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 $\dot{u}_1(t) = \rho_1(t)/\bar{p}_{11}$ and $\dot{u}_2(t) = \rho_2(t)/\bar{p}_{22}$:

$$\dot{u}_1 \equiv r_1 u_1 (1 - u_1 - a_{12} u_2),$$
$$\dot{u}_2 \equiv r_2 u_2 (1 - u_2 - a_{21} u_1),$$

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

(a) Show 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 $a_{21} > 1$ (strong competition). 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 what it means that the overall system is “bistable” for $a_{12} > 1, a_{21} > 1$.

Solution

Coexistence

For a fixed point, we need

$$u_1^* = 0 \implies u_2^* = 0 \text{ or } u_2^* = 1$$
$$u_1^* = 1 \implies u_2^* = 0$$
We note that in all of these cases, $0 < u_*^1, u_*^2 < 1$. Thus, we have four fixed points. Now, we look at linear stability near each fixed point. In general, we have

$$\frac{d}{d\tau} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} \partial_{u_1} u_1 & \partial_{u_1} u_2 \\ \partial_{u_2} u_1 & \partial_{u_2} u_2 \end{pmatrix} \begin{pmatrix} \delta u_1 \\ \delta u_2 \end{pmatrix} = \begin{pmatrix} r_1 (1 - a_{12}u_2^* - 2u_1^*) & -r_1 a_{12}u_1^* \\ -a_{21}r_2 u_2^* & r_2 (1 - a_{21}u_1^* - 2u_2^*) \end{pmatrix} \begin{pmatrix} \delta u_1 \\ \delta u_2 \end{pmatrix}$$

First, we consider the nontrivial case. Thus, we get that

$$\frac{d}{d\tau} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \frac{1}{1 - a_{12}a_{21}} \begin{pmatrix} (a_{12} - 1) r_1 & (a_{12} - 1) a_{12}r_1 \\ (a_{21} - 1) r_2 a_{21} & (a_{21} - 1) r_2 \end{pmatrix} \begin{pmatrix} \delta u_1 \\ \delta u_2 \end{pmatrix}$$

Thus, we see that the trace of the matrix is $\frac{(a_{12} - 1)r_1 + (a_{21} - 1)r_2}{1 - a_{12}a_{21}} < 0$. And we see that the determinant is $\frac{(a_{12} - 1)(a_{21} - 1)r_2}{1 - a_{12}a_{21}} < 0$. Thus, one eigenvalue is positive, and the other is negative. To refer to the stability, remember all we need to know are the trace and the determinant of the Jacobian, and we can refer to the Poincare Diagram:

Thus, the system is an unstable attractor (saddle-node), it is an attractor in one eigen-direction and repulser in the other direction.

**Extinction**

Now, we explore the fixed point at the origin, which is the case of extinction.

$$\frac{d}{d\tau} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \begin{pmatrix} \delta u_1 \\ \delta u_2 \end{pmatrix}$$
Thus, we see that the trace of the matrix is $r_1 + r_2 > 0$. And we see that the determinant is $r_1 r_2 > 0$. In fact, obviously, the eigenvalues are

$$\lambda_1 = r_1 > 0, \lambda_2 = r_2 > 0$$

Thus, the system is always unstable. This can also be seen from the Poincare Diagram.

**Dominance**

For the case of dominance of one species (let’s say species 1), we find that

$$\frac{d}{d\tau} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} -r_1 & -a_{12} r_1 \\ 0 & r_2 (1 - a_{21}) \end{pmatrix} \begin{pmatrix} \delta u_1 \\ \delta u_2 \end{pmatrix}$$

Thus, we see that the trace of the matrix is $r_2 (1 - a_{21}) - r_1 < 0$. And we see that the determinant is $r_1 r_2 (a_{21} - 1) > 0$. Thus, the eigenvalues are

$$\lambda_+ = -r_1 < 0, \lambda_- = r_2 (1 - a_{21}) < 0$$

which are both real and negative. Thus, the system is stable in either case and the system is bistable since there are two stable points, and the fixed point that is attained is decided by the initial conditions. The plot for the system looks as follows:
(b) In class, we showed by the graphical method 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 case you expect to occur.]

