

PHYS 239
Spatiotemporal Dynamics in Biological Systems
Winter 2022

Solution of Homework #2

Prepared by Leonardo Pacciani-Mori
lpaccianimori@physics.ucsd.edu

February 2nd, 2022

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 $u_2(t) = \rho_2(t)/\tilde{\rho}_{22}$:

$$\dot{u}_1 = r_1 u_1 \cdot (1 - u_1 - a_{12} u_2) \quad (1)$$

$$\dot{u}_2 = r_2 u_2 \cdot (1 - u_2 - a_{21} u_1) \quad (2)$$

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 $u_1^* = (1 - a_{12})/(1 - a_{12}a_{21})$, $u_2^* = (1 - a_{21})/(1 - a_{12}a_{21})$ 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 $a_{12} > 1$ and $a_{21} > 1$*

Solution

To show algebraically if each of the fixed point is stable or unstable, we compute the Jacobian matrix of the system:

$$J(u_1, u_2) = \begin{pmatrix} \frac{\partial \dot{u}_1}{\partial u_1} & \frac{\partial \dot{u}_1}{\partial u_2} \\ \frac{\partial \dot{u}_2}{\partial u_1} & \frac{\partial \dot{u}_2}{\partial u_2} \end{pmatrix} = \begin{pmatrix} r_1(1 - 2u_1 - a_{12}u_2) & -r_1 a_{12} u_1 \\ -r_2 a_{21} u_2 & r_2(1 - 2u_2 - a_{21}u_1) \end{pmatrix}$$

and evaluate it in the fixed points. Normally we would compute the eigenvalues explicitly and check if they are positive or negative, but in this case the computation of the eigenvalues can be complicated. To avoid this, we use a slightly different approach. Remember that the trace $\text{tr } M$ of any matrix M (which is the sum of all the elements on the diagonal) is equal to the sum of its eigenvalues, while the determinant $\det M$ is equal to their product, i.e.:

$$\text{tr } M = \lambda_1 + \lambda_2 \quad \det M = \lambda_1 \cdot \lambda_2$$

Therefore, by checking the signs of the trace and the determinant of a matrix, we can understand if one of the eigenvalues is positive/negative without computing them explicitly.

Now, for the nontrivial fixed point we have:

$$J(u_1^*, u_2^*) = \begin{pmatrix} \frac{r_1(1-a_{12})}{a_{12}a_{21}-1} & \frac{r_1a_{12}(1-a_{12})}{a_{12}a_{21}-1} \\ \frac{r_2a_{21}(1-a_{21})}{a_{12}a_{21}-1} & \frac{r_2(1-a_{21})}{a_{12}a_{21}-1} \end{pmatrix}$$

The trace and the determinant of this matrix are:

$$\begin{aligned} \text{tr } J(u_1^*, u_2^*) &= \frac{r_1(1-a_{12})}{a_{12}a_{21}-1} + \frac{r_2(1-a_{21})}{a_{12}a_{21}-1} = \frac{r_1(1-a_{12}) + r_2(1-a_{21})}{a_{12}a_{21}-1} < 0 \\ \det J(u_1^*, u_2^*) &= \frac{r_1r_2(1-a_{12})(1-a_{21})(1-a_{12}a_{21})}{a_{12}a_{21}-1} < 0 \end{aligned}$$

(where the inequalities come from the fact that $a_{12}, a_{21} > 1$). Therefore, since both the sum and the product of the eigenvalues are negative, one of them is positive and one of them is negative. Since one of the eigenvalues of the Jacobian matrix is positive, the fixed point is unstable.

Just as a reference, if we wanted to compute the eigenvalues of this matrix algebraically we would find:

$$\begin{aligned} \lambda_{\pm} &= \frac{1}{2(a_{12}a_{21}-1)} \left(r_1(1-a_{12}) + r_2(1-a_{21}) \pm \right. \\ &\quad \left. \pm \sqrt{[r_1(a_{12}-1) + r_2(a_{21}-1)]^2 - 4r_1r_2(a_{12}-1)(a_{21}-1)(a_{12}a_{21}-1)} \right) \end{aligned}$$

which is definitely a complicated expression to handle.

For $(u_1^* = 0, u_2^* = 0)$ we have:

$$J(0, 0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}$$

This is a diagonal matrix, so we can say immediately that its eigenvalues are r_1 and r_2 , which are both positive: $(u_1^* = 0, u_2^* = 0)$ is unstable.

