

PHYS 239
Spatiotemporal Dynamics in Biological Systems
Winter 2022

Solution of Homework #4

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1. Coexistence of 3 species on two nutrients

Consider the following Consumer-Resource model for 3 species (of densities ρ_i , $i \in \{1, 2, 3\}$) and 2 substitutable nutrients (of concentrations n_α , $\alpha \in \{A, B\}$).

$$\dot{\rho}_i = (v_{iA}n_A + v_{iB}n_B) \cdot \rho_i - \mu \cdot \rho_i$$

$$\dot{n}_\alpha = \mu \cdot (n_\alpha^0 - n_\alpha) - (v_{1\alpha}\rho_1 + v_{2\alpha}\rho_2 + v_{3\alpha}\rho_3) \cdot n_\alpha / Y_\alpha$$

Previously, we worked out that if there are two species with nutrient A preferred by species 1 and nutrient B preferred by species 2 (i.e., if $v_{1A} > v_{2A}$ and $v_{2B} > v_{1B}$), then coexistence of species 1 and 2 are expected for some range of the nutrient influx specified by (n_A^0, n_B^0) . In this problem, you are asked to work out what happens when a 3rd species is introduced. For simplicity, let this species have intermediate nutrient preference, i.e., $v_{1A} > v_{3A} > v_{2A}$ and $v_{2B} > v_{3B} > v_{1B}$, so that A is still most rapidly taken up by species 1 and B is by species 2.

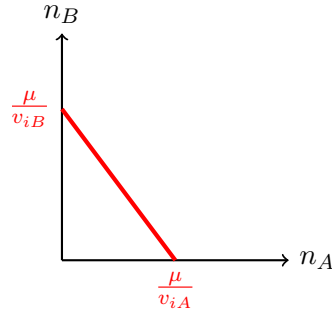
- (a) By setting $\frac{d}{dt}\rho_i = 0$ and demanding the steady state density $\rho_i^* > 0$ for all 3 species, obtain three conditions on the steady-state nutrient concentrations (n_A^*, n_B^*) . Sketch these three conditions in the (n_A, n_B) plane and show that there is generically no way to satisfy all three conditions simultaneously for arbitrary values of the nutrient uptake coefficients $v_{i\alpha}$. Consequently, one of the density must be at zero in steady state.

Solution

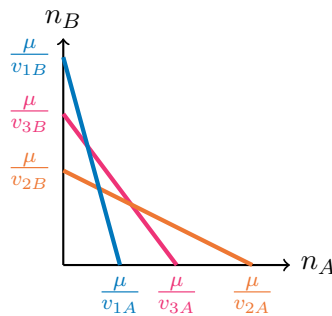
If we set $\frac{d}{dt}\rho_i = 0$, assuming $\rho_i^* \neq 0$ we get:

$$\mu = v_{iA}n_A + v_{iB}n_B$$

which is an equation for a line:



In order for the three species to coexist, we need three lines like this to intersect in one point. However, if the uptake coefficients $v_{i\alpha}$ have arbitrary values this never happens:



The intersections of these lines are three alternative steady states where only two species coexist.

- (b) Write down the three conditions if the nutrient uptake coefficients are of the special form motivated in class, $v_{i\alpha} = v_{\alpha}^0 \cdot \eta_{i\alpha}$, where $\eta_{i\alpha}$ describes the allocation of uptake enzymes for nutrient α by species i with $\eta_{iA} + \eta_{iB} = 1$ for each i . [Convince yourself that the nutrient preferences $v_{1A} > v_{3A} > v_{2A}$ and $v_{2B} > v_{3B} > v_{1B}$ implies that $\eta_{1A} > \eta_{3A} > \eta_{2A}$.] Show that there is a special pair of nutrient conditions (n_A^*, n_B^*) for which all three conditions are satisfied, hence all 3 species can coexist. Plot the three conditions in the (n_A, n_B) plane and show for yourself geometrically how this becomes possible. Show that if a 4th species is introduced with $v_{4\alpha} = v_{\alpha}^0 \eta_{4\alpha}$ and $\eta_{4A} + \eta_{4B} = 1$, the same solution (n_A^*, n_B^*) still holds (and hence the 4th species can also coexist).

Solution

If $v_{i\alpha} = v_{\alpha}^0 \cdot \eta_{i\alpha}$, then the three conditions become:

$$\mu = v_A^0 \eta_{iA} n_A^* + v_B^0 \eta_{iB} n_B^* \quad i \in \{1, 2, 3\}$$

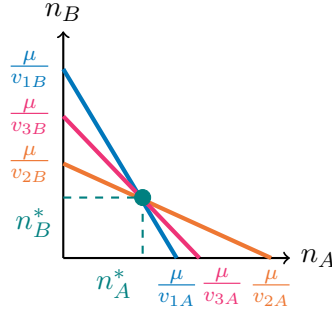
Since $\eta_{iA} + \eta_{iB} = 1$, these three equations can be solved if:

$$n_A^* = \frac{\mu}{v_A^0} \quad n_B^* = \frac{\mu}{v_B^0}$$

In fact, if we use these expressions in the above expression we get:

$$v_A^0 \eta_{iA} n_A^* + v_B^0 \eta_{iB} n_B^* = v_A^0 \eta_{iA} \frac{\mu}{v_A^0} + v_B^0 \eta_{iB} \frac{\mu}{v_B^0} = \mu(\eta_{iA} + \eta_{iB}) = \mu$$

which therefore solves the equation. Therefore, this time the three lines plotted above *do* intersect in a single point. Since $v_{1A} > v_{3A} > v_{2A}$ and $v_{2B} > v_{3B} > v_{1B}$, the situation is the following:



If we introduce a 4th species, the equations we have to solve now are:

$$\begin{cases} \mu = v_A^0 \eta_{1A} n_A^* + v_B^0 \eta_{1B} n_B^* \\ \mu = v_A^0 \eta_{2A} n_A^* + v_B^0 \eta_{2B} n_B^* \\ \mu = v_A^0 \eta_{3A} n_A^* + v_B^0 \eta_{3B} n_B^* \\ \mu = v_A^0 \eta_{4A} n_A^* + v_B^0 \eta_{4B} n_B^* \end{cases}$$

However, similarly to what was shown above, thanks to the fact that $\eta_{iA} + \eta_{iB} = 1$ this system still has $(n_A^*, n_B^*) = (\mu/v_A^0, \mu/v_B^0)$ as a solution¹. Therefore, the 4th species will coexist with the other three. Graphically speaking, there will be an additional line in the plot above that passes through the same (n_A^*, n_B^*) point.

- (c) From here on, we also take the slow dilution limit, $\mu \ll v_\alpha^0 n_\alpha^0$, to focus on inter-species competition. Let fractional species abundance be $\psi_i \equiv \rho_i^*/(\rho_1^* + \rho_2^* + \rho_3^*)$ and let the fraction of nutrient influx be $f_\alpha \equiv n_\alpha^0 Y_\alpha / (n_A^0 Y_A + n_B^0 Y_B)$. Show that in steady state, the abundances satisfy the condition

$$f_A = \eta_{1A} \psi_1 + \eta_{2A} \psi_2 + \eta_{3A} \psi_3$$

Plot the above condition as a plane in the space (ψ_1, ψ_2, ψ_3) for $f_A = 0.5$ and $(\eta_{1A}, \eta_{2A}, \eta_{3A}) = (0.75, 0.25, 0.5)$. Plot in the same space also the condition $\psi_1 + \psi_2 + \psi_3 = 1$ which follows from the definition of fractional abundance. Show that the two planes intersect to form a line with $\psi_1 > 0$. This line describes the possible abundance range for the coexisting species. Find the range of ψ_1 where all 3 species are present, and plot ψ_2, ψ_3 vs ψ_1 within this range. Comment on the degeneracy of the solutions.

Solution

Let's take the equation for nutrient α at steady state:

$$\dot{n}_\alpha = 0 \quad \Rightarrow \quad \mu(n_\alpha^0 - n_\alpha^*) = \frac{n_\alpha^*}{Y_\alpha} v_\alpha^0 (\eta_{1\alpha} \rho_1^* + \eta_{2\alpha} \rho_2^* + \eta_{3\alpha} \rho_3^*)$$

If we substitute $n_\alpha^* = \mu/v_\alpha^0$ we get:

$$\mu n_\alpha^0 - \frac{\mu^2}{v_\alpha^0} = \frac{\mu}{v_\alpha^0 Y_\alpha} v_\alpha^0 (\eta_{1\alpha} \rho_1^* + \eta_{2\alpha} \rho_2^* + \eta_{3\alpha} \rho_3^*) \quad \Rightarrow \quad n_\alpha^0 Y_\alpha = (\eta_{1\alpha} \rho_1^* + \eta_{2\alpha} \rho_2^* + \eta_{3\alpha} \rho_3^*) \quad (1)$$

¹Notice that when we plugged n_A^* and n_B^* in the computation shown above, the result is true for *any* species i . Therefore, as long as $\eta_{iA} + \eta_{iB} = 1$ for *all* species, we can add as many species as we want and they will *all* coexist.

where we have also neglected the term proportional to μ^2 , since we are in the slow dilution limit. If we now substitute $\psi_i = \rho_i^*/(\rho_1^* + \rho_2^* + \rho_3^*)$, we get:

$$n_\alpha^0 Y_\alpha = (\eta_{1\alpha}\psi_1 + \eta_{2\alpha}\psi_2 + \eta_{3\alpha}\psi_3) \cdot (\rho_1^* + \rho_2^* + \rho_3^*) \quad (2)$$

