1. Coexistence of 3 species on two nutrients. Consider the following Consumer-Resource model for 3 species (of densities \( \rho_i, i \in \{1,2,3\} \)) and 2 substitutable nutrients (of concentrations \( n_\alpha, \alpha \in \{A,B\} \)).

\[
\dot{\rho}_i = (v_{iA} n_A + v_{iB} n_B) \cdot \rho_i - \mu \cdot \rho_i \\
\dot{n}_\alpha = \mu \cdot (n_\alpha^0 - n_\alpha) - (v_{1a} \rho_1 + v_{2a} \rho_2 + v_{3a} \rho_3) \cdot n_\alpha / Y_\alpha.
\]

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.

(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 \( \alpha \) b 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 \( v_{4A} = v_{4A}^0 \cdot \eta_{4A} \) 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, \( \mu \ll v_{\alpha}^0 n_\alpha^0 \), 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 \((\psi_1, \psi_2, \psi_3)\) 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 \( \psi_1 \) where all 3 species are present, and plot \( \psi_2, \psi_3 \) vs \( \psi_1 \) 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 \( \eta_3A \) also falling in between \( \eta_1A \) and \( \eta_2A \)). 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 \( \psi_1 \) where all 3 species can coexist. [This should be as an area in the \((f_A, \psi_1)\) space.]

(e) Repeat the above plot in the space of \((f_A, \psi_3)\). 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 \( \rho_1, \rho_2, \rho_3 \)) and 3 substitutable nutrients (of concentrations \( n_A, n_B, n_C \)):

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

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

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

(a) Write down the conditions on \( \rho_i \) 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, \( f_\alpha \equiv n^0_\alpha Y_\alpha / \sum_\beta n^0_\beta Y_\beta \).

(b) Use \( \psi_2 = 1 - \psi_1 - \psi_2 \) to reduce the 3 equations in (a) to two equations for \( \psi_1 \) and \( \psi_2 \). Solve the two linear equations to obtain expressions for \( \psi_1 \) and \( \psi_2 \). 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 \((\eta_{1A}, \eta_{1B})\) form a triangle. Take \((\eta_{3A}, \eta_{3B})\) 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 \( v_{4\alpha} = v^0_\alpha \cdot \eta_{4\alpha} \), 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 \( \psi_1 \) and \( \psi_2 \). 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 \((\eta_{1A}, \eta_{1B}), (\eta_{2A}, \eta_{2B}), (\eta_{3A}, \eta_{3B})\), then feasibility conditions for coexistence obtained above are unchanged with \( \psi_4 > 0 \).

Problems 3, 4 to be posted later