamma_A < v_{2A}\gamma_B \\ v_{1A}v_{2B} < v_{1B}v_{2A} \end{cases} \quad \Rightarrow$$

$$\Rightarrow \begin{cases} m_2 > \gamma_B/\gamma_A \\ m_1 < m_2 \end{cases} \quad \text{or} \quad \begin{cases} m_2 < \gamma_B/\gamma_A \\ m_1 > m_2 \end{cases}$$

Similarly, we have that $\rho^*_2 > 0$ when:

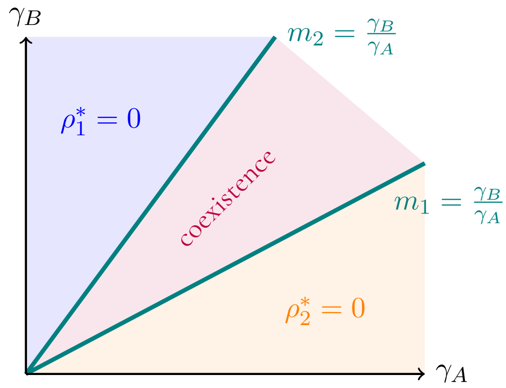
$$\begin{cases} m_1 > \gamma_B/\gamma_A \\ m_1 > m_2 \end{cases} \quad \text{or} \quad \begin{cases} m_1 < \gamma_B/\gamma_A \\ m_1 < m_2 \end{cases}$$

Therefore, putting together these results, we have:

$$m_1 < \frac{\gamma_B}{\gamma_A} < m_2 \qquad \text{when} \quad m_1 < m_2$$

$$m_2 < \frac{\gamma_B}{\gamma_A} < m_1 \qquad \text{when} \quad m_1 > m_2$$

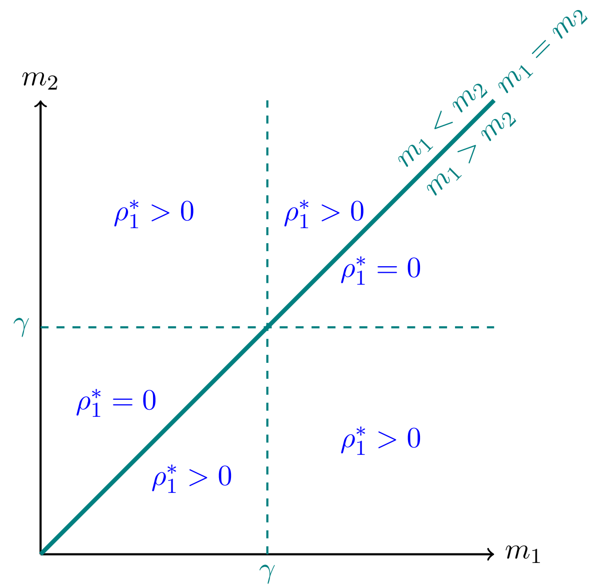
Therefore, the "ecological phase diagram" in (γ_A, γ_B) space looks like this (in the case $m_1 < m_2$):



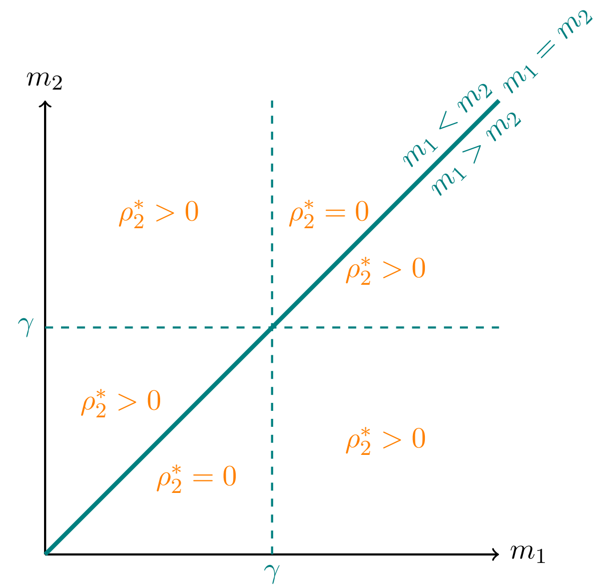
(c) *For a fixed environment parameterized by $\gamma \equiv \gamma_B/\gamma_A$ (which indicates the relative nutrient availability), plot the "physiological phase diagram" in the space (m_1, m_2) by indicating which regions of this space give coexistence, and which regions give dominance of species 1 or 2.*