From Eq (1) we can determine the value of $\rho_1^* + \rho_2^* + \rho_3^*$:

$$\begin{cases} n_A^0 Y_A = \eta_{1A}\rho_1^* + \eta_{2A}\rho_2^* + \eta_{3A}\rho_3^* \\ n_B^0 Y_B = \eta_{1B}\rho_1^* + \eta_{2B}\rho_2^* + \eta_{3B}\rho_3^* \end{cases} \Rightarrow \text{we sum the equations} \Rightarrow$$

$$\Rightarrow n_A^0 Y_A + n_B^0 Y_B = \underbrace{(\eta_{1A} + \eta_{1B})}_{=1} \rho_1^* + \underbrace{(\eta_{2A} + \eta_{2B})}_{=1} \rho_2^* + \underbrace{(\eta_{3A} + \eta_{3B})}_{=1} \rho_3^* \Rightarrow$$

$$\Rightarrow \rho_1^* + \rho_2^* + \rho_3^* = n_A^0 Y_A + n_B^0 Y_B$$

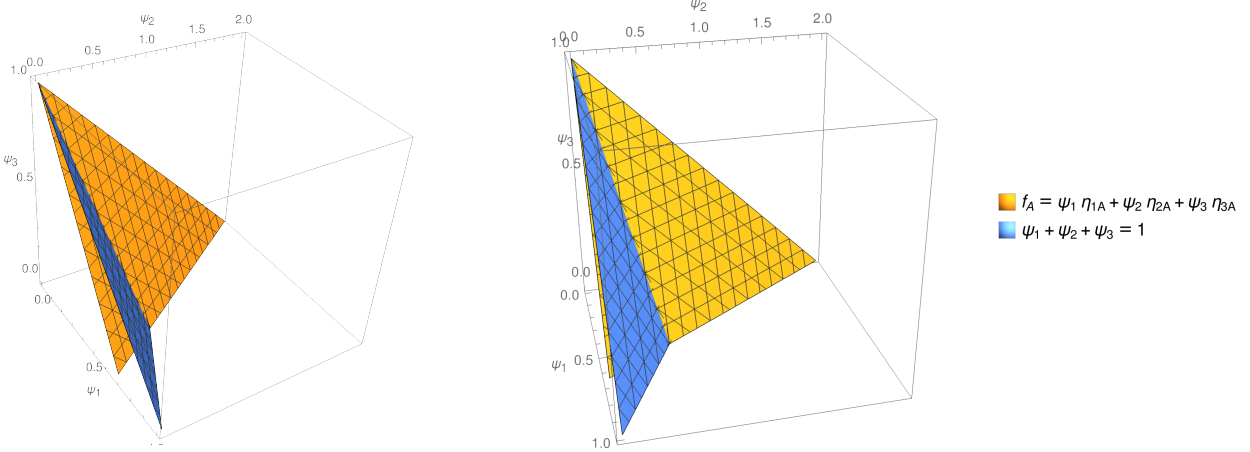
Therefore, using this in Eq. (2):

$$\frac{n_\alpha^0 Y_\alpha}{n_A^0 Y_A + n_B^0 Y_B} = f_\alpha = \eta_{1\alpha}\psi_1 + \eta_{2\alpha}\psi_2 + \eta_{3\alpha}\psi_3$$

In particular, for resource A we have:

$$f_A = \eta_{1A}\psi_1 + \eta_{2A}\psi_2 + \eta_{3A}\psi_3$$

The plot of the plane and the condition $\psi_1 + \psi_2 + \psi_3 = 1$ is the following:



We can see from the plots that the line where the two surfaces intersect lies in the part of the space where $\psi_1 \geq 0$. In order to find the range of ψ_1 where all species coexist and in order to plot ψ_2 and ψ_3 vs ψ_1 , it is convenient to write the parametric equation of the line (i.e., the intersection of the two planes). In order to do this, we can treat ψ_1 as a “free parameter”² and solve:

$$\begin{cases} f_A = \eta_{1A}\psi_1 + \eta_{2A}\psi_2 + \eta_{3A}\psi_3 \\ \psi_1 + \psi_2 + \psi_3 = 1 \end{cases}$$

²This is the general strategy to find the parametric equation of a line in three dimensions: you treat one of the variables as a parameter and solve the equations of the intersecting planes.

(which is now a system of two equations in two unknowns, since we are treating ψ_1 as a parameter). We obtain:

$$\psi_2 = \frac{f_A - \eta_{3A} + (\eta_{3A} - \eta_{1A})\psi_1}{\eta_{2A} - \eta_{3A}} \quad \psi_3 = \frac{-(f_A - \eta_{2A}) + (\eta_{1A} - \eta_{2A})\psi_1}{\eta_{2A} - \eta_{3A}}$$

If we plug in the numbers provided in the text, we get:

$$\psi_2 = \psi_1 \quad \psi_3 = 1 - 2\psi_1$$

Therefore, the range of ψ_1 where all three species are present will be given by:

$$\begin{cases} \psi_2 > 0 \\ \psi_3 > 0 \end{cases} \Rightarrow \begin{cases} \psi_1 > 0 \\ \psi_1 < \frac{1}{2} \end{cases}$$

Therefore, the range of ψ_1 where all species coexist is³ $0 < \psi_1 < 1/2$. The plots of ψ_2 and ψ_3 vs ψ_1 will therefore be:



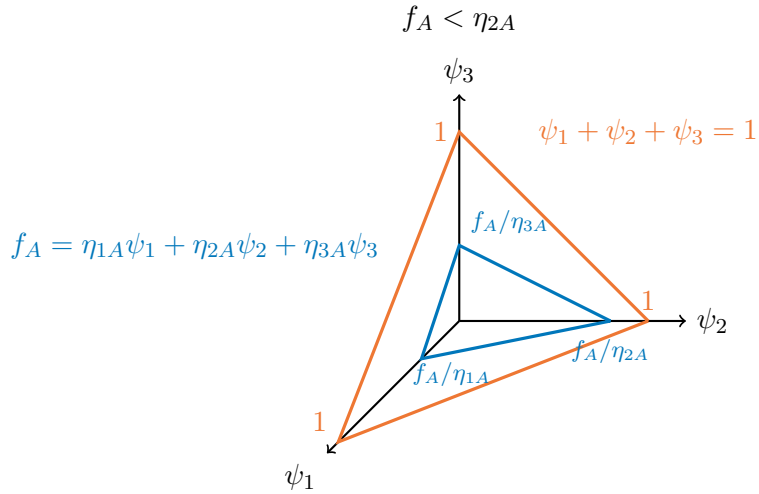
In this case we have a continuous space of possible steady-state points (the line given by the intersection of the planes as shown above). In other words, there are infinitely many possible steady states, each one with different fractional species abundances (ψ_1, ψ_2, ψ_3).

- (d) Show that the 3 species can coexist as long as $\eta_{2A} < f_A < \eta_{3A}$ (for η_{3A} also falling in between η_{1A} and η_{2A}). For $(\eta_{1A}, \eta_{2A}, \eta_{3A}) = (0.75, 0.25, 0.5)$, plot the ecological landscape, e.g., for each value of f_A , the range of ψ_1 where all 3 species can coexist. [This should be as an area in the (f_A, ψ_1) space.]

Solution

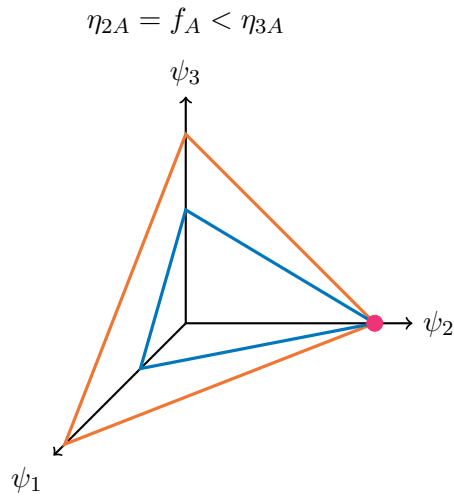
We can show that the three species coexist when $\eta_{2A} < f_A < \eta_{3A}$ by plotting the two planes for different values of f_A . For example, when $f_A < \eta_{2A}$ we have:

³Notice that this is also a mathematical way to show that the line where the two planes intersect has $\psi_1 > 0$



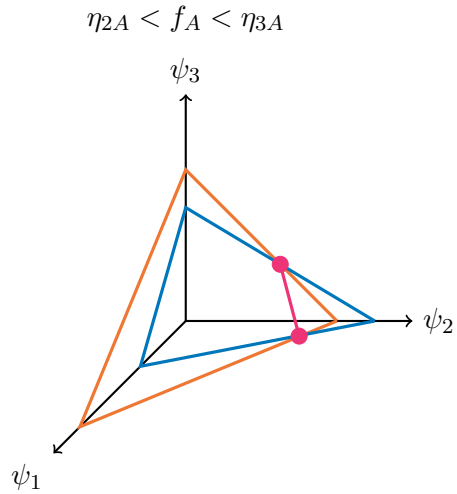
where we have taken into account that, since $\eta_{1A} > \eta_{3A} > \eta_{2A}$, we have $\frac{f_A}{\eta_{2A}} > \frac{f_A}{\eta_{3A}} > \frac{f_A}{\eta_{1A}}$. Therefore, since the two planes *don't* intersect in this case, the three species will not be able to coexist.

When $\eta_{2A} = f_A < \eta_{3A}$ we have:



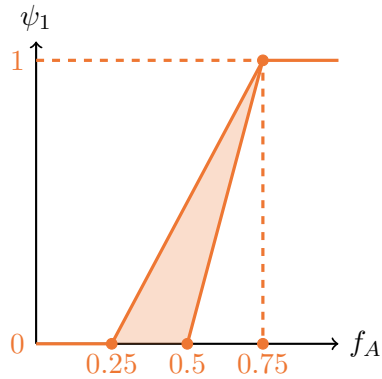
Since now $f_A/\eta_{2A} = 1$, the two planes intersect in one point where all three species coexist.

If we now consider $\eta_{2A} < f_A < \eta_{3A}$:



Now $f_A/\eta_{2A} > 1$ and the two planes intersect in a line. Therefore, the three species can coexist.