For $(u_1^* = 1, u_2^* = 0)$ we have:

$$J(1, 0) = \begin{pmatrix} -r_1 & -r_1a_{12} \\ 0 & r_2(1-a_{21}) \end{pmatrix}$$

whose trace and determinant are:

$$\text{Tr } J(1, 0) = r_2(1-a_{21}) - r_1 < 0 \quad \det J(1, 0) = -r_1r_2(1-a_{21}) > 0$$

Since the product of the eigenvalues is positive but their sum is negative, both of them are negative and so the fixed point is stable. As a reference, the eigenvalues of the Jacobian matrix in this case are $\lambda_1 = -r_1 < 0$ and $\lambda_2 = r_2(1-a_{21}) < 0$.

Similarly, for $(u_1^* = 0, u_2^* = 1)$ we have:

$$J(0, 1) = \begin{pmatrix} r_1(1-a_{12}) & 0 \\ -r_2a_{21} & -r_2 \end{pmatrix}$$

whose trace and determinant are:

$$\text{tr } J(0, 1) = r_1(1 - a_{12}) - r_2 < 0 \quad \det J(0, 1) = -r_1 r_2(1 - a_{12}) > 0$$

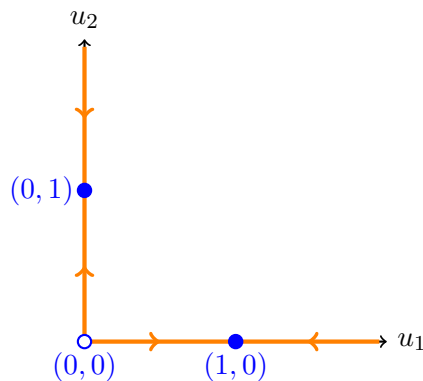
so also in this case both eigenvalues are negative (as a reference, $\lambda_1 = r_1(1 - a_{12}) < 0$ and $\lambda_2 = -r_2 < 0$), and the fixed point is stable.

When we say that the system is “bistable” for $a_{12} > 1$ and $a_{21} > 1$ we mean that the system exhibits two stable fixed points, and the initial conditions will determine whether the system will end up in one or the other.

- (b) Using the graphical method, 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 would occur. What about the case $a_{21} = 1$ and $a_{21} < 1$?]

Solution

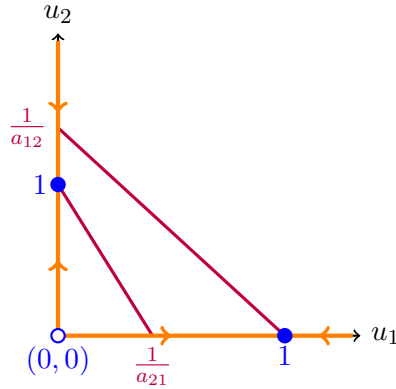
First of all, if $u_2 = 0$ we have $\dot{u}_1 = r_1 u_1(1 - u_1)$ and if $u_1 = 0$ we have $\dot{u}_2 = r_2 u_2(1 - u_2)$, so the flow along the axes will look like this:



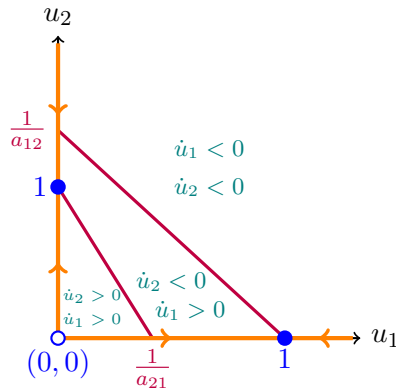
Looking at the equations of the system, we will have:

$$\begin{cases} \dot{u}_1 > 0 \\ \dot{u}_2 > 0 \end{cases} \Rightarrow \begin{cases} 1 - u_1 - a_{12}u_2 > 0 \\ 1 - u_2 - a_{21}u_1 > 0 \end{cases} \Rightarrow \begin{cases} u_2 < \frac{1-u_1}{a_{12}} \\ u_2 < 1 - a_{21}u_1 \end{cases}$$

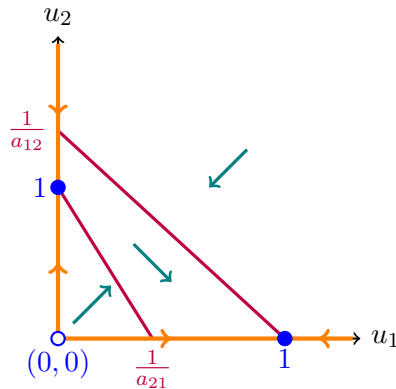
where in the first step we have divided by u_1 and u_2 since $u_1, u_2 \neq 0$. The two nullclines look like this:



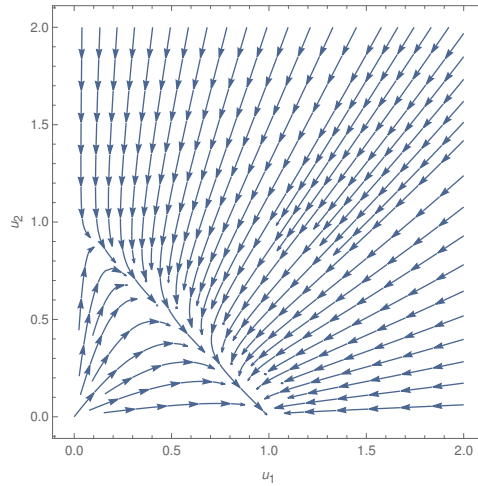
These are the areas where \dot{u}_1 and \dot{u}_2 are positive/negative:



and therefore this is the general behavior of the flow in the three areas:

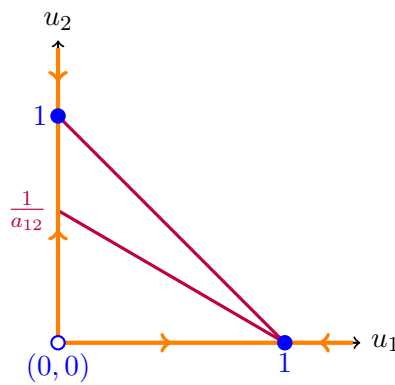


We can therefore see that, if $u_1(0), u_2(0) \neq 0$ the solutions will approach the region near the line that connects the points $(0, 1)$ and $(1, 0)$ and then move towards $(1, 0)$, i.e. the fixed point where species 1 dominates and species 2 is extinct. As a reference, this is how the *actual* streamplot of the system looks like for $r_1 = r_2 = 1$, $a_{12} = 0.75$ and $a_{21} = 1.25$:

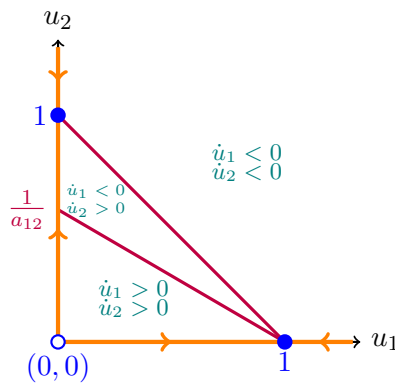


Therefore, as soon as $u_1(0) > 0$ the system will *always* end up in the fixed point ($u_1^* = 1, u_2^* = 0$) where species 1 dominates and species 2 is extinct.

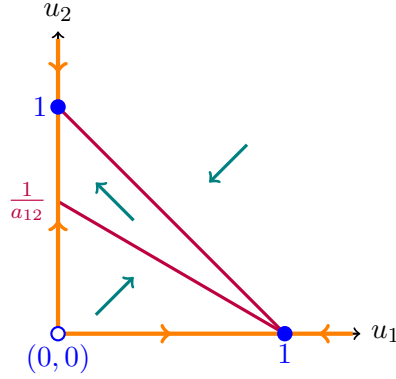
Let us now consider the case $a_{21} = 1, a_{12} > 1$. In this case the nullclines look like this:



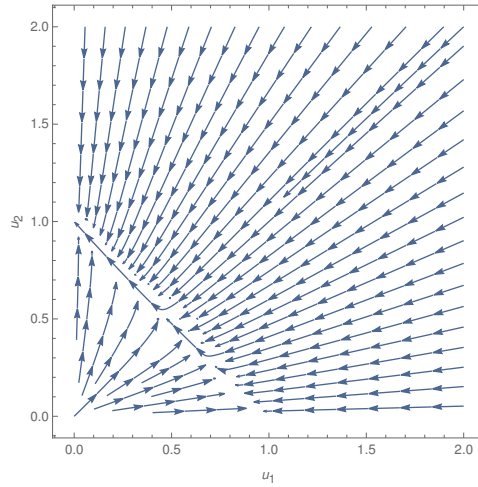
and the areas where \dot{u}_1 and \dot{u}_2 are positive/negative are:



so the general behavior of the flow is:



Therefore, in this case the solutions of the system will *always* go towards $(u_1^* = 0, u_2^* = 1)$, i.e., species 2 dominates and species 1 is extinct. This means that there can't be bistability in the case $a_{21} = 1$ and $a_{12} > 1$. This is how the *actual* streamplot of the system looks like for $r_1 = r_2 = 1$, $a_{12} = 1.1$ and $a_{21} = 1$:



Let's see how to show this mathematically. Let us Taylor expand the system around $(u_1^* = 1, u_2^* = 0)$ by defining

$$x := u_1 - 1 \quad y := u_2$$

and rewriting the equations of the system. By ignoring all the terms beyond first order in x and y , we get:

$$\begin{cases} \dot{x} = -x - a_{12}y \\ \dot{y} = y(-x - y) \end{cases} \Rightarrow \frac{d}{dt} (\ln y - x) = (a_{12} - 1)y \Rightarrow \ln \frac{y(t)}{y(0)} - (x(t) - x(0)) = (a_{12} - 1) \int_0^t y(t') dt'$$

The integral is always positive because $y(t) = u_2(t) > 0$. Therefore, if $a_{12} > 1$ we have:

$$\ln \frac{y(t)}{y(0)} - (x(t) - x(0)) = (a_{12} - 1) \int_0^t y(t') dt' > 0 \Rightarrow \ln \frac{y(t)}{y(0)} > (x(t) - x(0)) \Rightarrow y(t) > y(0)e^{x(t) - x(0)}$$

The plot of $y(t) = y(0)e^{x(t) - x(0)}$ is the following:

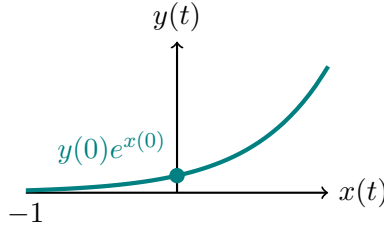


Figure 1: Plot of $y(t)$ as a function of $x(t)$.

When $a_{12} > 1$, for any initial condition the solution will *never* go towards the fixed point $(x^* = 0, y^* = 0) = (u_1^* = 1, u_2^* = 0)$ because $y(t)$ will *always* stay above the curve shown in figure 1. Therefore, there cannot be bistability in this case¹.

On the other hand, if $a_{12} < 1$ we have:

$$\ln \frac{y(t)}{y(0)} - (x(t) - x(0)) = (a_{12} - 1) \int_0^t y(t') dt' < 0 \Rightarrow \ln \frac{y(t)}{y(0)} < (x(t) - x(0)) \Rightarrow y(t) < y(0)e^{x(t) - x(0)}$$

The solution will always stay below the curve in figure 1, so the only fixed point towards which we can go is $(x^* = 0, y^* = 0) = (u_1^* = 1, u_2^* = 0)$ and thus also in this case there cannot be bistability.

- (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 nontrivial 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 du_2/du_1 .]

Solution

The equations of the system in this case are:

$$\begin{cases} \dot{u}_1 = r_1 u_1^* (1 - u_1^* - u_2^*) \\ \dot{u}_2 = r_2 u_2^* (1 - u_2^* - u_1^*) \end{cases}$$

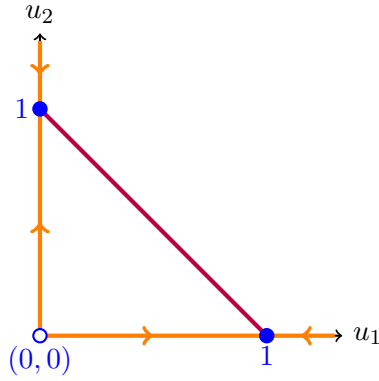
The expression of the fixed points is:

$$\begin{cases} \dot{u}_1 = 0 \\ \dot{u}_2 = 0 \end{cases} \Rightarrow \begin{cases} r_1 u_1^* (1 - u_1^* - u_2^*) = 0 \\ r_2 u_2^* (1 - u_2^* - u_1^*) = 0 \end{cases} \Rightarrow u_1^* + u_2^* = 1$$

where we have assumed $u_1^*, u_2^* \neq 0$. This is one linear equation in two variables, and as such admits infinite solutions²: the fixed points will lie on the line that connects $(u_1^* = 0, u_2^* = 1)$ to $(u_1^* = 1, u_2^* = 0)$:

¹Remember: a system is *bistable* if there are two (or more) possible stable fixed points, and the initial conditions determine in which one we end up. Since we have just shown that we can *never* end up in one of the two fixed points of the system, there cannot be bistability.