Solution

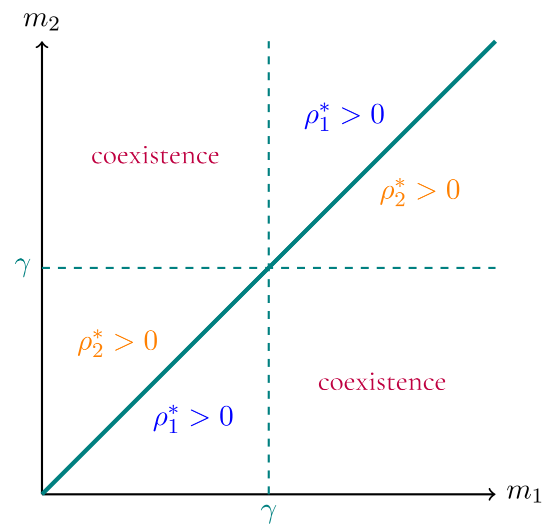
By looking at the conditions found above, in the (m_1, m_2) space we have that $\rho_1^* > 0$ and $\rho_1^* = 0$ when:



Similarly, for ρ_2^* we have:



Therefore, the "physiological phase diagram" in (m_1, m_2) space looks like this:

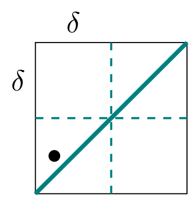


(d) *What is the 'optimal' value of m_1 that species 1 should take on to maximize its existence (i.e., survival) if it expects species 2 to take on a random value of m_2? or if it expects species 2 to take on the 'optimal' value of m_2? If the m values of both species are close to this 'optimal' value, what would be the probability that one species becomes extinct if the environmental parameter γ can take on a value within a finite range δ about a mean value, $\overline{\gamma}$ with equal probability? [Assume the environment can vary rapidly while m_i, determined by genetics, is frozen over the scale of environmental variation.] What range of m_i should each species i take on to maximize its existence in a fluctuating environment if it can coordinate with the other species which is also interested in maximizing its existence? What danger is there if the other species 'cheats'? [Note: Your response to **(d)** is not expected to be quantitative.]*

Solution
The "optimal" value that m_1 should take to maximize the survival of species 1 is γ in both cases.

Let's now consider the case m_1, $m_2 \approx \gamma$ and the environmental parameter can take value within a finite range δ around its mean value $\overline{\gamma}$. As the hint suggest, we can assume that the point (m_1, m_2) that describes the species is fixed and γ changes rapidly. In this case there are three possibilities: we either end up in one of the two "quadrants" where coexistence is possible, or we end up in one branch of the two "half-quadrants" where one of the species goes to extinction. Let's consider for example species 1: the probability that species 1 goes extinct as γ changes will be proportional to the angles occupied by the quadrant $\rho_2^* > 0$, and since each quadrant is spanned by an angle of $45°$, the probability of going extinct is $2 \cdot 2 \cdot 45/360 = 1/2$ (alternatively, we can compute this probability as the complementary of the probability of both species coexisting, i.e. $1 - 2 \cdot 90/360 = 1 - 1/2 = 1/2$).

A more formal way to see the same thing is the following. If we fix $(m_1^*, m_2^*) \approx (\gamma, \gamma)$ and then we let the environmental parameter γ vary within a range δ, we can "zoom in" the physiological phase diagram:



and the system now will be in a point (e.g., the one shown in the figure above) that can be thought of as randomly drawn in this square. Therefore, the probability that (for example) species 1 will go extinct will be equal to the ratio between the area inside that square where $\rho_1^* = 0$ and the total area of the square. Since $\rho_1^* = 0$ in two right triangles of base and height δ, the probability of extinction is:

$$\frac{2 \cdot \delta^2/2}{(2\delta)^2} = \frac{\delta^2}{4\delta^2} = \frac{1}{4}$$