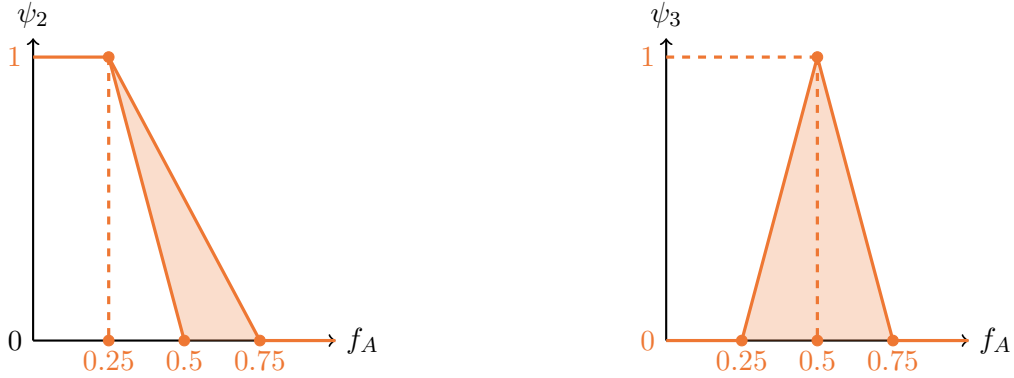
If we now use $(\eta_{1A}, \eta_{2A}, \eta_{3A}) = (0.75, 0.25, 0.5)$, the ecological landscape is:



- (e) Repeat the above plot in the space of (f_A, ψ_3) . For what environmental parameter (f_A) can you expect the abundance of the “intermediate species” (species 3 in this case) be maximal? What happens to the other two species in this case? Contrast this with the dominance conditions for the two “key-stone species” (species 1 and 2). [It may be useful to repeat the plots of part (c) for f_A at selected special values.]

Solution

The plots for ψ_2 and ψ_3 are:



Therefore, the value of f_A for which ψ_3 is maximal is $f_A = 0.5 = \eta_{3A}$. From the three ecological plots we see that each species' population is maximized when $f_A = \eta_{iA}$: the population of a species is maximized when the nutrient influx matches the species' uptake.

Finally, when ψ_3 is maximized (i.e., $f_A = \eta_{3A} = 0.5$), as we can see from the ecological phase diagram we can have $\psi_3 = 1$ but it is not the only choice (the whole line that goes from $\psi_3 = 0$ to $\psi_3 = 1$ at $f_A = 0.5$ is part of the phase diagram). On the other hand, when either ψ_1 or ψ_2 is maximized, the only possibilities are $\psi_1 = 1$ and $\psi_2 = 1$, respectively. In other words, when f_A is such that either of the two "keystone species" is maximized (i.e., $f_A = \eta_{1A}$ or $f_A = \eta_{2A}$) the other two are extinct, but when $f_A = \eta_{3A}$ we can still have all three species coexisting.

2. Ecological phase diagram for 3 nutrients

Consider the Consumer-Resource model for 3 species (of densities ρ_1, ρ_2, ρ_3) and 3 substitutable nutrients (of concentrations n_A, n_B, n_C):

$$\begin{aligned}\dot{\rho}_i &= (v_{iA}n_A + v_{iB}n_B + v_{iC}n_C) \cdot \rho_i - \mu \cdot \rho_i \\ \dot{n}_\alpha &= \mu \cdot (n_\alpha^0 - n_\alpha) - (v_{1\alpha}\rho_1 + v_{2\alpha}\rho_2 + v_{3\alpha}\rho_3) \cdot n_\alpha / Y_\alpha\end{aligned}$$

Let the nutrient uptake coefficients be of the special form $v_{i\alpha} = v_\alpha^0 \cdot \eta_{i\alpha}$ where $\sum_\alpha \eta_{i\alpha} = 1$. Let us also take the slow dilution limit, $\mu \ll v_\alpha^0 n_\alpha^0$, to focus on inter-species competition.

- (a) Write down the conditions on ρ_i obtained from the steady-state conditions $\dot{n}_\alpha = 0$. Add up these equations to recover the constraint on mass conservation. Express these 3 conditions in terms of the fractional species abundance $\psi_i \equiv \rho_i / \sum_j \rho_j$, and the fractional nutrient influx, $f_\alpha \equiv n_\alpha^0 Y_\alpha / \sum_\beta n_\beta^0 Y_\beta$.

Solution

From $\dot{n}_\alpha = 0$ we get:

$$\mu n_\alpha^0 - \mu n_\alpha^* = \frac{n_\alpha^*}{Y_\alpha} (v_{1\alpha}\rho_1^* + v_{2\alpha}\rho_2^* + v_{3\alpha}\rho_3^*)$$

Similarly to what has been done above, we can substitute $n_\alpha^* = \mu / v_\alpha^0$ (which is still a solution for the system) and neglect the quadratic term in μ to obtain:

$$n_\alpha^0 Y_\alpha = \eta_{1\alpha}\rho_1^* + \eta_{2\alpha}\rho_2^* + \eta_{3\alpha}\rho_3^*$$

If we sum these three expressions for $\alpha = A, B, C$ and use $\eta_{iA} + \eta_{iB} + \eta_{iC} = 1$, we get:

$$\rho_1^* + \rho_2^* + \rho_3^* = n_A^0 Y_A + n_B^0 Y_B + n_C^0 Y_C$$

If we now substitute ψ_i in the above equation and use the constraint on mass conservation, we get:

$$n_\alpha^0 Y_\alpha = (\eta_{1\alpha}\psi_1 + \eta_{2\alpha}\psi_2 + \eta_{3\alpha}\psi_3) \cdot (\rho_1^* + \rho_2^* + \rho_3^*)$$

and therefore:

$$\frac{n_\alpha^0 Y_\alpha}{n_A^0 Y_A + n_B^0 Y_B + n_C^0 Y_C} = f_\alpha = \eta_{1\alpha}\psi_1 + \eta_{2\alpha}\psi_2 + \eta_{3\alpha}\psi_3$$

- (b) Use $\psi_3 = 1 - \psi_1 - \psi_2$ to reduce the 3 equations in (a) to two equations for ψ_1 and ψ_2 . Solve the two linear equations to obtain expressions for ψ_1 and ψ_2 . From the conditions $\psi_1 \geq 0$ and $\psi_2 \geq 0$, obtain two constraints involving $f_\alpha - \eta_{3\alpha}$ and $\eta_{i\alpha} - \eta_{3\alpha}$.

Solution

The three equations are:

$$f_A = \eta_{1A}\psi_1 + \eta_{2A}\psi_2 + \eta_{3A}\psi_3$$

$$f_B = \eta_{1B}\psi_1 + \eta_{2B}\psi_2 + \eta_{3B}\psi_3$$

$$f_C = \eta_{1C}\psi_1 + \eta_{2C}\psi_2 + \eta_{3C}\psi_3$$

We can for example substitute $\psi_3 = 1 - \psi_1 - \psi_2$ in the first two equations to get:

$$(\eta_{1A} - \eta_{3A})\psi_1 + (\eta_{2A} - \eta_{3A})\psi_2 = f_A - \eta_{3A}$$

$$(\eta_{1B} - \eta_{3B})\psi_1 + (\eta_{2B} - \eta_{3B})\psi_2 = f_B - \eta_{3B}$$

Which can also be written in matrix form:

$$\underbrace{\begin{pmatrix} \eta_{1A} - \eta_{3A} & \eta_{2A} - \eta_{3A} \\ \eta_{1B} - \eta_{3B} & \eta_{2B} - \eta_{3B} \end{pmatrix}}_{:=M} \begin{pmatrix} \psi_1 \\ \psi_2 \end{pmatrix} = \begin{pmatrix} f_A - \eta_{3A} \\ f_B - \eta_{3B} \end{pmatrix}$$

The solution of this equation is given by:

$$\begin{pmatrix} \psi_1 \\ \psi_2 \end{pmatrix} = \frac{1}{\det M} \begin{pmatrix} (\eta_{2B} - \eta_{3B})(f_A - \eta_{3A}) - (\eta_{2A} - \eta_{3A})(f_B - \eta_{3B}) \\ -(\eta_{1B} - \eta_{3B})(f_A - \eta_{3A}) + (\eta_{1A} - \eta_{3A})(f_B - \eta_{3B}) \end{pmatrix}$$

If we now assume⁴ $\det M > 0$, from $\psi_1 \geq 0$ we get:

$$(\eta_{2B} - \eta_{3B})(f_A - \eta_{3A}) \geq (\eta_{2A} - \eta_{3A})(f_B - \eta_{3B}) \quad \Rightarrow \quad \frac{f_B - \eta_{3B}}{f_A - \eta_{3A}} \leq \frac{\eta_{2B} - \eta_{3B}}{\eta_{2A} - \eta_{3A}}$$

On the other hand, $\psi_2 \geq 0$ yields:

$$(\eta_{1A} - \eta_{3A})(f_B - \eta_{3B}) \geq (\eta_{1B} - \eta_{3B})(f_A - \eta_{3A}) \quad \Rightarrow \quad \frac{f_B - \eta_{3B}}{f_A - \eta_{3A}} \geq \frac{\eta_{1B} - \eta_{3B}}{\eta_{1A} - \eta_{3A}}$$

⁴This corresponds to assuming that:

$$\frac{\eta_{1A} - \eta_{3A}}{\eta_{2A} - \eta_{3A}} > \frac{\eta_{1B} - \eta_{3B}}{\eta_{2B} - \eta_{3B}}$$

As shown below, this assumption has some consequences in part (d).

(c) Apply the condition $\psi_1 + \psi_2 \leq 1$ (from $\psi_3 \geq 0$) to obtain a 3rd constraint on the parameters.

