PHYSICS 239 Spatiotemporal Biodynamics

Homework #2

Due Wednesday February 2, 2022

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

1. Lotka-Volterra model of 2-species competition. In class, we discussed the LV model of 2-species competition, which takes on the following form for the dimensionless density variables $u_1(t) = \rho_1(t)/\tilde{\rho}_{11}$ and $u_2(t) = \rho_2(t)/\tilde{\rho}_{22}$:

$$\dot{u_1} = r_1 u_1 \cdot (1 - u_1 - a_{12} u_2), \tag{1}$$

$$\dot{u_2} = r_2 u_2 \cdot (1 - u_2 - a_{21} u_1), \tag{2}$$

with the interaction parameters a_{12} and a_{21} both positive.

(a) In class, we discussed the case of strong competition with $a_{12} > 1$ and $a_{21} > 1$ using the graphic method. Here you are asked to show the result *algebraically*, that the nontrivial fixed point at $u_1^* = (1 - a_{12})/(1 - a_{12} \cdot a_{21})$, $u_2^* = (1 - a_{21})/(1 - a_{12} \cdot a_{21})$ is an unstable attractor of the dynamics if $a_{12} > 1$ and $a_{21} > 1$. Show that of the remaining 3 fixed points, $(u_1^* = 0, u_2^* = 0)$ is always unstable, while $(u_1^* = 1, u_2^* = 0)$ and $(u_1^* = 0, u_2^* = 1)$ are both stable for this case of strong competition. Explain in words what it means that the overall system is "bistable" for $a_{12} > 1$, $a_{21} > 1$.

(b) Using the graphical method, i.e., sketch the phase flow in (u_1, u_2) space, to show that if $a_{12} < 1$ and $a_{21} > 1$, species 1 will dominate and species 2 will be extinct. The case of $a_{21} = 1$ and $a_{12} > 1$ is borderline between the single species dominance phase and the bistable phase of part **(a)**. This borderline case might exhibit single species dominance or bistability. Sketch the phase flow in (u_1, u_2) space for this case and show how either scenario might occur.

[Bonus for the more mathematically oriented: construct a mathematical argument to show which scenario should occur. What about the case $a_{21} = 1$ and $a_{21} < 1$?]

(c) For the special case $a_{12} = a_{21} = 1$, first show that any nontrivial fixed point must satisfy the constraint $u_1^* + u_2^* = 1$. Further, show that there could be an infinite number of such non-trivial fixed points, each corresponding uniquely to the initial condition $u_1(0), u_2(0)$. [Hint: Solve for the class of trajectories $u_2(u_1)$ in the (u_1, u_2) space by writing down an expression for $\frac{du_2}{du_1}$.]

(d) Continuing on the problem studied in part **(c)**: Suppose $r_1/r_2 = 2$. We start with initial condition $u_1(0) = 0.05$ and $u_2(0) = 0.05$. What will the final densities u_1^*, u_2^* be? Suppose we take this final population, dilute it by 10-fold and start the process over again, what would the new final densities be? If we keep on iterating the process, every time with 10x dilution, what would we eventually end up with? Explain in words what is happening in this process.

(e) Suppose you perform the same iterative process for the case $a_{12} = 0.5$, $a_{21} = 0.5$, what do you expect will happen? What is the difference between this case and the one in **(d)**?

2*. Lotka-Volterra model with mixed interaction. In this problem, we will work through the 2-species Lotka-Volterra model with mixed interaction, i.e., with species 1 retarding the growth of species 2, and species 2 enhancing the growth of species 1. In term of the parameters in Eqs. (1) and (2) above, this corresponds to $a_{21} > 0$, $a_{12} < 0$. For convenience, we define $a \equiv a_{21}$ and $b \equiv -a_{12}$ such that both a and b are positive.

(a) Sketch the phase flow for the two cases $a > 1$ and $a < 1$. Explain the nature of the fixed point in each region (i.e., what phase of the 2-species system each corresponds to.) Describe the possible dynamical behaviors in each region.

(b) Carry out perturbative analysis around the nontrivial fixed point for the case $a < 1$. Show that the fixed point is stable by showing that the real parts of the associated eigenvalues are negative.

(c) Next examine the discriminant Δ of the analysis in **(b)**, which depends on the parameters a, b, and $r \equiv r_2/r_1$. Show that if $r = 1$, the discriminant is never negative in the allowed phase space $0 < a < 1$ and $b > 0$; hence, no oscillation is expected. This can be done by finding the *minima* of Δ, located along a line $a^* = h(b)$, and showing that the minimum value of Δ is 0 along this line. Plot this line of minima $a^* = h(b)$ in the parameter space (a, b).

(d) For r slightly deviating from 1, i.e., for $r = 1 + \varepsilon$ where $|\varepsilon| \ll 1$, the value of the discriminant $\Delta(a, b; r)$ can be obtained around $r = 1$ using Taylor expansion: Show that along the line $a^* = h(b)$, $\Delta < 0$ only if $\varepsilon > 0$ (i.e., if $r_2 > r_1$). Show further that the region of negative Δ (which corresponds to damped oscillation) extends to some width $\delta(b)$ to either side of the line $a^* = h(b)$. Show that this width is small for the entire range $0 > b > \infty$ if ε is small.

(e) We learned from part **(d)** that the region of damped oscillation occurs as a narrow stripe around the line $a^* = h(b)$ for $r_2 \gtrsim r_1$. Explain qualitatively why this occurs for $r_2 > r_1$ but not for $r_1 > r_2$. Does the dependence of this region on a and b make sense? For r_2 larger than and not too close to r_1, this stripe actually expands to occupy a big part of the parameter space in the allowed region $0 < a < 1$ and $b > 0$. Demonstrate this by numerically solving the region where $\Delta(a, b; r) < 0$ for $r = 2$.

3*. Relaxational oscillator. In class we discussed the FitzHugh-Nagumo model of relaxational oscillator. Consider the following form of the model:

$$\dot{v} = f(v) - w + I_a, \tag{3}$$

$$\dot{w} = \epsilon \cdot (v - w). \tag{4}$$

We will adopt the following form of $f(v)$ that facilitates explicit solution:

$$f(v) = \begin{cases} v \cdot (v-1) & \text{for } v \leq 1 \\ (2-v) \cdot (v-1) & \text{for } v \geq 1 \end{cases}$$

(a) Calculate the value and slope of $f(v)$ at the mid-point $v = 1$ to verify the continuity of $f(v)$ and $f'(v)$ at $v = 1$. Sketch the null clines for $I_a = 1/2,\ 1,\ 2$, and sketch the flow diagram for each case. Describe qualitatively what type of dynamics you might expect the system to exhibit for each case (e.g., oscillation, threshold dynamics).

(b) Work out the eigenvalues of perturbative dynamics around the non-trivial fixed point associated for arbitrary I_a. Find the range of I_a where the system is expected to exhibit a stable limit cycle.

(c) The stable limit cycles found in **(b)** becomes relaxational oscillation if the parameter ϵ in Eq. (4) is very small. For the case $I_a = 1$, work out the values of $f(v)$ at its local minimum and maximum, denoted $f_{\min}$ and $f_{\max}$, respectively, and write down the four pieces of the trajectory of the corresponding limit cycle in the limit of small ϵ. Indicate which pieces correspond to slow and fast dynamics. Find the period of the oscillation by assuming the time spent on the fast-legs are negligible and work out the time spent on the slow-legs. The latter can be done by directly integrating the equation of motion for the slow variable. [Hint: you should get a definite integral of the form $\int dx/[x + b\sqrt{x} + c]$ which you can look up or leave as is.]