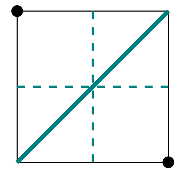
If the species want to maximize their existence in a fluctuating environment and can coordinate with each other, they should set their m_i so that the system will end up surely in one of the two "quadrants" where coexistence is possible, i.e.:

$$m_1 < \gamma < m_2 \qquad \text{or} \qquad m_2 < \gamma < m_1$$

For example, if $\gamma \in [\overline{\gamma} - \delta, \overline{\gamma} + \delta]$, they should set:

$$\begin{cases} m_1 = \overline{\gamma} + \delta \\ m_2 = \overline{\gamma} - \delta \end{cases} \qquad \text{or} \qquad \begin{cases} m_1 = \overline{\gamma} - \delta \\ m_2 = \overline{\gamma} + \delta \end{cases} \tag{12}$$

which, referring to the "zommed in" figure shown above, means putting the system in either of these two points:



Finally, if one of the two species "cheats" (i.e., it doesn't coordinate with the other as discussed above) there is the risk that either one of the two species will go extinct[1].

4. **Competition for essential nutrients**
The dependence of the growth of bacterial species i on two essential nutrients A and B is given by

$$r_i(n_A, n_B) = \left[\frac{1}{v_{iA} n_A} + \frac{1}{v_{iB} n_B}\right]^{-1} \tag{13}$$

where $v_{i\alpha}$ is the single-nutrient consumption efficiency (when the other nutrient is in saturation) and n_α is the concentration of nutrient α as in Problem #2. Unlike substitutable nutrients, the uptake of nutrient α by species i is given by $r_i \cdot \rho_i / Y_\alpha$, where ρ_i is the density of species i, and Y_α is the yield of either species for nutrient α. This leads to the following set of consumer-resource equations

$$\dot{\rho}_1 = r_1(n_A, n_B) \cdot \rho_1 - \mu \rho_1$$
$$\dot{\rho}_2 = r_2(n_A, n_B) \cdot \rho_2 - \mu \rho_2$$
$$\dot{n}_A = \mu(n_A^0 - n_A) - r_1(n_A, n_B)\frac{\rho_1}{Y_{1,A}} - r_2(n_A, n_B)\frac{\rho_2}{Y_{2,A}}$$
$$\dot{n}_B = \mu(n_B^0 - n_B) - r_1(n_A, n_B)\frac{\rho_1}{Y_{1,B}} - r_2(n_A, n_B)\frac{\rho_2}{Y_{2,B}}$$

for a chemostat-based system where μ is the dilution rate and n_α^0 is the inflow concentration of nutrient α. In this problem, you will derive the feasibility conditions for this system using Tilman's graphical approach.

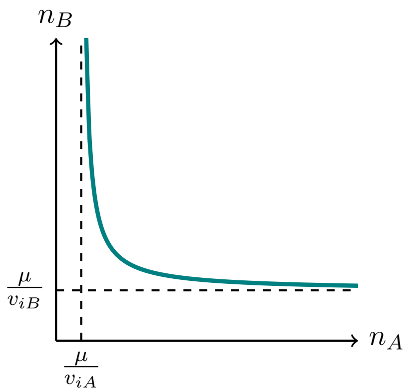
(a) *Without solving the equations algebraically, sketch the conditions for $\dot{\rho}_i = 0$ in the (n_A, n_B) plane. Indicate the location of (n_A^*, n_B^*) where both ρ_1 and ρ_2 are finite. On the plot, also mark the point (n_A^0, n_B^0) which is proportional to the nutrient inflow. Next, find an algebraic expression for n_A^*, n_B^* in terms of the environmental and physiological parameters. [Hint: You can first use the matrix inversion formula for n_α^{-1} .]*

Solution
From $\dot{\rho}_i = 0$ we have:

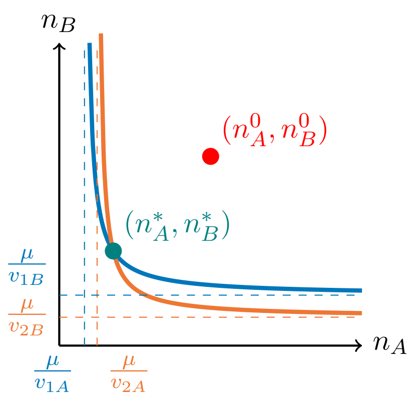
$$\frac{1}{v_{iA} n_A} + \frac{1}{v_{iB} n_B} = \frac{1}{\mu} \quad \Rightarrow \quad n_B = \frac{v_{iA}}{v_{iB}} \cdot \frac{n_A}{\frac{v_{iA} \cdot n_A}{\mu} - 1}$$

which is a hyperbola that looks like this:

[1]Notice: even the species that is cheating can go extinct: a cheater can drive itself to extinction, if it doesn't cheat in the "right" way!