Solution

If we set $\psi_1 + \psi_2 \leq 1$, we get:

$$\begin{aligned}
 (\eta_{2B} - \eta_{3B})(f_A - \eta_{3A}) - (\eta_{2A} - \eta_{3A})(f_B - \eta_{3B}) - (\eta_{1B} - \eta_{3B})(f_A - \eta_{3A}) + (\eta_{1A} - \eta_{3A})(f_B - \eta_{3B}) &\leq \det M = \\
 &= (\eta_{1A} - \eta_{3A})(\eta_{2B} - \eta_{3B}) - (\eta_{1B} - \eta_{3B})(\eta_{2A} - \eta_{3A})
 \end{aligned}$$

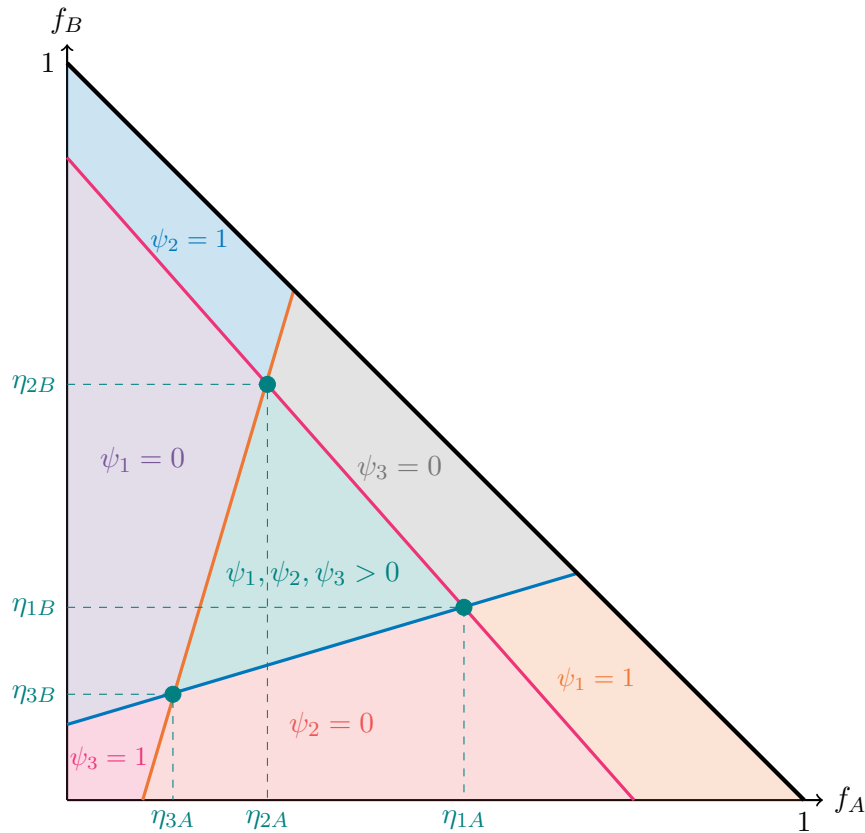
which can be simplified to:

$$\frac{f_B - \eta_{1B}}{f_A - \eta_{1A}} \leq \frac{\eta_{2B} - \eta_{1B}}{\eta_{2A} - \eta_{1A}}$$

(d) Show the constraints obtained in (b) and (c) have a simple geometric representation in the (f_A, f_B) space. [Hint: The 3 points (η_{iA}, η_{iB}) form a triangle. Take (η_{3A}, η_{3B}) as the origin and plot the 3 lines of the 3 constraints from above.] For each of the 7 regions partitioned by the lines, indicate the phase of the region, e.g., $\psi_1 = 0, \psi_2 > 0, \psi_3 > 0$.

Solution

The constraints obtained in (b) and (c) can all be represented as lines in the (f_A, f_B) space. The representation of the constraints is the following:



Notice that this plot is in agreement with the assumption

$$\det M > 0 \quad \Rightarrow \quad \frac{\eta_{1A} - \eta_{3A}}{\eta_{2A} - \eta_{3A}} > \frac{\eta_{1B} - \eta_{3B}}{\eta_{2B} - \eta_{3B}}$$

that we have introduced before. In fact, this assumption can be rewritten as:

$$\frac{\eta_{1B} - \eta_{3B}}{\eta_{1A} - \eta_{3A}} < \frac{\eta_{2B} - \eta_{3B}}{\eta_{2A} - \eta_{3A}}$$

which means that the slope of the blue line in the plot above is smaller than the slope of the orange line.

- (e) For the more mathematically oriented: Add a 4th species, characterized by $v_{4\alpha} = v_{\alpha}^0 \cdot \eta_{4\alpha}$, to the community with 3 nutrients. Show that $\dot{\rho}_i/\rho_i = 0$ still holds with $\rho_i > 0$ for $i \in \{1, 2, 3, 4\}$. Repeat the analysis in (a) through (c) to obtain modified conditions on ψ_1 and ψ_2 . Explain that if the representation of $\eta_{4\alpha}$ in the (f_A, f_B) space is a point located in the interior of the triangle defined by the 3 vertices (η_{1A}, η_{1B}) , (η_{2A}, η_{2B}) , (η_{3A}, η_{3B}) , then feasibility conditions for coexistence obtained above are unchanged with $\psi_4 > 0$.

Solution

For $i \in \{1, 2, 3, 4\}$ we can write:

$$\frac{\dot{\rho}_i}{\rho_i} = v_{iA}n_A + v_{iB}n_B + v_{iC}n_C - \mu$$

and therefore at steady state we have:

$$\frac{\dot{\rho}_i}{\rho_i^*} = v_{iA}n_A^* + v_{iB}n_B^* + v_{iC}n_C^* - \mu$$

if we substitute $n_{\alpha}^* = \mu/v_{\alpha}^0$ and $v_{i\alpha} = v_{\alpha}^0\eta_{i\alpha}$:

$$\frac{\dot{\rho}_i}{\rho_i^*} = v_A^0\eta_{iA}\frac{\mu}{v_A^0} + v_B^0\eta_{iB}\frac{\mu}{v_B^0} + v_C^0\eta_{iC}\frac{\mu}{v_C^0} - \mu = \mu(\eta_{iA} + \eta_{iB} + \eta_{iC} - 1) = 0 \quad (3)$$

Furthermore, from $\dot{n}_{\alpha} = 0$ we have:

$$\eta_{1\alpha}\psi_1 + \eta_{2\alpha}\psi_2 + \eta_{3\alpha}\psi_3 + \eta_{4\alpha}\psi_4 = f_{\alpha}$$

and plugging in $\psi_3 = 1 - \psi_1 - \psi_2 - \psi_4$:

$$(\eta_{1A} - \eta_{3A})\psi_1 + (\eta_{2A} - \eta_{3A})\psi_2 + (\eta_{4A} - \eta_{3A})\psi_4 = f_A - \eta_{3A}$$

$$(\eta_{1B} - \eta_{3B})\psi_1 + (\eta_{2B} - \eta_{3B})\psi_2 + (\eta_{4B} - \eta_{3B})\psi_4 = f_B - \eta_{3B}$$

This is equivalent to “shifting” f_A and f_B in the conditions found above to:

$$f'_A = f_A - (\eta_{4A} - \eta_{3A})\psi_4 \quad f'_B = f_B - (\eta_{4B} - \eta_{3B})\psi_4$$

so the results found above (including the feasibility conditions) are still valid with $f_{\alpha} \rightarrow f'_{\alpha}$.

3. Mutualistic interaction in the batch culture

In class, we consider the problem where a species (1) of bacteria consumes a substance A and excretes a substance B , with B being toxic to the excreting species but taken up as nutrient for growth by another species (2). Consider the case where species 1 and 2 are placed in a “batch culture” (e.g., a flask) where the substance A is provided in saturating concentration, and there is no dilution. Assume that the flask is very large so you don’t have to worry about cells getting too dense. Let ρ_1, ρ_2 denote the density of the two species and n_B denote the concentration of substance B . Let the replication rate of the two species be $r_1(n_B) = r_{1,0}/(1 + n_B/K_I)$ and $r_2 = r_{2,0}n_B/(n_B + K_B)$ where $r_{1,0}$ and $r_{2,0}$ are the growth rates of the two species under saturating nutrient, K_I is the half-inhibitory concentration, and K_B is the Monod constant for species 2 to grow on B . Finally, B is excreted by species 1 at rate γ per cell and the yield of species 2 growing on B is Y_B .

- (a) Find the growth rate λ where the two species grow at the same rate. Find the nutrient concentration n_B^* at this steady state, and find the ratio of the two species.

Solution

The equations of the system are the following:

$$\dot{\rho}_1 = r_1(n_B)\rho_1 \quad \dot{\rho}_2 = r_2(n_B)\rho_2 \quad \dot{n}_B = \gamma\rho_1 - r_2(n_B)\frac{\rho_2}{Y_B}$$

When the two species grow at the same rate we have $r_1(n_B^*) = r_2(n_B^*)$, i.e.:

$$\frac{r_{1,0}}{1 + \frac{n_B^*}{K_I}} = r_{2,0}\frac{n_B^*}{n_B^* + K_B} \quad \Rightarrow \quad \frac{r_{2,0}}{K_I}(n_B^*)^2 + (r_{2,0} - r_{1,0})n_B^* - r_{1,0}K_B = 0$$

and the only acceptable (i.e., positive) solution of this quadratic equation is:

$$n_B^* = \frac{K_I}{2r_{2,0}} \left[r_{1,0} - r_{2,0} + \sqrt{(r_{2,0} - r_{1,0})^2 + 4r_{1,0}r_{2,0}\frac{K_B}{K_I}} \right]$$

Therefore, the growth rate at which both species are growing at the same rate is:

$$\lambda = r_1(n_B^*) = \dots = \frac{2r_{1,0}r_{2,0}}{r_{1,0} + r_{2,0} + \sqrt{(r_{1,0} + r_{2,0})^2 + 4r_{1,0}r_{2,0}\frac{K_B}{K_I}}}$$