Solution

Thus, we see that the solution is bistable in that for an initial concentration of $u_2 = 0$, the system will go towards the dominance of species 1, but if there is a small perturbation and $u_2 > 0$, then species 2 will eventually dominate.

To see it mathematically, we can just use the solution above as it still holds. First, we note that we have no non-trivial fixed point. The only fixed points are the cases of dominance, and extinction. For the case of dominance of species 1, we have that the determinant is 0, and the trace is $-r_1 < 0$. Thus, the eigenvalues are 0 and $-r_1$ and the solution is stable along one eigenvector. This happens to be the case along the $u_2 = 0$ axis. ¹ If we look at the case of dominance of species 2, we see that $\lambda = -r_2, -r_1 \left( a_{12} - 1 \right) < 0$, thus the system is stable.

¹As an aside, in general, one cannot make any statement regarding the stability of a fixed point in the case that one of the eigenvalues is 0 (do not trust the Poincare diagram above for this case, that is only for linear dynamics). Even if it is stable in one eigendirection, it may be unstable in the other. And in fact, the behaviour of the system is actually determined non-locally as high order terms start playing a role. To understand the dynamics of a system when one of the eigenvalues has a vanishing real part, we have to explore the center manifold, and if an eigenvalue is exactly zero, we have to explore the slow manifold. These can be complicated mathematical structures, and we won’t explore it. Usually, plotting the system is sufficient.
(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 $\frac{du_2}{du_1}$.

Solution

\[ \dot{u}_1 = 0 \implies u_1 = 0 \text{ or } u_1 + u_2 = 1 \]
\[ \dot{u}_2 = 0 \implies u_2 = 0 \text{ or } u_1 + u_2 = 1 \]

Thus, we have two sets of solutions: $(u_1, u_2) = (0, 0)$, or the line of fixed points, $u_1 + u_2 = 1$. We will now see that the entire set of fixed non-trivial points is accessed, and is stable. We look at the trajectory of densities for an initial density of $u_1(0), u_2(0)$.

\[
\frac{du_2}{du_1} = \frac{r_2 u_2}{r_1 u_1} \implies \frac{du_2}{r_2 u_2} = \frac{du_1}{r_1 u_1} \implies \ln \frac{u_2(t)}{u_2(0)} = \frac{r_2}{r_1} \ln \frac{u_1(t)}{u_1(0)} \implies \frac{u_2(t)}{u_2(0)} = \left( \frac{u_1(t)}{u_1(0)} \right)^{\frac{r_2}{r_1}}
\]

At $t = \infty$, $u_1^* = 1 - u_2^*$

\[ u_1^* + (u_1^*)^{\frac{r_2}{r_1}} \frac{u_2(0)}{u_1(0)^{\frac{r_2}{r_1}}} = 1 \]

We define

\[ \frac{u_2(0)}{u_1(0)^{\frac{r_2}{r_1}}} \equiv a, \frac{r_2}{r_1} \equiv r \]

\[ \implies u_1^* + a (u_1^*)^r = 1 \]

We will simplify the algebra by using $u \equiv u_1^*$

\[ au^r = 1 - u \]

We know that there is always a unique solution to this, by simply plotting the two curves. $au^r$ is always a monotonically increasing function starting from the origin, and $1 - u$ is a straight line. They must intersect at exactly one point. Thus, for each $a, r$, there is a solution (we can even show that for $a_1 \neq a_2$, the solutions are different for the same $r$, but it should also be obvious from the graph), and by varying $a$ or $r$, we note that we get different solutions, and thus we have an infinite number of solutions.
The graph of such a solution is as follows:
(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.

Solution

In this case, following our notation from earlier, $r = 1/2$, $a = \sqrt{0.05} \approx 0.22$. Thus,

$$\sqrt{0.05}u = 1 - u \implies u \approx 0.8 \implies (u_1^*, u_2^*) = (0.8, 0.2)$$

If we dilute 10x again, then $(u_1^0, u_2^0) = (0.08, 0.02) \implies a = 0.07$. Thus, $u = 0.93 \implies (u_1^*, u_2^*) = (0.93, 0.07)$. Thus, with each step, the concentration increases. Eventually, we expect that $(u_1^*, u_2^*) \to (1, 0)$. This is because species 1 grows much faster, thus it will always end up with a greater proportion than species 2.