Therefore, putting together the two species we will have, for example:



where we have also shown the point proportional to nutrient inflow.

In order to find the algebraic expression of n_A^* and n_B^*, we start from $\dot{\rho}_i = 0$ as above:

$$\begin{cases} \frac{1}{v_{1A}} \cdot \frac{1}{n_A^*} + \frac{1}{v_{1B}} \cdot \frac{1}{n_B^*} = \frac{1}{\mu} \\ \frac{1}{v_{2A}} \cdot \frac{1}{n_A^*} + \frac{1}{v_{2B}} \cdot \frac{1}{n_B^*} = \frac{1}{\mu} \end{cases} \quad \Rightarrow \quad \begin{pmatrix} \frac{1}{v_{1A}} & \frac{1}{v_{1B}} \\ \frac{1}{v_{2A}} & \frac{1}{v_{2B}} \end{pmatrix} \begin{pmatrix} \frac{1}{n_A^*} \\ \frac{1}{n_B^*} \end{pmatrix} = \begin{pmatrix} \frac{1}{\mu} \\ \frac{1}{\mu} \end{pmatrix}$$

If we now call M the matrix on the left and use the inversion formula, we get:

$$\begin{pmatrix} \frac{1}{n_A^*} \\ \frac{1}{n_B^*} \end{pmatrix} = \frac{1}{\det M} \begin{pmatrix} \frac{1}{v_{2B}} & -\frac{1}{v_{1B}} \\ -\frac{1}{v_{2A}} & \frac{1}{v_{1A}} \end{pmatrix} \begin{pmatrix} \frac{1}{\mu} \\ \frac{1}{\mu} \end{pmatrix}$$

where:

$$\det M = \frac{1}{v_{1A} v_{2B}} - \frac{1}{v_{1B} v_{2A}} \quad \Rightarrow \quad \frac{1}{\det M} = \frac{v_{1A} v_{1B} v_{2A} v_{2B}}{v_{1B} v_{2A} - v_{1A} v_{2B}}$$

Therefore, we get:

$$\frac{1}{n_A^*} = \frac{1}{\mu} \cdot \frac{v_{1A} v_{2A} (v_{1B} - v_{2B})}{v_{1B} v_{2A} - v_{1A} v_{2B}} \qquad \frac{1}{n_B^*} = \frac{1}{\mu} \cdot \frac{v_{1B} v_{2B} (v_{2A} - v_{1A})}{v_{1B} v_{2A} - v_{1A} v_{2B}}$$

and thus:

$$n_A^* = \mu \cdot \frac{v_{1B}v_{2A} - v_{1A}v_{2B}}{v_{1A}v_{2A}(v_{1B} - v_{2B})} \qquad\qquad n_B^* = \mu \cdot \frac{v_{1B}v_{2A} - v_{1A}v_{2B}}{v_{1B}v_{2B}(v_{2A} - v_{1A})}$$

(b) *Show the balance of nutrient fluxes at (n_A^*, n_B^*) graphically using a vector relation among the nutrient influx $\vec{J}_0$ and the consumption fluxes $\vec{J}_1$, $\vec{J}_2$, as done in class. Describe the condition for coexistence graphically, and write down the corresponding algebraic expression involving the constraint on n_A^0, n_B^0.*

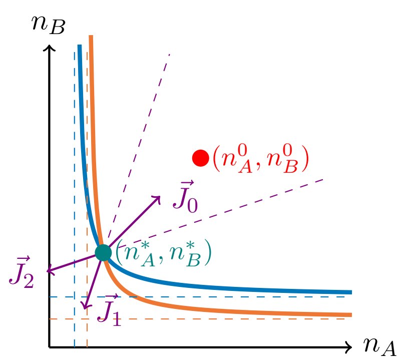
Solution

We can rewrite the equations for $\dot{n}_A$ and $\dot{n}_B$ as follows:

$$\begin{cases} \dot{n}_A = \mu(n_A^0 - n_A) - r_1(n_A, n_B)\frac{\rho_1}{Y_{1,A}} - r_2(n_A, n_B)\frac{\rho_2}{Y_{2,A}} \\ \dot{n}_B = \mu(n_B^0 - n_B) - r_1(n_A, n_B)\frac{\rho_1}{Y_{1,B}} - r_2(n_A, n_B)\frac{\rho_2}{Y_{2,B}} \end{cases} \qquad \Rightarrow$$

$$\Rightarrow \quad \begin{pmatrix} \dot{n}_A \\ \dot{n}_B \end{pmatrix} = \mu \underbrace{\begin{pmatrix} n_A^0 - n_A \\ n_B^0 - n_B \end{pmatrix}}_{:=\vec{J}_0} - \rho_1 \underbrace{\begin{pmatrix} r_1/Y_{1,A} \\ r_1/Y_{1,B} \end{pmatrix}}_{:=\vec{J}_1} - \rho_2 \underbrace{\begin{pmatrix} r_2/Y_{2,A} \\ r_2/Y_{2,B} \end{pmatrix}}_{:=\vec{J}_2}$$

Therefore, the consumption fluxes $\vec{J}_1$ and $\vec{J}_2$ point in directions with slopes $Y_{1,B}/Y_{1,A}$ and $Y_{2,B}/Y_{2,A}$, respectively. If we use $(n_A, n_B) = (n_A^*, n_B^*)$, the system looks like this:



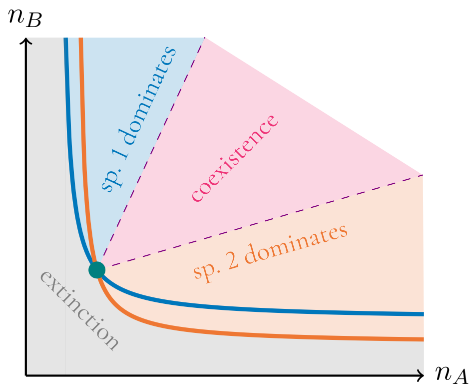
Where we have also highlighted the directions along which $\vec{J}_1$ and $\vec{J}_2$ lie, i.e. the lines passing through (n_A^*, n_B^*) and with slopes $Y_{1,B}/Y_{1,A}$ and $Y_{2,B}/Y_{2,A}$. Coexistence will be possible if the slope of $\vec{J}_0$, i.e. $(n_B^0 - n_B^*)/(n_A^0 - n_A^*)$, lies between the slopes of these two lines:

$$\frac{Y_{2,B}}{Y_{2,A}} < \frac{n_B^0 - n_B^*}{n_A^0 - n_A^*} < \frac{Y_{1,B}}{Y_{1,A}}$$

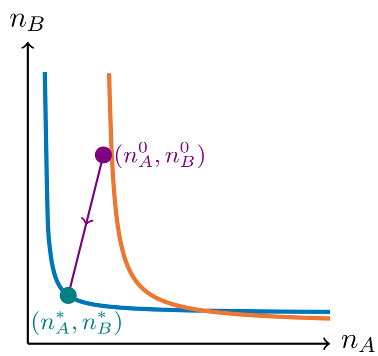
(c) *Show graphically what happens if (n_A^0, n_B^0) lies outside of the constraint, and write down the algebraic expression for the steady-state concentrations n_A^*, n_B^* and densities ρ_1^*, ρ_2^* corresponding to the two types of outcomes that would arise.*

Solution

Referring to the figure above, if (n_A^0, n_B^0) lies outside of the coexistence region we can have either one or both species going to extinction. In particular, if (n_A^0, n_B^0) lies between the blue hyperbola and the direction of $\vec{J}_1$ species 1 will dominate, and conversely species 2 will outcompete species 1 if (n_A^0, n_B^0); finally, if (n_A^0, n_B^0) lies below the two hyperbolas, both species will go to extinction:



Let's assume for example that (n_A^0, n_B^0) lies in the area where species 1 dominates (the case for species 2 is symmetrical). The point will follow $\vec{J}_1$ and thus move along the line passing through (n_A^0, n_B^0) with the same slope as $\vec{J}_1$. At the steady state, (n_A^*, n_B^*) will lie on the intersection between this line and the nullcline $\dot{\rho}_1 = 0$:



Therefore, can find n_A^*, n_B^* by finding the intersection of these two curves. The nullcline $\dot{\rho}_1 = 0$ is:

$$\frac{1}{v_{1A} n_A} + \frac{1}{v_{1B} n_B} = \mu$$

On the other hand, the line along which the system moves is:

$$n_B = q + m \cdot n_A$$

where $m = Y_{1,B}/Y_{1,A}$ (the slope of $\vec{J}_1$) and q can be found from the fact that the line passes through (n_A^0, n_B^0):

$$n_B^0 = q + \frac{Y_{1,B}}{Y_{1,A}} n_A^0 \quad \Rightarrow \quad q = n_B^0 - \frac{Y_{1,B}}{Y_{1,A}} n_A^0$$

Therefore, the point (n_A^*, n_B^*) can be found by solving:

$$\frac{1}{v_{1A} n_A^*} + \frac{1}{v_{1B} n_B^*} = \mu \qquad\qquad n_B^* = q + m \cdot n_A^*$$

This can be done, for example, by taking the reciprocal of the equation of the line:

$$\frac{1}{n_B^*} = \frac{1}{1 + m n_A^*}$$

and substituting in the equation of the nullcline:

$$\frac{1}{v_{1A} n_A^*} + \frac{1}{v_{1B}(1 + m n_A^*)} = \mu \;\Rightarrow\; \mu = \frac{v_{1B}(1 + m n_A^*) + v_{1A} n_A^*}{v_{1A} v_{1B} n_A^* (q + m n_A^*)} \;\Rightarrow$$

$$\Rightarrow\; \mu v_{1A} v_{1B} m \cdot (n_A^*)^2 + (\mu v_{1A} v_{1B} q - v_{1B} m - v_{1A}) n_A^* - v_{1B} q = 0 \;\Rightarrow$$

$$\Rightarrow\; n_A^* = \frac{1}{2\mu m v_{1A} v_{1B}} \left(v_{1B} m + v_{1A} - \mu q v_{1A} v_{1B} + \sqrt{(\mu q v_{1A} v_{1B} - v_{1B} m - v_{1A})^2 + 4 \mu m q v_{1A} v_{1B}^2} \right)$$

(which is the only acceptable solution, since the other one is negative). Substituting in the equation for the straight line we get $n_B^* = q + m \cdot n_A^*$.
Finally, from the equation for $\dot{\rho}_1$ at steady state we get:

$$\rho_1(r_1(n_A^*, n_B^*) - \mu) = 0 \qquad \Rightarrow \qquad r_1(n_A^*, n_B^*) = \mu \tag{14}$$

and therefore, from the equation for $\dot{n}_A$:

$$\mu(n_A^0 - n_A^*) - r_1(n_A^*, n_B^*) \frac{\rho_1^*}{Y_{1,A}} \qquad \Rightarrow \qquad \rho_1^* = Y_{1,A}(n_A^0 - n_A^*)$$

as stated above, the case where species 2 dominates is symmetrical, so:

$$n_A^* = \frac{1}{2\mu m v_{2A} v_{2B}} \left(v_{2B} m + v_{2A} - \mu q v_{2A} v_{2B} + \sqrt{(\mu q v_{2A} v_{2B} - v_{2B} m - v_{2A})^2 + 4 \mu m q v_{2A} v_{2B}^2} \right)$$

$$\text{where:} \qquad m = \frac{Y_{2,B}}{Y_{2,A}} \qquad q = n_B^0 - \frac{Y_{2,B}}{Y_{2,A}} n_A^0$$

and furthermore:

$$\rho_2^* = Y_{2,A}(n_A^0 - n_A^*)$$

(d) *Describe and explain the difference of the behavior obtained here compared to the ones obtained in class for two substitutable nutrients.*

Solution
In the case of substitutable resources, if we inflow of either of the two resources is very large, one of the two species will dominate (according to their preferences). This happens because the nullclines intersect the axes and therefore the area in the (n_A, n_B) space where both species go to extinction is finite. Here, however, this

is not true for essential resources: since the nullclines are now hyperbolas with non-trivial asymptotes (i.e., the asymptotes are not the axes, see also the representation of the system in point **(a)**) the area where extinction is possible extends to infinity. This means that even if we put a very large amount of one resource, let's say resource A for example, it is not guaranteed that species 2 will dominate (if we refer to the phase diagrams plotted above). In fact, since both resources are essential species 2 also needs a minimum supply of resource 1 to grow. If this supply is not provided, species 2 will not be able to dominate the system even though resource A is very abundant.