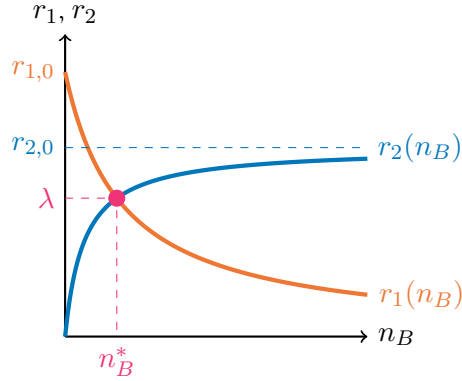
or alternatively:

$$\lambda = r_2(n_B^*) = \dots = \frac{K_I}{2(K_B - K_I)} \left[-(r_{1,0} + r_{2,0}) + \sqrt{(r_{1,0} - r_{2,0})^2 + 4r_{1,0}r_{2,0}\frac{K_B}{K_I}} \right]$$

These two expressions are equivalent. In fact, if we call $S := (r_{1,0} - r_{2,0})^2 + 4r_{1,0}r_{2,0}\frac{K_B}{K_I}$ we have:

$$\begin{aligned}
r_1(n_B^*) = r_2(n_B^*) &\Rightarrow \frac{2r_{1,0}r_{2,0}}{r_{1,0} + r_{2,0} + \sqrt{S}} = \frac{K_I}{2(K_B - K_I)} \left[-(r_{1,0} + r_{2,0}) + \sqrt{S} \right] \Rightarrow \\
&\Rightarrow 2r_{1,0}r_{2,0} \cdot 2(K_B - K_I) = K_I \left(r_{1,0} + r_{2,0} + \sqrt{S} \right) \left(-r_{1,0} - r_{2,0} + \sqrt{S} \right) \Rightarrow \\
&\Rightarrow 4r_{1,0}r_{2,0}(K_B - K_I) = K_I \left[-(r_{1,0} + r_{2,0})^2 + S \right] = \\
&= K_I \left[-(r_{1,0} + r_{2,0})^2 + (r_{1,0} - r_{2,0})^2 + 4r_{1,0}r_{2,0}\frac{K_B}{K_I} \right] = \\
&= K_I \left(-4r_{1,0}r_{2,0} + 4r_{1,0}r_{2,0}\frac{K_B}{K_I} \right) = \\
&= K_I \cdot 4r_{1,0}r_{2,0} \left(\frac{K_B}{K_I} - 1 \right) = 4r_{1,0}r_{2,0}(K_B - K_I)
\end{aligned}$$

and so $4r_{1,0}r_{2,0}(K_B - K_I) = 4r_{1,0}r_{2,0}(K_B - K_I) \Rightarrow 1 = 1$, which means the equation $r_1(n_B^*) = r_2(n_B^*)$ is solved. Graphically, the situation is the following:



To find the ratio of the two species at steady state, we can plug $\lambda = r_2(n_B^*)$ into $\dot{n}_B = 0$:

$$\gamma\rho_1^* = \lambda\frac{\rho_2^*}{Y_B} \Rightarrow \frac{\rho_2^*}{\rho_1^*} = \frac{\gamma Y_B}{\lambda} \quad (4)$$

- (b) Show that this steady state is stable by considering what happens if the nutrient concentration is transiently different from n_B^* .

Solution

If $n_B \gtrsim n_B^*$ we have $r_2(n_B) \gtrsim r_1(n_B)$ and therefore $\rho_2 > \rho_1$. This, however, means that $\dot{n}_B < 0$, which

means that the nutrient concentration goes back down towards n_B^* .

On the other hand, if $n_B \lesssim n_B^*$, $r_2(n_B) \lesssim r_1(n_B)$ and so $\rho_2 < \rho_1$ and $\dot{n}_B > 0$, which means the resource concentration goes back up towards n_B^* . Therefore, however we perturb the resource concentration it will go back to n_B^* , which is therefore stable.

- (c) Next consider the case where species 2 is absent. Let the starting density be $\rho_1(0) = \rho_0$ at time $t = 0$. Derive a relation between $\rho_1(t)$ and $n_B(t)$ by observing that $d\rho_1/dn_B = \dot{\rho}_1/\dot{n}_B$ has a simple form that can be integrated. Use the relation derived to obtain a nonlinear ODE for $\rho_1(t)$. The solution of this ODE cannot be expressed in terms of elementary functions. To see what it describes, you can solve the non-dimensionalized version of the ODE numerically, plot $\ln(\rho_1(t)/\rho_0)$ vs time. Show that behavior of the solution at small and large time are very different and obtain the approximate form numerically for these two regimes. Explain what the two regimes mean biologically. Find and rationalize the time scale t_\times separating the two regimes.

[For the more mathematically inclined: show that the increase of $\rho_1(t)$ at large time is in between logarithmic and linear dependence.]

Solution

If species 2 is absent, the equations of the system are:

$$\dot{\rho}_1 = r_1(n_B)\rho_1 = \frac{r_{1,0}}{1 + \frac{n_B}{K_I}}\rho_1 \quad \dot{n}_B = \gamma\rho_1$$

Therefore:

$$\frac{d\rho_1}{dn_B} = \frac{\dot{\rho}_1}{\dot{n}_B} = \frac{r_{1,0}}{\gamma} \frac{1}{1 + \frac{n_B}{K_I}} \Rightarrow \rho_1(t) - \rho_1(0) = \frac{r_{1,0}}{\gamma} \int_{n_B(0)=0}^{n_B(t)} \frac{dn_B}{1 + \frac{n_B}{K_I}} = \frac{r_{1,0}K_I}{\gamma} \ln\left(1 + \frac{n_B(t)}{K_I}\right)$$

Thus:

$$1 + \frac{n_B(t)}{K_I} = e^{\frac{\gamma}{r_{1,0}K_I}[\rho_1(t) - \rho_0]} \Rightarrow r_1(n_B) = r_{1,0}e^{-\frac{\gamma}{r_{1,0}K_I}[\rho_1(t) - \rho_0]}$$

We can therefore rewrite the equation for $\dot{\rho}_1$ as:

$$\dot{\rho}_1 = r_{1,0}e^{-\frac{\gamma}{r_{1,0}K_I}[\rho_1(t) - \rho_0]} \cdot \rho_1$$

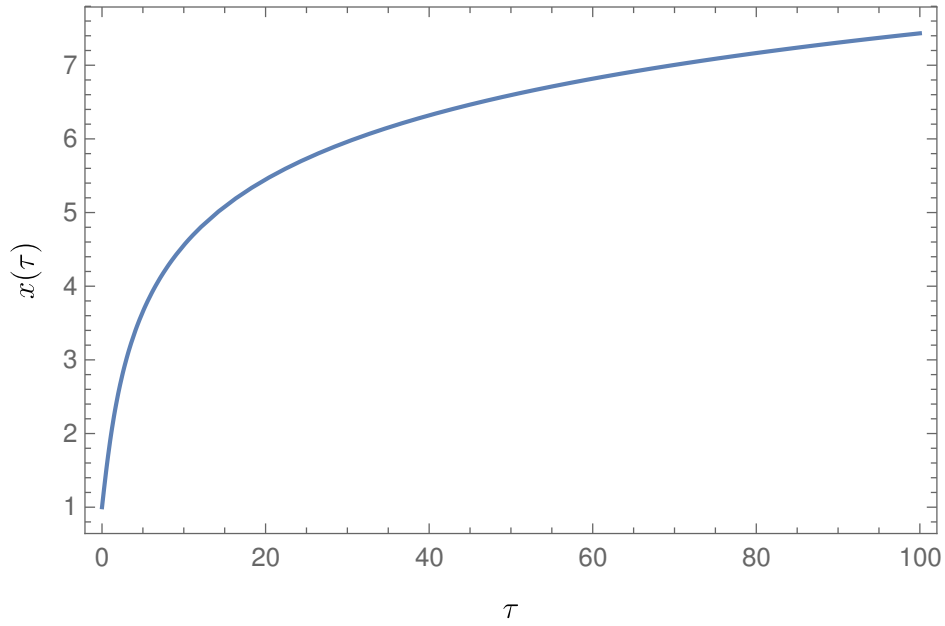
We can make this equation non-dimensional by defining:

$$x := \frac{\gamma\rho_1(t)}{r_{1,0}K_I} \quad x_0 := \frac{\gamma\rho_0}{r_{1,0}K_I} \quad \tau = r_{1,0}t$$

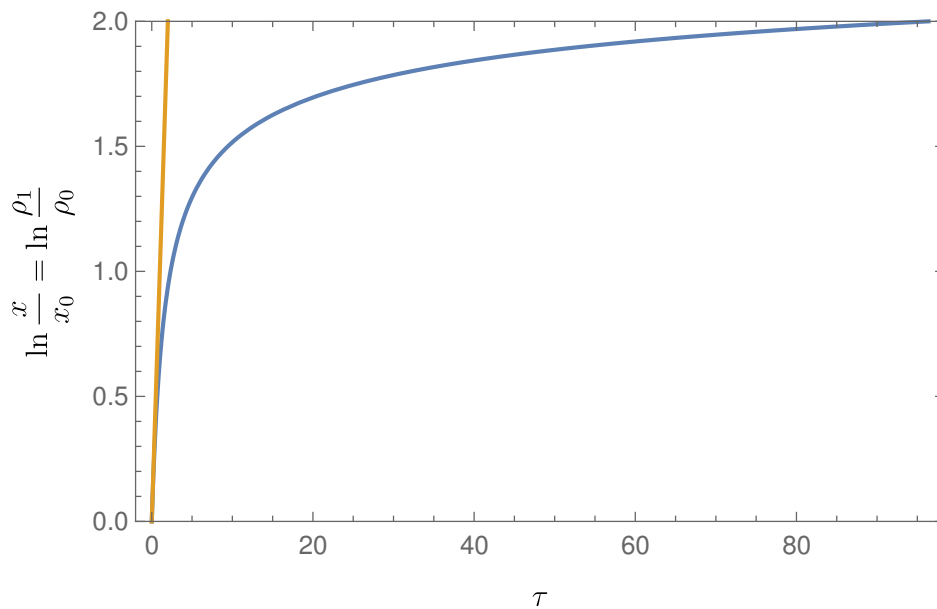
which leads to the non-dimensional equation:

$$\frac{dx}{d\tau} = xe^{-(x-x_0)}$$

The plot of the numerical solution of this equation with $x_0 = 1$ is:



Since $\rho_1/\rho_0 = x/x_0$, from this plot we can also obtain the plot of $\ln(\rho_1/\rho_0)$:



In the small time regime $\ln \rho_1/\rho_0$ is linear, meaning that species 1 is growing exponentially; this is possible because the population is still small, and so the abundance of the toxic substrate n_B is still low. On the other hand, at large times growth is greatly inhibited (in particular $\ln \rho_1/\rho_0$ is logarithmic, which means the population is growing linearly) because species 1 has produced a lot of the toxic substrate n_B , which is now slowing down its own growth.