(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 that in (d)?

Solution

In the case of $a_{12} < 1, a_{21} < 1$, we had that there was a globally stable fixed point which was the case of coexistence. Thus, we will always obtain that solution, regardless of how we do our dilutions. The non-trivial fixed point in this case is $(u_1^*, u_2^*) = (2/3, 2/3)$. The difference in this case is because there is a single global fixed point for every initial condition. We also note for the same reason, the differences in $r_i$ do not end up mattering.
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), (2) above, this corresponds to $a_{21} > 0, a_{12} < 0$. For convenience, we define $a \equiv a_{21} > 0$ and $b \equiv -a_{12}$ such that both $a$ and $b$ are positive.

\[
\begin{align*}
\dot{u}_1 &\equiv r_1 u_1 (1 - u_1 + bu_2), \\
\dot{u}_2 &\equiv r_2 u_2 (1 - u_2 - au_1),
\end{align*}
\]

(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.

Solution

The two flows are plotted below (left for $a > 1$, and right for $a < 1$), with nullclines (blue for $\dot{u}_1 = 0$, and orange for $\dot{u}_2 = 0$).

Thus, for $a > 1$, we have dominance of species 1 (which makes sense as this is the case of strong competition due to species 1), and there is coexistence for $a < 1$ (as this is the case of weak competition from species 1). In neither case will species 2 win, because the presence of species 2 is actually beneficial to species 1. If $a > 1$, then it is exactly as earlier, and the only stable fixed point is the case of dominance of species 1. If $a < 1$, at the fixed point of coexistence, the determinant is $> 0$ and the trace is $< 0$. Thus, depending on the $r_1, r_2$, we have either a spiral sink or a simple sink.

In general, we note that first there is a large change in $u_1$, and then there is movement along the nullcline for $\dot{u}_1 = 0$. Thus, species 2 doesn't really drive the dynamics of the system: it just helps species 1 get where it wants to be, and then species 1 equilibrates to the global
fixed point. We also note that the carrying capacity of species 1 is no longer 1, as species 2 allows for a larger number to be supported.

(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.

**Solution**

Why repeat calculations when we did it in generality already? We can borrow the result from earlier (Prob. 1a), and we see that the trace of the matrix is

\[
Tr(M) = \frac{(a_{12} - 1) r_1 + (a_{21} - 1) r_2}{1 - a_{12}a_{21}} = \frac{(-b - 1) r_1 + (a - 1) r_2}{1 + ab} < 0.
\]

And we see that the determinant is

\[
det(M) = \frac{(a_{12} - 1)(a_{21} - 1) r_1 r_2}{1 - a_{12}a_{21}} = \frac{(b + 1)(1 - a) r_1 r_2}{1 + ab} < 0.
\]

Thus, the real parts of the eigenvalues are less than 0 and the system is stable.

(c) Next examine the discriminant \( \Delta \) 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 \( b > 0 \) and \( 0 < a < 1 \); hence, no oscillation. This can be done by finding the minima of \( \Delta \), located along a line \( a^* = h(b) \), and showing that the minimum value is 0 along this line. Plot this line of minima \( a^* = h(b) \) in the parameter space \( (a, b) \).

**Solution**

\[
\Delta = \frac{Tr(M)^2}{4} - \det A = \left(\frac{(-b - 1) r_1 + (a - 1) r_2}{2 (1 + ab)}\right)^2 - \frac{(b + 1)(1 - a) r_1 r_2}{1 + ab}
\]

Now we plug in \( r_2 = r_1 \) and factor it out

\[
\Delta = r_1^2 \left[ \left(\frac{(-b - 1) + (a - 1)}{2 (1 + ab)}\right)^2 - \frac{(b + 1)(1 - a)}{1 + ab} \right]
\]

In fact, we find that \( \Delta \) is a perfect square:

\[
\Delta = \left(\frac{r_1 (a - b + 2ab)}{2 (1 + ab)}\right)^2
\]

We could also have done it by noting that \( \frac{\partial \Delta}{\partial a} = 0 \) along the line \( a^* = \frac{b}{1 + 2b} \). Along this line, \( \Delta = 0 \), and thus, the minimum is 0. Thus, there is never an oscillation. We plot \( a^* = h(b) = \frac{b}{1 + 2b} \) below:
(d) For $r$ slightly deviating from 1, i.e., for $r = 1 + \epsilon$ where $|\epsilon| \ll 1$, 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 $\epsilon > 0$ (i.e., if $r_2 > r_1$). Show further that the region of negative $\Delta$ (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 of $0 < b < \infty$ if $\epsilon$ is small.

