PHYSICS 239 Spatiotemporal Biodynamics

Homework #4

Due Monday March 9, 2022

[Note: Those not from math/physics background need not attempt problem(s) indicated by *]

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, $\alpha \in \{A, B\}$).

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

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

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 $\nu_{1A} > \nu_{2A}$ and $\nu_{2B} > \nu_{1B}$), 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., $\nu_{1A} > \nu_{3A} > \nu_{2A}$ and $\nu_{2B} > \nu_{3B} > \nu_{1B}$, 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 $\nu_{i\alpha}$. Consequently, one of the density must be at zero in steady state.

(b) Write down the three conditions if the nutrient uptake coefficients are of the special form motivated in class, $\nu_{i\alpha} = \nu_\alpha^0 \cdot \eta_{i\alpha}$, where $\eta_{i\alpha}$ describes the allocation of uptake enzymes for nutrient α b species i with $\eta_{iA} + \eta_{iB} = 1$ for each i. [Convince yourself that the nutrient preferences $\nu_{1A} > \nu_{3A} > \nu_{2A}$ and $\nu_{2B} > \nu_{3B} > \nu_{1B}$ 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 $\nu_{4\alpha} = \nu_\alpha^0 \cdot \eta_{4\alpha}$ and $\eta_{4A} + \eta_{4B} = 1$, the same solution (n_A^*, n_B^*) still holds (and hence the 4th species can also coexist).

(c) From here on, we also take the slow dilution limit, $\mu \ll \nu_\alpha^0 n_\alpha^0$, 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.

(d) Show that the 3 species can coexist as long as $\eta_{1A} < f_A < \eta_{2A}$ (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.]

(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.]

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):

$$\dot{\rho}_i = (\nu_{iA} n_A + \nu_{iB} n_B + \nu_{iC} n_C) \cdot \rho_i - \mu \rho_i,$$

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

Let the nutrient uptake coefficients be of the special form $\nu_{i\alpha} = \nu_\alpha^0 \cdot \eta_{i\alpha}$ where $\sum_\alpha \eta_{i\alpha} = 1$. Let us also take the slow dilution limit, $\mu \ll \nu_\alpha^0 n_\alpha^0$, 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, $f_\alpha \equiv n_\alpha^0 Y_\alpha / \sum_\beta n_\beta^0 Y_\beta$.

(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 $\eta_{i\alpha} - \eta_{3\alpha}$.

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

(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., $\psi_1 = 0, \psi_2 > 0, \psi_3 > 0$.

(e) For the more mathematically oriented: Add a 4th species, characterized by $\nu_{4\alpha} = \nu_\alpha^0 \cdot \eta_{4\alpha}$, 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 $\psi_4 > 0$.

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 $r_1(n_B) = r_{1,0}/(1 + \frac{n_B}{K_I})$ 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.

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

(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 $\frac{d\rho_1}{dn_B} = \frac{\dot{\rho}_1}{\dot{n}_B}$ 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.]

(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.

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:

$$\dot{\rho}_1 = (\nu_{1A} n_A + \nu_{1B} n_B) \cdot \rho_1 - \mu \cdot \rho_1,$$

$$\dot{\rho}_2 = (\nu_{2A} n_A + \nu_{2B} n_B) \cdot \rho_2 - \mu \cdot \rho_2$$

$$\dot{n}_A = \gamma_{1A} \rho_1 - \mu n_A - (\nu_{1A} \rho_1 + \nu_{2A} \rho_2) \cdot n_A$$

$$\dot{n}_B = \gamma_{2B} \rho_2 - \mu n_B - (\nu_{1B} \rho_1 + \nu_{2B} \rho_2) \cdot n_B$$

where $\nu_{i\alpha}$ are the nutrient uptake matrix introduced before, μ is the dilution rate, and γ_{1A}, γ_{2B} 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 $\rho_i \propto \mu^2$.

(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 expression 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.

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

(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?

(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 $\nu_{1A} = \nu_{2B} \equiv \nu$, $\nu_{2A} = \nu_{1B} \equiv \nu'$, and $\gamma_{1A} = \gamma_{2B} \equiv \gamma$.] 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) $\nu_{1A} > \nu_{2A}$ and $\nu_{2B} > \nu_{1B}$, and ii) $\nu_{1A} < \nu_{2A}$ and $\nu_{2B} < \nu_{1B}$.

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