At small times, $x \approx x_0$ so $x \sim x_0 e^\tau$. This means that the population is growing exponentially. The exponential

factor in the equation “kicks in” when $x(t_\times) - x_0 \approx 1$. Therefore:

$$x_0 e^{t_\times} = 1 + x_0 \quad \Rightarrow \quad t_\times = \ln \left(1 + \frac{1}{x_0} \right) = \ln \left(1 + \frac{r_{1,0} K_I}{\gamma \rho_0} \right)$$

On the other hand, at large times we have $x \gg x_0$, so we can Taylor expand:

$$e^{-(x-x_0)} = \frac{1}{e^{x-x_0}} \sim \frac{1}{1+x-x_0}$$

so that the equation of the system becomes:

$$\frac{dx}{d\tau} = \frac{x}{x + (1 - x_0)}$$

We can separate the variables to obtain:

$$d\tau = dt \left(1 + \frac{1-x_0}{x} \right) \quad \Rightarrow \quad \tau = x - x_0 + (1-x_0) \ln \frac{x}{x_0}$$

However, since x is large we can approximate this to $x = x_0 + \tau$ (i.e., we can neglect the term involving $\ln x$). Now, in order to show formally that the increase of x at large times is between linear and logarithmic we can do the following. The expression of $dx/d\tau$ is bounded by these two functions:

$$x_0 e^{-(x-x_0)} \leq \frac{dx}{d\tau} = x e^{-(x-x_0)} \leq \frac{x}{x + (1-x_0)}$$

By integrating the lower bound we have:

$$\frac{dx}{d\tau} \geq x_0 e^{-(x-x_0)} \quad \Rightarrow \quad x(t) \geq x_0 + \ln(1 + x_0 \tau)$$

While from what we have shown above for large times, for the upper bound we have:

$$\frac{dx}{d\tau} \leq \frac{x}{x + (1-x_0)} \quad \Rightarrow \quad x \leq x_0 + \tau$$

Therefore:

$$\ln(1 + x_0 \tau) \leq x - x_0 \leq \tau$$

which can be rewritten as:

$$1 + \frac{r_{1,0} K_I}{\gamma \rho_0} \ln \left(1 + \frac{\gamma \rho_0}{K_I} t \right) \leq \frac{\rho_1}{\rho_0} \leq 1 + \frac{r_{1,0} K_I}{\gamma \rho_0} t$$

which indeed shows that the increase of ρ_1 is between logarithmic and linear.

- (d) Compare your answer to part (a) and (c) to assess the effect of species 2 on species 1. Explain why this effect is so different from the effect obtained in class for the same system in a chemostat.

Solution

In the presence of species 2 we have seen that $\rho_1 \propto e^{\lambda t}$. Therefore, the presence of species 2 gives a large boost to the fitness of species 1. This happens because as species 1 grows it excretes a substance that is toxic for itself, but can be uptaken by species 2. Therefore, the presence of species 2 makes it possible to remove the toxic substrate, allowing species 1 to grow more. This result is very different from the chemostat case because particularly when we are close to the washout limit, species 1 will not be able to grow to a high enough density and produce enough resource B to support the growth of species 2.

4. Production and cross-feeding of substitutable nutrients

Consider two species of bacteria with density ρ_1, ρ_2 , which generate nutrients n_A and n_B , respectively. Take these two nutrients to be substitutable. Examples could be the polymers chitin and alginate, both of which can be broken down into monomeric sugars by special (and different) enzymes. The population dynamics of this system in a chemostat can be described by the following system of ODEs:

$$\begin{aligned}\dot{\rho}_1 &= (v_{1A}n_A + v_{1B}n_B) \cdot \rho_1 - \mu \cdot \rho_1 \\ \dot{\rho}_2 &= (v_{2A}n_A + v_{2B}n_B) \cdot \rho_2 - \mu \cdot \rho_2 \\ \dot{n}_A &= \gamma_{1A}\rho_1 - \mu n_A - (v_{1A}\rho_1 + v_{2A}\rho_2) \cdot n_A \\ \dot{n}_B &= \gamma_{2B}\rho_2 - \mu n_B - (v_{1B}\rho_1 + v_{2B}\rho_2) \cdot n_B\end{aligned}$$

where $v_{i\alpha}$ are the nutrient uptake matrix introduced before, μ is the dilution rate, and γ_{1A}, γ_{1B} are the two nutrient production rates. The yield factor has been set to unity for simplification.

- (a) In the limit of small μ , show that steady state solution would have $n_\alpha^* \propto \mu$ and $\rho_i^* \propto \mu^2$.

Solution

Considering the equations for the populations, at steady state we have:

$$\begin{aligned}\begin{cases} v_{1A}n_A^* + v_{1B}n_B^* = \mu \\ v_{2A}n_A^* + v_{2B}n_B^* = \mu \end{cases} &\Rightarrow \begin{pmatrix} v_{1A} & v_{1B} \\ v_{2A} & v_{2B} \end{pmatrix} \begin{pmatrix} n_A^* \\ n_B^* \end{pmatrix} = \begin{pmatrix} \mu \\ \mu \end{pmatrix} \Rightarrow \\ &\Rightarrow \begin{pmatrix} n_A^* \\ n_B^* \end{pmatrix} = \frac{1}{v_{1A}v_{2B} - v_{1B}v_{2A}} \begin{pmatrix} \mu(v_{2B} - v_{1B}) \\ \mu(v_{1A} - v_{2A}) \end{pmatrix}\end{aligned}$$

and so indeed $n_\alpha^* \propto \mu$. From the equation for the resources, on the other hand:

$$\begin{aligned}\begin{cases} \gamma_{1A}\rho_1^* - \mu n_A^* - (v_{1A}\rho_1^* + v_{2A}\rho_2^*)n_A^* = 0 \\ \gamma_{1B}\rho_1^* - \mu n_B^* - (v_{1B}\rho_1^* + v_{2B}\rho_2^*)n_B^* = 0 \end{cases} &\Rightarrow \\ \Rightarrow \begin{pmatrix} \gamma_{1A} - v_{1A}n_A^* & -v_{2A}n_A^* \\ \gamma_{1B} - v_{1B}n_B^* & -v_{2B}n_B^* \end{pmatrix} \begin{pmatrix} \rho_1^* \\ \rho_2^* \end{pmatrix} = \begin{pmatrix} \mu n_A^* \\ \mu n_B^* \end{pmatrix} &\Rightarrow \\ \Rightarrow \begin{pmatrix} \rho_1^* \\ \rho_2^* \end{pmatrix} = \frac{1}{(v_{1A}v_{2B} - v_{1B}v_{2A})n_A^*n_B^* + v_{2A}\gamma_{1B}n_A^* - v_{2B}\gamma_{1A}n_B^*} \begin{pmatrix} -v_{2B}n_B^* & v_{2A}n_A^* \\ v_{1B}n_B^* - \gamma_{1B} & \gamma_{1A} - v_{1A}n_A^* \end{pmatrix} \begin{pmatrix} \mu n_A^* \\ \mu n_B^* \end{pmatrix} \\ \Rightarrow \begin{pmatrix} \rho_1^* \\ \rho_2^* \end{pmatrix} = \frac{1}{(v_{1A}v_{2B} - v_{1B}v_{2A})n_A^*n_B^* + v_{2A}\gamma_{1B}n_A^* - v_{2B}\gamma_{1A}n_B^*} \begin{pmatrix} (v_{2A} - v_{2B})\mu n_A^*n_B^* \\ (v_{1B}n_B^* - v_{1A}n_A^* + \gamma_{1A} - \gamma_{1B})\mu n_A^*n_B^* \end{pmatrix}\end{aligned}$$

Now, since $n_\alpha \propto \mu$ we have:

$$(v_{1A}v_{2B} - v_{1B}v_{2A})n_A^*n_B^* + v_{2A}\gamma_{1B}n_A^* - v_{2B}\gamma_{1A}n_B^* \propto a\mu^2 + b\mu$$

$$(v_{2A} - v_{2B})\mu n_A^* n_B^* \propto c\mu^3$$

$$(v_{1B}n_B^* - v_{1A}n_A^* + \gamma_{1A} - \gamma_{1B})\mu n_A^* n_B^* \propto d\mu^4 + e\mu^3$$

In the limit of small μ , these expressions can be approximated as:

$$(v_{1A}v_{2B} - v_{1B}v_{2A})n_A^* n_B^* + v_{2A}\gamma_{1B}n_A^* - v_{2B}\gamma_{1A}n_B^* \sim b\mu$$

$$(v_{2A} - v_{2B})\mu n_A^* n_B^* \sim c\mu^3$$

$$(v_{1B}n_B^* - v_{1A}n_A^* + \gamma_{1A} - \gamma_{1B})\mu n_A^* n_B^* \sim e\mu^3$$

Therefore:

$$\begin{pmatrix} \rho_1^* \\ \rho_2^* \end{pmatrix} \sim \frac{1}{b\mu} \begin{pmatrix} c\mu^3 \\ e\mu^3 \end{pmatrix} \Rightarrow \rho_i^* \propto \mu^2$$

- (b) By setting $\dot{n}_\alpha = 0$, solve for the steady state condition $n_A^*(\rho_1, \rho_2)$ and $n_B^*(\rho_1, \rho_2)$. Find the leading order dependence on ρ_1 and ρ_2 in the limit of small μ . Substitute these expressions into the ODEs for ρ_1 and ρ_2 to obtain two nonlinear ODEs involving only ρ_1 and ρ_2 to the leading order for small μ .