Solution

\[
\Delta = \left(\frac{(-b - 1) r_1 + (a - 1) r_2}{2 (1 + ab)}\right)^2 - \frac{(b + 1) (1 - a) r_1 r_2}{1 + ab}
\]

\[
= \left(\frac{r_1}{1 + ab}\right)^2 \left[ (1 + b + r (1 - a))^2 - 4r (1 + b) (1 - a) (1 + ab) \right]
\]

\[
\frac{\partial \Delta}{\partial r} = \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2 (1 + b + r (1 - a)) (1 - a) - 4 (1 + b) (1 - a) (1 + ab) \right]
\]

\[
\left. \frac{\partial \Delta}{\partial r} \right|_{r=1} = \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2 (1 + (1 - a)) (1 - a) - 4 (1 + b) (1 - a) (1 + ab) \right]
\]

\[
= \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2 (1 - a) (2 + b - a - 2 (1 + ab)) \right]
\]

\[
= \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2 (1 - a)(-a - 2ab - b - 2ab^2) \right]
\]

\[
= \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2 (a - 1)(a + 2ab + b + 2ab^2) \right]
\]

We Taylor expand $\Delta$ around $r = 1$

\[
\Delta \approx \Delta_{r=1} + \left(\frac{r_1}{1 + ab}\right)^2 \left[ 2\epsilon (a - 1)(a + 2ab + b + 2ab^2) \right]
\]

Along the line $a^* = h(b)$

\[
\Delta \approx 2\epsilon \left(\frac{r_1}{1 + ab}\right)^2 \frac{2b (1 + b)^2}{1 + 2b} (a - 1) = -2\epsilon \left(\frac{r_1^2 (1 + 2b)}{(1 + b)^2}\right) \frac{2b}{1 + 2b} = -\epsilon \frac{4br_1^2}{1 + b}
\]
Thus, $\Delta < 0$ if $\epsilon > 0$. Thus, we see that there are damped oscillations in this regime of mixed interactions. Now, we want to see how for we can deviate from this line and still have $\Delta < 0$. For this, we will Taylor expand around $a^* = \frac{b}{1 + 2b}$

$$
\Delta = \left(\frac{(-b - 1) r_1 + (a - 1) r_2}{2 (1 + ab)}\right)^2 - \frac{(b + 1) (1 - a) r_1 r_2}{1 + ab}
$$

$$
\frac{\partial \Delta}{\partial a} = \frac{(-1 + a) (1 + b) r^2 r_1^2}{2 (1 + ab)^3}
$$

$$
\frac{\partial \Delta}{\partial a}\bigg|_{a = \frac{b}{1 + 2b}} = \frac{(b + 2b^2 - r) (r - 1) (r_1 + 2br_1)^2}{2 (1 + b)^4}
$$

But $\frac{\partial \Delta}{\partial a} \bigg|_{a = \frac{b}{1 + 2b}, r = 1} = 0$, so we must go to the 2nd term in the Taylor series

$$
\frac{\partial^2 \Delta}{\partial a^2}\bigg|_{a = \frac{b}{1 + 2b}, r = 1} = \frac{(1 + 2b)^4 r_1^2}{2 (1 + b)^4}
$$

Now we consider $\Delta$ at $r = 1 + \epsilon$ and $a = \frac{b}{1 + 2b} + \delta$

$$
\Rightarrow \Delta \approx \frac{\delta^2 (1 + 2b)^4 r_1^2}{2 (1 + b)^4} - \frac{4br_1^2}{1 + b}
$$

$$
\Delta < 0 \Rightarrow \frac{\delta^2 (1 + 2b)^4 r_1^2}{2 (1 + b)^4} < \epsilon \frac{4br_1^2}{1 + b}
$$

$$
\Rightarrow -4\sqrt{\epsilon} \sqrt{\frac{b (1 + b)^3}{(1 + 2b)^2}} < \delta < 4\sqrt{\epsilon} \sqrt{\frac{b (1 + b)^3}{(1 + 2b)^2}}
$$

