PHYSICS 239 Spatiotemporal Biodynamics

Homework #4a

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 $\psi_4 > 0$.

Problems 3, 4 to be posted later