Solution

From $\dot{n}_A = 0$ and $\dot{n}_B = 0$ (i.e., we assume that the time evolution of the resources is fast) we have:

$$\gamma_{1A}\rho_1 - \mu n_A^* - (v_{1A}\rho_1 + v_{2A}\rho_2)n_A^* = 0 \quad \gamma_{1B}\rho_1 - \mu n_B^* - (v_{1B}\rho_1 + v_{2B}\rho_2)n_B^* = 0$$

which yields:

$$n_A^* = \frac{\gamma_{1A}\rho_1}{\mu + v_{1A}\rho_1 + v_{2A}\rho_2} \quad n_B^* = \frac{\gamma_{1B}\rho_1}{\mu + v_{1B}\rho_1 + v_{2B}\rho_2}$$

and by substituting this in the equations for $\dot{\rho}_i$ we get:

$$\dot{\rho}_1 = \rho_1 \left[\frac{v_{1A}\gamma_{1A}}{\mu + v_{1A}\rho_1 + v_{2A}\rho_2} + \frac{v_{1B}\gamma_{1B}}{\mu + v_{1B}\rho_1 + v_{2B}\rho_2} - \mu \right]$$

In the limit of small μ , since $\rho_i \propto \mu^2$ we can approximate:

$$n_A^* = \frac{\gamma_{1A}\rho_1}{\mu + v_{1A}\rho_1 + v_{2A}\rho_2} \sim \frac{\gamma_{1A}}{\mu} \rho_1 \quad n_B^* = \frac{\gamma_{1B}\rho_1}{\mu + v_{1B}\rho_1 + v_{2B}\rho_2} \sim \frac{\gamma_{1B}}{\mu} \rho_1$$

and so we can write:

$$\dot{\rho}_1 \simeq \rho_1 \left(\frac{v_{1A}\gamma_{1A}}{\mu} \rho_1 + \frac{v_{1B}\gamma_{1B}}{\mu} \rho_2 - \mu \right) \quad \dot{\rho}_2 \simeq \rho_2 \left(\frac{v_{2A}\gamma_{1A}}{\mu} \rho_1 + \frac{v_{2B}\gamma_{1B}}{\mu} \rho_2 - \mu \right)$$

- (c) Plot the null-clines and sketch the phase flow of the ODEs obtained in part (b) for i) $v_{1A} > v_{2A}$ and $v_{2B} > v_{1B}$, and ii) $v_{1A} < v_{2A}$ and $v_{2B} < v_{1B}$. Describe the dynamics of the system in words for each regime, in particular, the dependence on initial densities $\rho_1(0)$ and $\rho_2(0)$.

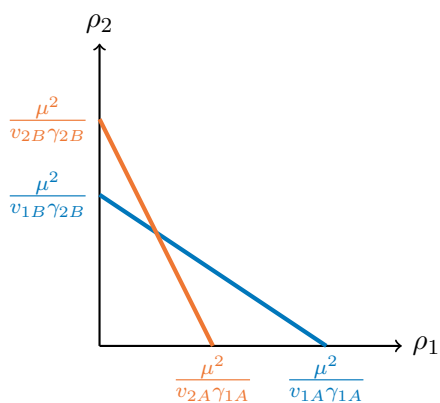
Solution

The nullclines are the two lines given by:

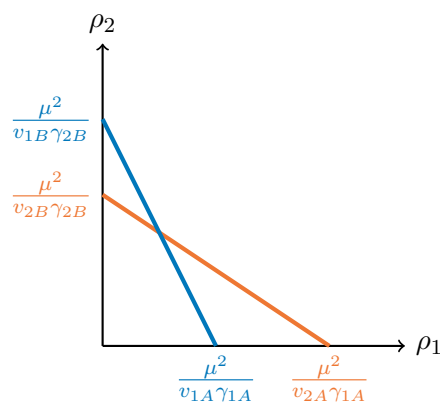
$$\frac{v_{1A}\gamma_{1A}}{\mu} \rho_1 + \frac{v_{1B}\gamma_{1B}}{\mu} \rho_2 = \mu \quad \frac{v_{2A}\gamma_{1A}}{\mu} \rho_1 + \frac{v_{2B}\gamma_{1B}}{\mu} \rho_2 = \mu$$

which can be represented as follows:

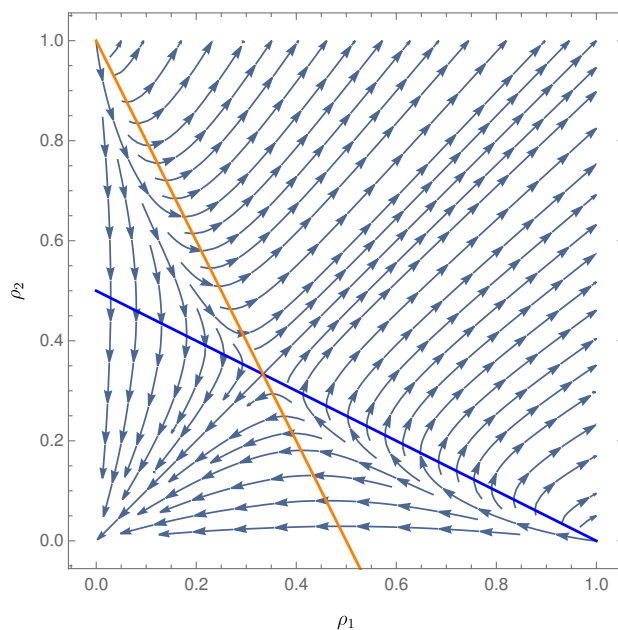
$$v_{1A} < v_{2A}, v_{2B} < v_{1B}$$



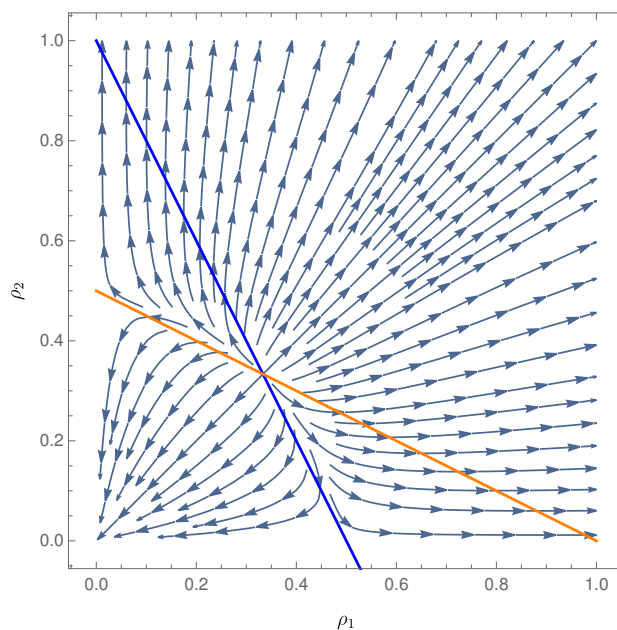
$$v_{1A} > v_{2A}, v_{2B} > v_{1B}$$



The phase flow of the system for $\gamma_{1A} = \gamma_{2B} = \mu = 1$ is the following:



$$v_{1A} = v_{2B} = 1, v_{2A} = v_{1B} = 2$$



$$v_{1A} = v_{2B} = 2, v_{2A} = v_{1B} = 1$$

where we are also representing the nullclines.

In both cases, depending on the initial condition $(\rho_1(0), \rho_2(0))$ the system can either end up in $(0, 0)$ (i.e., both species go to extinction) or go towards (∞, ∞) (i.e., both species grow without limit). In this latter case, the ratio of the two populations remains constant (the flow is well approximated by lines in the (ρ_1, ρ_2) space in this case), and the value of the ratio depends on the initial condition.

- (d) Investigate the growth phase at high densities (the runaway part of (c)) by assuming the nutrients have reached constant concentrations of values n_A^* and n_B^* , while the two species grow exponentially with rates λ_1 and λ_2 . Find the values of n_A^* and n_B^* for i) $\lambda_1 > \lambda_2$ and ii) $\lambda_1 < \lambda_2$. Relate the resulting dynamics to the simple producer-cheater relation discussed in class and use the results derived in class to describe the parameter regime where species 1 dominates, species 2 dominates,

or when either species can dominate. In the last case, what is species dominance determined by?

Solution

From the assignment, when $n_A = n_A^*$ and $n_B = n_B^*$ we have $\rho_i \propto e^{\lambda_i t}$ with $i = 1, 2$. If $\lambda_1 > \lambda_2$, in the long time limit we have $\rho_1 \gg \rho_2$. From the equations of the system, we see that this leads to $\dot{n}_B < 0$ because the uptake term $-v_{1B}n_B\rho_1$ is going to be much larger than the production rate $\gamma_{2B}\rho_2$. Therefore, in the large time limit $n_B^* \rightarrow 0$; if we now set $\dot{n}_A = 0$ we have:

$$\gamma_{1A}\rho_1 = v_{1A}n_A^*\rho_1 \quad \Rightarrow \quad n_A^* = \frac{\gamma_{1A}}{v_{1A}}$$

In this case, therefore, since resource B is completely removed from the system by species 1, species 2 is behaving as a cheater because it grows on resource A , which is being produced by species 1. This situation is stable (i.e., species 1 will dominate) if $v_{1A} > v_{2A}$ (i.e., if species 1 uptakes the only available resource faster than species 2).