Thus, as $b \to \infty$, $-\sqrt{\epsilon} < \delta < \sqrt{\epsilon}$. Thus, even if $b$ is very large, this strip is thin for small $\epsilon$. We should note that even if $\epsilon$ is large, as we had shown earlier, this strip only exists for $0 < a < 1$. We can see the plot for the regions where $\Delta < 0$ for a wide range of $\epsilon$ below.
(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 \( b \) and \( a \) 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 \( b > 0 \) and \( 0 < a < 1 \). Demonstrate this by numerically solving the region where \( \Delta(a,b;r) < 0 \) for \( r = 2 \).

**Solution**

In our case, species 1 is aided by the presence of species 2. Thus, the reason why you have a damped oscillation in this case is because species 2 wants to grow really fast, but this only benefits species 1, which in turn harms species 2. Thus, there is an oscillation about the fixed point, until the system stabilises. It can be understood as an oscillator of the following form:

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This can be seen in the dynamics below for \( r > 1 \)
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For $r_1 > r_2$, species 1, which is benefiting in this relationship, is able to utilise the presence of species 2 to quickly stabilise (we can see this below as the flow quickly goes to the nullcline for $\dot{u}_1 = 0$).

As $r \to \infty$, we see (in the grid of figures shown above) that it slowly occupies the entire region where damped oscillations are possible: $0 < a < 1$
3 Relaxational oscillator

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

\[ \dot{v} \equiv f(v) - w + I_a, \quad (5) \]
\[ \dot{w} \equiv \epsilon (v - w) \quad (6) \]

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 isoclines 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).

Solution

\( f(v = 1) = 0 \) for both pieces of the piece function, thus it is continuous. \( f'(v = 1) = 1 \) in both cases, and thus the function is differentiable. We have the flow diagrams for each case below:

In this case, we see the presence of a version of threshold dynamics: If we start at a point where \( \dot{v} < 0 \), then the system quickly goes to the stable fixed point. However, if we start at a point where \( \dot{v} > 0 \), then the system will first lead to an increase in \( v \), and then we enter a regime of damped oscillations.
In this case, we see always have oscillations (actually, it is a canard trajectory, see explanation below), regardless of where we start. This is because no matter where we start, there is no region where the flow leads directly to the fixed point.

In this case, we again have a version of threshold dynamics, but the cases are reversed: If we start at a point where $\dot{v} > 0$, then the system quickly goes to the stable fixed point. However, if we start at a point where $\dot{v} < 0$, then the system will first lead to an increase in $v$, and then we enter a regime of damped oscillations.

It must be noted that the FitzHugh-Nagumo model does not have a well-defined firing threshold. This feature is the consequence of the absence of all-or-none responses (threshold
phenomena), and it is related, from the mathematical point of view, to the absence of a saddle equilibrium. The apparent illusion of threshold dynamics and all-or-none responses is due to the existence of the “quasi-threshold”, which is a canard trajectory\(^2\) that follows the unstable (middle) branch of the N-shaped V-nullcline. Nearby trajectories diverge sharply away from the canard trajectory to the left or right, producing an apparently “all-or-none” response and threshold-like behavior. (A point moving along a canard trajectory is like a tightrope walker walking slowly along a rope; if he loses his balance, he quickly falls away from the rope to one side or the other.).

(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.