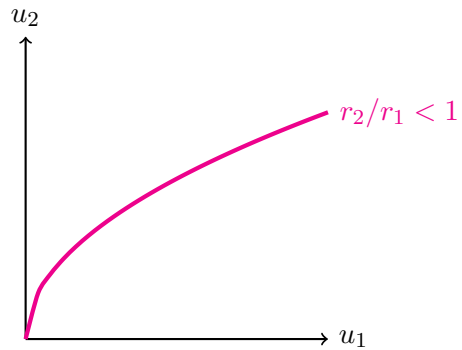
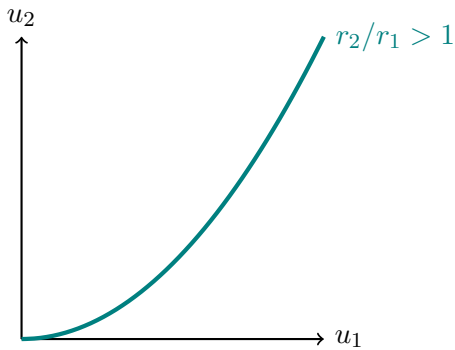
²Remember: if you have in general a system of E linear equations in V variables, if $V > E$ the system will admit infinite solutions



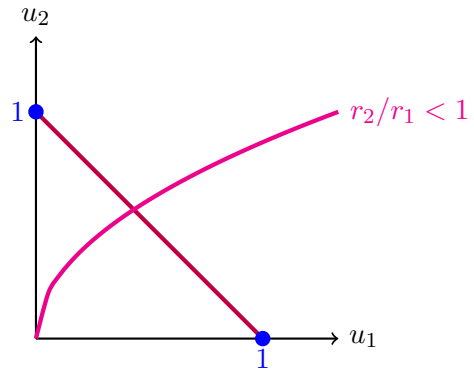
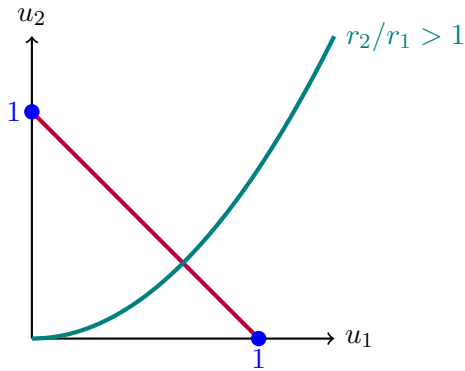
To show that each point on this line corresponds uniquely to a different initial condition, let's compute the trajectories $u_2(u_1)$ as the hint suggests:

$$\begin{aligned} \frac{du_2}{du_1} &= \frac{r_1 u_1 (1 - u_1 - u_2)}{r_2 u_2 (1 - u_2 - u_1)} = \frac{r_1 u_1}{r_2 u_2} \Rightarrow \frac{du_2}{u_2} = \frac{r_2}{r_1} \frac{du_1}{u_1} \Rightarrow \\ &\Rightarrow \ln \frac{u_2}{u_2(0)} = \frac{r_2}{r_1} \ln \frac{u_1}{u_1(0)} \Rightarrow u_2(u_1) = u_2(0) \left(\frac{u_1}{u_1(0)} \right)^{r_2/r_1} \Rightarrow \\ &\Rightarrow u_2(u_1) = \frac{u_2(0)}{u_1(0)^{r_2/r_1}} (u_1)^{r_2/r_1} \end{aligned}$$

where we have called $u_1(0)$ and $u_2(0) = u_2(u_1(0))$ the initial conditions. Therefore, the trajectories in (u_1, u_2) space behave like powers of u_1 , and their "shape" will depend on if $r_1 > r_2$ or $r_2 > r_1$:



We can easily see that in both cases ($r_1 > r_2$ and $r_2 > r_1$) the trajectories will intersect the line of fixed points $u_1^* + u_2^* = 1$ in a unique point:



The intersection between the curve and the line will be the fixed point towards which the system tends. Furthermore, from the expression of the trajectories found above:

$$u_2(u_1) = \frac{u_2(0)}{u_1(0)^{r_2/r_1}} (u_1)^{r_2/r_1}$$

We can see that by changing initial conditions we will change the curvature of the trajectory. Therefore, to each initial condition corresponds a unique trajectory, and therefore a unique fixed point at the intersection with the line $u_1^* + u_2^* = 1$.