The case $\lambda_1 < \lambda_2$ is equivalent to the previous one, provided we substitute species 1 \leftrightarrow species 2 and resource $A \leftrightarrow$ resource B . In particular, when $\lambda_1 < \lambda_2$ we will have $n_A^* = 0$ and $n_B^* = \gamma_{2B}/v_{2B}$. This time it's species 1 that is behaving as a cheater, and species 2 dominates if $v_{2B} > v_{1B}$.

When $v_{1A} < v_{2A}$ or $v_{2B} < v_{1B}$ either species can dominate. In particular the system is bistable, and species dominance is determined by the initial conditions.

- (e) Continuing the investigation above, we next study the case $\lambda_1 = \lambda_2$ (and refer to both as λ). Find n_A^* and n_B^* in this case and the growth rate λ in terms of the model parameters. [To simplify the algebra, you may take $v_{1A} = v_{2B} \equiv v$, $v_{2A} = v_{1B} = v'$, and $\gamma_{1A} = \gamma_{1B} \equiv \gamma$.] To see whether the fixed point solution obtained here is stable, apply Tilman's analysis in the space of (n_A, n_B) for the two parameter regimes discussed in (c): i) $v_{1A} > v_{2A}$ and $v_{2B} > v_{1B}$, and ii) $v_{1A} < v_{2A}$ and $v_{2B} < v_{1B}$.

Solution

Since $\lambda_1 = \lambda_2 = \lambda$, we can write $r_i(n_A^*, n_B^*) = r^*$. Therefore, by definition we have:

$$v_{1A}n_A^* + v_{1B}n_B^* = r^* \quad v_{2A}n_A^* + v_{2B}n_B^* = r^*$$

which is a system of two equations in two variables. The solution of this system is:

$$\begin{pmatrix} v_{1A} & v_{1B} \\ v_{2A} & v_{2B} \end{pmatrix} \begin{pmatrix} n_A^* \\ n_B^* \end{pmatrix} = \begin{pmatrix} r^* \\ r^* \end{pmatrix} \quad \Rightarrow \quad \begin{pmatrix} n_A^* \\ n_B^* \end{pmatrix} = \frac{r^*}{v_{1A}v_{2B} - v_{1B}v_{2A}} \begin{pmatrix} v_{2B} - v_{1B} \\ v_{1A} - v_{2A} \end{pmatrix}$$

As suggested, we simplify the algebra by setting $v_{1A} = v_{2B} = v$ and $v_{2A} = v_{1B} = v'$, which yields:

$$\begin{pmatrix} n_A^* \\ n_B^* \end{pmatrix} = \frac{r^*}{v^2 - (v')^2} \begin{pmatrix} v - v' \\ v - v' \end{pmatrix} = \begin{pmatrix} \frac{r^*}{v+v'} \\ \frac{r^*}{v+v'} \end{pmatrix}$$

Therefore:

$$n_A^* = n_B^* = \frac{r^*}{v + v'}$$

We now have to express r^* in terms of the model parameters. We can do so by using the equations for n_α at steady state:

$$\gamma_{1A}\rho_1^* = v_{1A}n_A^*\rho_1^* + v_{2A}n_A^*\rho_2^* \quad \gamma_{2B}\rho_2^* = v_{1B}n_B^*\rho_1^* + v_{2B}n_B^*\rho_2^*$$

We can rearrange these equations as:

$$(\gamma_{1A} - v_{1A}n_A^*)\rho_1^* = v_{2A}n_A^*\rho_2^* \quad (\gamma_{2B} - v_{2B}n_B^*)\rho_2^* = v_{1B}n_B^*\rho_1^*$$

By multiplying each sides of these equations, we get:

$$(\gamma_{1A} - v_{1A}n_A^*)(\gamma_{2B} - v_{2B}n_B^*) = v_{2A}n_A^*v_{1B}n_B^*$$

If we now introduce the algebraic simplifications (including $\gamma_{1A} = \gamma_{2B} = \gamma$) this becomes:

$$(\gamma - vn_A^*)(\gamma - vn_B^*) = (v')^2n_A^*n_B^*$$

and by also plugging in the expression of n_A^* and n_B^* :

$$\left(\gamma - v\frac{r^*}{v+v'}\right)^2 = \left(v'\frac{r^*}{v+v'}\right)^2$$

By taking the square root on both sides, and considering only the positive root:

$$\gamma - v\frac{r^*}{v+v'} = v'\frac{r^*}{v+v'} \Rightarrow r^*\frac{v+v'}{v+v'} = \gamma \Rightarrow r^* = \gamma$$

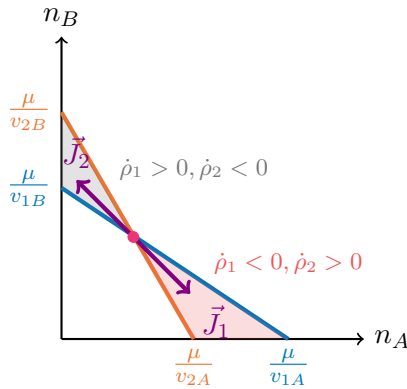
Therefore, $\lambda = r^* = \gamma$.

For Tilman's graphical analysis, we can rewrite the equations for \dot{n}_α as:

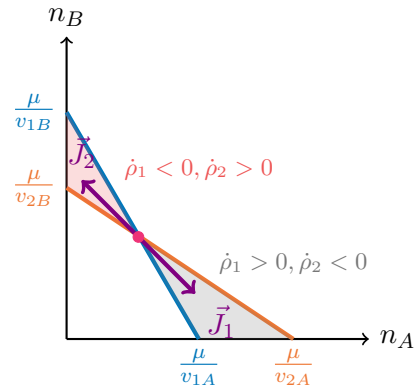
$$\begin{pmatrix} \dot{n}_A \\ \dot{n}_B \end{pmatrix} = \rho_1^* \underbrace{\begin{pmatrix} \gamma_{1A} - v_{1A}n_A \\ -v_{1B}n_B \end{pmatrix}}_{\vec{J}_1} + \rho_2^* \underbrace{\begin{pmatrix} -v_{2A}n_A \\ \gamma_{2B} - v_{2B}n_B \end{pmatrix}}_{\vec{J}_2}$$

where we are neglecting the terms proportional to μ , since we are in the slow dilution rate. Graphically, the situation in the two cases is the following:

$$v_{1A} < v_{2A}, v_{2B} < v_{1B}$$



$$v_{1A} > v_{2A}, v_{2B} > v_{1B}$$

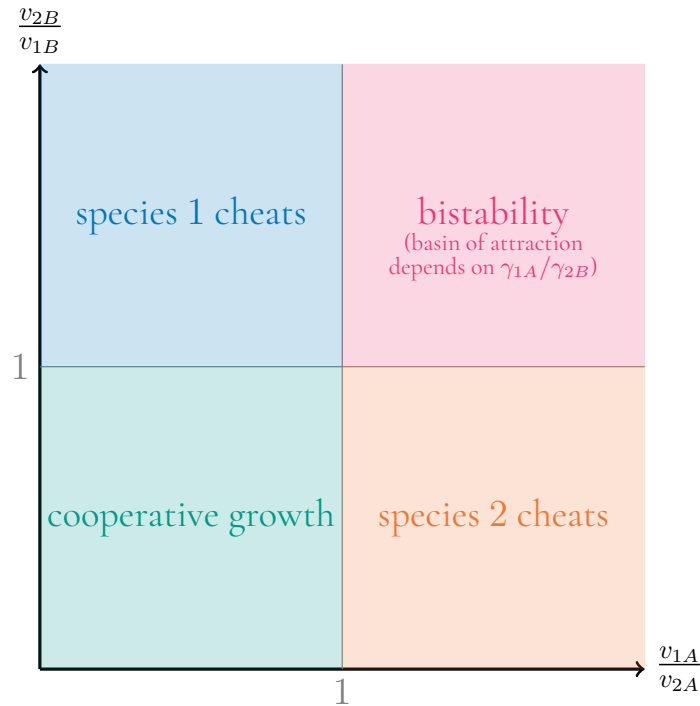


Therefore, when $v_{1A} < v_{2A}$ and $v_{2B} < v_{1B}$ an increase in ρ_1 results in $\dot{\rho}_1 < 0$, and similarly an increase in ρ_2 yields $\dot{\rho}_2 < 0$: the system is stable. On the other hand, when $v_{1A} > v_{2A}$ and $v_{2B} > v_{1B}$ an increase in ρ_i leads to $\dot{\rho}_i > 0$: the system is unstable.

- (f) Summarize your findings in parts (d) and (e) by indicating the phase diagram in the space of $(v_{1A}/v_{2A}, v_{2B}/v_{1B})$. Compare your result to the conditions derived in class for the case of essential nutrients. Discuss the differences between the two cases.

Solution

The phase diagram is:



With respect to the conditions derived for the case of essential nutrients, the “quadrants” of bistability and cooperative growth are switched. In other words, in the case of essential nutrients the species coexist when $v_{1A} > v_{2A}$ and $v_{2B} > v_{1B}$, while either of the two species will dominate when $v_{1A} < v_{2A}$ and $v_{2B} < v_{1B}$. This difference arises from the different effect that a low resource has on population growth: when the resources are substitutable, if one of them runs low each species can grow by uptaking the other, while if both resources are essential then both species will slow down if either of the two resources is scarce. Therefore, when resources are essential having two species that uptake faster their “own” resource (i.e., the resource that they are producing) has a stabilizing effect, because if either of the two populations becomes larger both of them will be slowed down by the decreased availability of resources. On the other hand, with substitutable resource this situation is de-stabilizing because in this case if each species uptakes faster its “own” resource any increase in ρ_i will have a positive effect on species i but not on the other. Conversely, when resources are substitutable having species 1 that uptakes faster the resource made by species 2 and viceversa has a stabilizing effect because any increase in ρ_i will have a positive effect on the *other* species, bringing the system back to equilibrium.