Solution

For a solution to exist in the regime \(v \leq 1\), we need

\[
v \cdot (v - 1) + I_a = v \implies v^* = 1 - \sqrt{1 - I_a}
\]

Similarly, for a solution to exist in the regime \(v \geq 1\), we need

\[
(2 - v) \cdot (v - 1) + I_a = v \implies v^* = 1 + \sqrt{I_a - 1}
\]

Thus, if \(I_a \leq 1\), then the only solution is \(1 - \sqrt{1 - I_a}\), and if \(I_a \geq 1\), then the only solution is \(1 + \sqrt{I_a - 1}\). In either case, we note that \(f'(v^*) = 1 - 2\sqrt{|I_a - 1|}\) To find the eigenvalues, we note that the Jacobian is

\[
J = \begin{pmatrix}
    f'(v^*) & -1 \\
    \epsilon & -\epsilon
\end{pmatrix}
\]

For stable limit cycles, we need \(Tr(J) > 0\), thus \(f'(v^*) > \epsilon\). Thus,

\[
1 - 2\sqrt{|I_a - 1|} > \epsilon \implies \sqrt{|I_a - 1|} < \frac{1 - \epsilon}{2}
\]

\[
\implies |I_a - 1| < \left(\frac{1 - \epsilon}{2}\right)^2 \implies 1 \leq I_a < 1 + \left(\frac{1 - \epsilon}{2}\right)^2 \quad \text{or} \quad 1 - \left(\frac{1 - \epsilon}{2}\right)^2 < I_a \leq 1
\]

Thus, for stable limit cycles, we need:

\[
1 - \left(\frac{1 - \epsilon}{2}\right)^2 < I_a < 1 + \left(\frac{1 - \epsilon}{2}\right)^2
\]

We note that we do not care about the discriminant, since this is a closed system: there must be a stable limit cycle if there is no sink.

\(^2\)A canard is a solution of a singularly perturbed system which follows an attracting slow manifold \(S_a\), passes close to a bifurcation point \(p \in L\) of the critical manifold, and then follows a repelling slow manifold \(S_r\) for a considerable amount of time. In other words, it is a solution which passes close to the nullcline and then leaves the nullcline to move quickly to be near another nullcline, and repeats the process over and over again.
(c) The stable limit cycles found in (b) becomes relaxational oscillation if the parameter $\epsilon$ 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 $f_{\text{min}}$ and $f_{\text{max}}$, respectively, and write down the four pieces of the trajectory of the corresponding limit cycle in the limit of small $b$. 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.

**Solution**

The minimum for $f$ occurs at $v = 1/2$, and $f_{\text{min}} = -1/4$. The maximum of $f$ occurs at $v = 3/2$, and $f_{\text{max}} = 1/4$. In the limit of $b \to 0$, we get the following limit cycle (thanks to Palka for the beautiful figure!)

![Diagram showing the limit cycle and nullclines](image)

Along this trajectory, (suppose we start at an arbitrary point, (1,0)), first we move quickly to the right to the $\dot{v} = 0$ nullcline. The dynamics push us just over the nullcline (as $\dot{w} > 0$), and then we follow the nullcline (just marginally to the right of it) slowly, as $w$ changes very slowly. Then, once we reach the point of $f_{\text{max}}$, we note that $\dot{w} > 0$. So we do not follow the nullcline anymore, and move to the left. As we are no longer following the slow nullcline, change in $v$ is rapid, and we move very quickly to the left in leg B, until we hit the $\dot{v} = 0$ nullcline again on the left side of the N-curve. Again, we quickly fall into the left side of this nullcline (since now $\dot{w} < 0$), and we follow the nullcline slowly until we reach the point of $f_{\text{min}}$ in leg C. Now again, we can no longer follow the nullcline and so we make a dash for the right side of the nullcline in leg D.

We note that as the change in $v$ is much more rapid than the change in $w$, the fast legs are B and D, and the slow legs are A and C. We will ignore the time spent on the fast legs, and integrate over the slow legs. The slow legs happen over the $\dot{v} = 0$ nullcline, and thus, we have that $w = f(v) + I_a$. Let’s start by looking at the leg A. In this case, we have the following equation for $v$:

$$w = (2 - v)(v - 1) + 1 = 3v - 1 - v^2 \implies v = \frac{3}{2} \pm \sqrt{\frac{5}{4} - w}$$
We note that the A leg starts after the maximum of $f(v)$, and thus $v > 3/2 \implies v = \frac{3}{2} + \sqrt{\frac{5}{4} - w}$

$$\frac{dw}{dt} = \epsilon \left( \frac{3}{2} + \sqrt{\frac{5}{4} - w - w} \right)$$

$$\implies t_A = \frac{1}{\epsilon} \int_{3/4}^{5/4} \frac{dw}{\frac{3}{2} + \sqrt{\frac{5}{4} - w - w}}$$