As a reference, here is how the *actual* streamplot of the system looks like when $a_{12} = a_{21} = 1$:

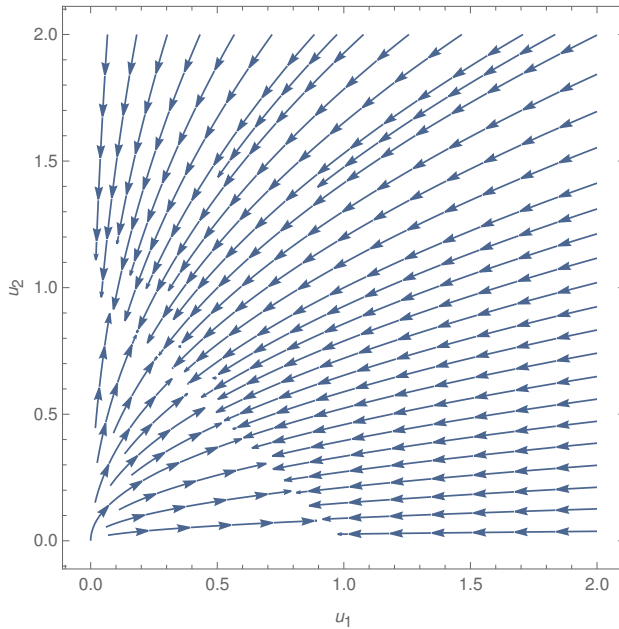


Figure 2: Streamplot of the system for $r_1 = 2, r_2 = 1$.

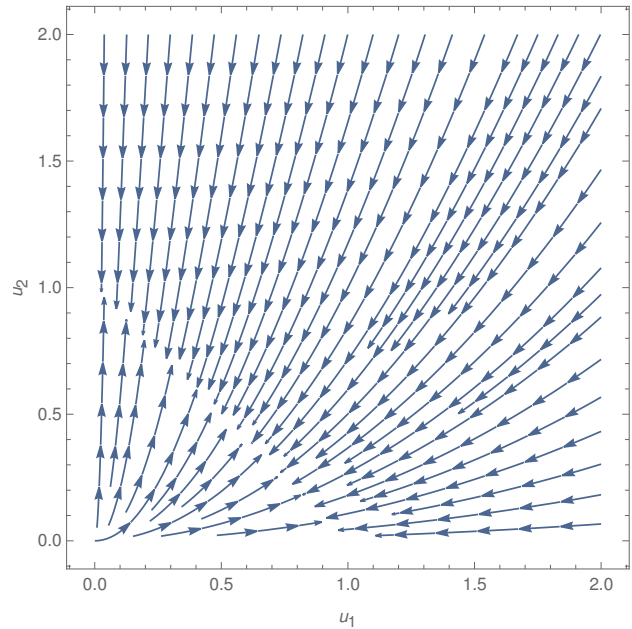


Figure 3: Streamplot of the system for $r_1 = 1, r_2 = 2$.

- (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

With the given r_1/r_2 and initial conditions, the final fixed point (u_1^*, u_2^*) where we will end up is given by the solution of:

$$\begin{cases} u_1^* + u_2^* = 1 \\ u_2^* = \frac{0.05}{\sqrt{0.05}} \sqrt{u_1^*} = \sqrt{0.05u_1^*} \end{cases} \Rightarrow 1 - u_1^* = \sqrt{0.05u_1^*} \Rightarrow (1 - u_1^*)^2 = 0.05u_1^* \Rightarrow \\ \Rightarrow (u_1^*)^2 - 2.05u_1^* + 1 = 0 \Rightarrow u_1^* = \frac{2.05 \pm \sqrt{2.05^2 - 4}}{2} = \frac{2.05 \pm \sqrt{0.2025}}{2} = \frac{2.05 \pm 0.45}{2}$$

One of the solutions is $u_1^* = 1.25$, which is not acceptable because it doesn't agree with the conditions $u_1^* + u_2^* = 1$. The other solution is $u_1^* = 0.8$ and therefore $u_2^* = 0.2$.

If we now dilute 10-fold, we will have $(u_1(0) = 0.08, u_2(0) = 0.02)$ and repeating the same process we obtain $(u_1^* \approx 0.93, u_2^* \approx 0.07)$. If we do this repeatedly, overall we get:

$$(u_1^*, u_2^*) \rightarrow (0.8, 0.2) \rightarrow (0.93, 0.07) \rightarrow (0.98, 0.02) \rightarrow (0.99, 0.01)$$

It is therefore very clear that we are moving towards the fixed point $(u_1^* = 1, u_2^* = 0)$, i.e. species 2 is going to extinction. This is happening because species 1 grows twice as fast as species 2 ($r_1 = 2r_2$). Therefore, at every dilution species 1 will grow much more than species 2, and the advantage of species 1 becomes larger at every dilution until eventually only species 1 is left.