The limits of the leg are from when $f_{\text{min}} + I_a$ to $f_{\text{max}} + I_a$. We make a simple substitution: $s \equiv \frac{5}{4} - w$, and thus we get:

$$\implies t_A = \frac{1}{\epsilon} \int_{0}^{1/2} \frac{ds}{\frac{1}{4} + s + \sqrt{s}}$$

Again by substituting $u = \sqrt{s}$, we get

$$\implies t_A = \frac{1}{\epsilon} \int_{0}^{1/\sqrt{2}} \frac{2udu}{\frac{1}{4} + u^2 + u} = \frac{1}{\epsilon} \int_{0}^{1/\sqrt{2}} \frac{2udu}{(u + 1/2)^2}$$

Again, $x \equiv u + 1/2$

$$\implies t_A = \frac{1}{\epsilon} \int_{1/2}^{1/2 + 1/\sqrt{2}} \frac{(2x - 1)dx}{x^2}$$

$$\implies t_A = \frac{1}{\epsilon} \int_{1/2}^{1/2 + 1/\sqrt{2}} \frac{2dx}{x} - \frac{dx}{x^2}$$

$$\implies t_A = \frac{2}{\epsilon} \left( -2 + \sqrt{2} + \ln \left( 1 + \sqrt{2} \right) \right)$$

Similarly, for part C,

$$\frac{dw}{dt} = \epsilon \left( \frac{1}{2} - \sqrt{w - \frac{3}{4} - w} \right)$$

$$\implies t_C = \frac{1}{\epsilon} \int_{3/4}^{5/4} \frac{dw}{\frac{1}{2} - \sqrt{w - \frac{3}{4} - w}}$$

The limits of the leg are from when $f_{\text{min}} + I_a$ to $f_{\text{max}} + I_a$. We make a simple substitution: $s \equiv w - \frac{3}{4}$, and thus we get:

$$\implies t_C = \frac{1}{\epsilon} \int_{0}^{1/2} \frac{ds}{\frac{1}{4} + s + \sqrt{s}} = \frac{2}{\epsilon} \left( -2 + \sqrt{2} + \ln \left( 1 + \sqrt{2} \right) \right)$$

Thus, total time period of oscillation is

$$t \approx \frac{4}{\epsilon} \left( -2 + \sqrt{2} + \ln \left( 1 + \sqrt{2} \right) \right)$$
4 Competition for nutrient

Two species described by densities $\rho_1(t)$ and $\rho_2(t)$ grow on the same nutrient source, of concentration $n(t)$. Suppose the growth rate of species $i$ is given by the Monod growth law, 
\[ r_i(n) = r_i^0 \cdot \frac{n}{n + K_i} \]

The death rate is given by $\mu_i$ and the nutrient influx is $j_0$. Find a criterion on the physiological parameters $(r_i^0, K_i, \mu_i)$ in order for species $i$ to survive in the steady state.

Solution

Suppose species 1 survives. Thus, nutrient concentration is 
\[ n_1^* = \frac{K_1 \mu_1}{r_1^0 - \mu_1} \]

Let’s check the stability of the point. The Jacobian is given by
\[
J = \begin{pmatrix}
\frac{r_1^0 n_1^*}{n_1^* + K_1} - \mu_1 & 0 \\
0 & \frac{r_2^0 n_2^*}{n_2^* + K_2} - \mu_2
\end{pmatrix}
\]

Thus, for the system to be stable, we need:
\[
\frac{r_2^0 n_2^*}{n_1^* + K_2} - \mu_2 < 0 \implies \frac{r_2^0 n_2^*}{n_1^* + K_2} < \mu_2 \implies n_1^* = \frac{K_1 \mu_1}{r_1^0 - \mu_1} < \frac{K_2 \mu_1}{r_2^0 - \mu_2}
\]

By symmetry, the condition for survival of species 2 is $n_2^* < n_1^*$. Thus, the species that needs the lower concentration at steady state survives. This can be understood intuitively as the less food you need, the better you are at surviving!