- (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)?

Solution

Since $a_{12}, a_{21} < 1$ this is the case of weak competition, for which we have seen in class that there is one nontrivial stable fixed point (because the two nullclines this time intersect in one point) given by:

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}} = \frac{2}{3} \quad u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}} = \frac{2}{3}$$

Since this is the *only* nontrivial stable equilibrium of the system, the same iterative process outlined in (c) will eventually lead the system to this fixed point where the two species coexist. Notice that this result does not depend on the ratio r_1/r_2 (i.e., on the "intrinsic" growth rates of the two species): the competitive interaction slows down species 1 enough to allow both species to coexist.

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 terms of the parameters in Eqs. (1) and (2) above, this corresponds to $a_{21} > 0, a_{12} < 0$. For convenience, we define $a := a_{21}$ and $b = -a_{12}$ so 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.

Solution

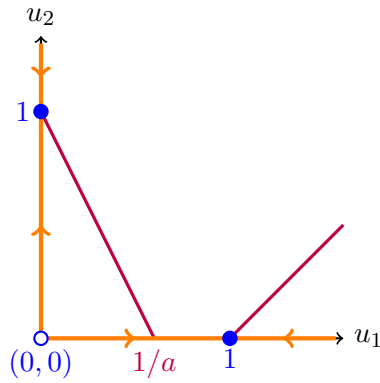
The equations of the system are:

$$\begin{cases} \dot{u}_1 = r_1 u_1 (1 - u_1 + b u_2) \\ \dot{u}_2 = r_2 u_2 (1 - u_2 - a u_1) \end{cases}$$

Therefore, \dot{u}_1 and \dot{u}_2 will be positive when:

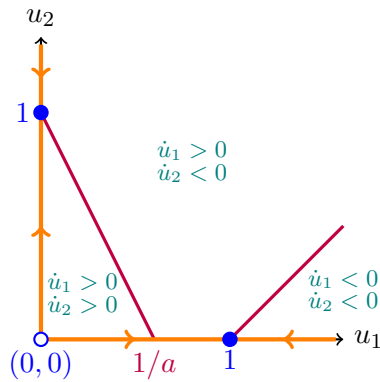
$$\begin{cases} 1 - u_1 + bu_2 > 0 \\ 1 - u_2 - au_1 > 0 \end{cases} \Rightarrow \begin{cases} u_2 > \frac{u_1 - 1}{b} \\ u_2 < 1 - au_1 \end{cases}$$

which also gives the expression of the nullclines of the system. For $a > 1$, the nullclines look like this:

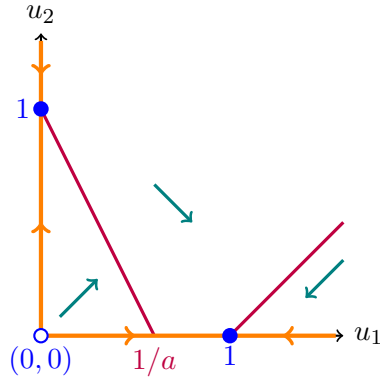


where $(u_1^* = 0, u_2^* = 0)$, $(u_1^* = 0, u_2^* = 1)$ and $(u_1^* = 1, u_2^* = 0)$ are the only fixed points, and where we have also added the flow on the axes (which is determined exactly as in the previous problem).

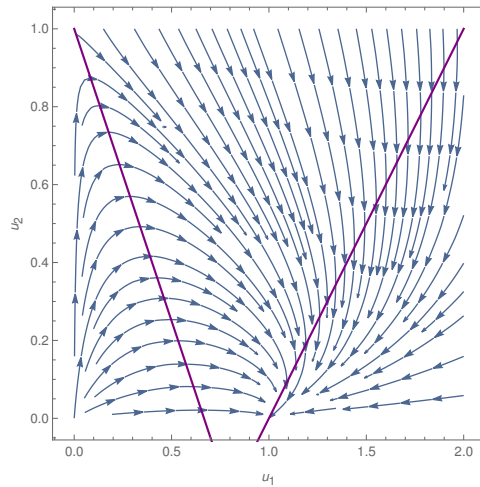
Therefore, these are the areas of the (u_1, u_2) space where \dot{u}_1 and \dot{u}_2 are positive/negative:



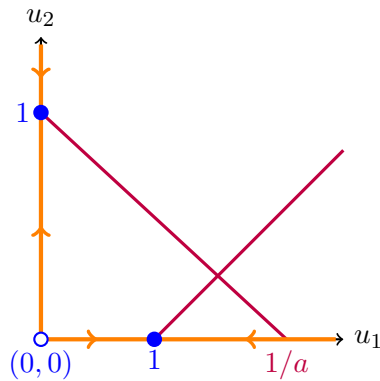
and so the general behavior of the flow is:



We can therefore guess that the flow of the system will *always* be directed towards the fixed point $(u_1^* = 1, u_2^* = 0)$, i.e. to the fixed point where species 1 dominates and species 2 is extinct. In fact, the case $a > 1$ corresponds to species 1 having a strong competitive effect on species 2, so even if the growth of species 2 would “help” species 1, the strong competitive interaction drives species 2 to extinction. As a reference, here is how the flow of this system looks like for $r_1 = r_2 = 1, a = 1.5$ and $b = 1$ (with the nullclines superimposed):



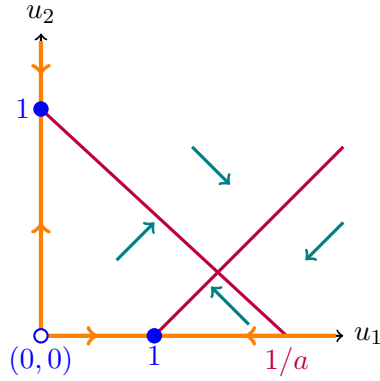
On the other hand, when $a < 1$ the nullclines look like this:



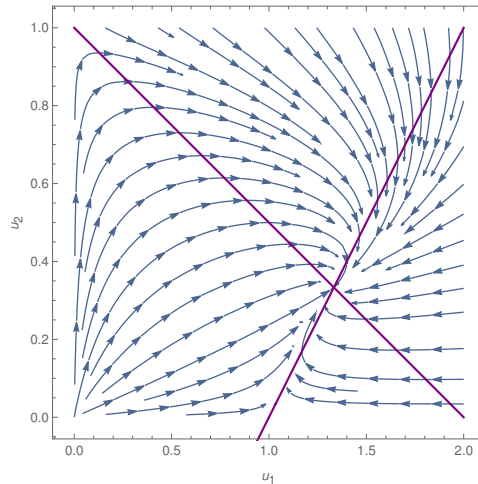
and so now the system will exhibit a nontrivial fixed point where both species coexist. The expression of the nontrivial fixed point this:

$$u_1^* = \frac{1+b}{1+ab} \quad u_2^* = \frac{1-a}{1+ab}$$

This time, the general behavior of the flow is:



and so the solutions *may* oscillate³ towards the fixed point. In this case, since the competitive effect of species 1 on species 2 is weak, species 1 does not drive species 2 to complete extinction, and both species can coexist. As a reference, this is how the *actual* streamplot of the system looks like for $r_1 = r_2 = 1$, $a = 0.5$ and $b = 1$:



- (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

In order to show this, we first have to compute the Jacobian matrix of the system:

$$J(u_1, u_2) = \begin{pmatrix} r_1(1 - 2u_1 + bu_2) & r_1bu_1 \\ -r_2au_2 & r_2(1 - 2u_2 - au_1) \end{pmatrix} \quad (3)$$

³This qualitative approach does not allow us yet to determine if the solutions indeed oscillate or not.

and evaluate it in the nontrivial fixed point:

$$J(u_1^*, u_2^*) = \begin{pmatrix} -\frac{r_1(1+b)}{1+ab} & \frac{r_1b(1+b)}{1+ab} \\ -\frac{r_2a(1-a)}{1+ab} & -\frac{r_2(1-a)}{1+ab} \end{pmatrix}$$

The trace and the determinant of this matrix are:

$$\text{tr } J(u_1^*, u_2^*) = \frac{-r_1(1+b) - r_2(1-a)}{1+ab} \quad \det J(u_1^*, u_2^*) = \frac{r_1r_2(1-a)(1+b)}{1+ab}$$

and since we are considering the case $a < 1$:

$$\text{tr } J(u_1^*, u_2^*) < 0 \quad \det J(u_1^*, u_2^*) > 0$$

Therefore, since the sum of the eigenvalues of $J(u_1^*, u_2^*)$ is negative and their product is positive, they both have negative real part and so (u_1^*, u_2^*) is indeed a stable fixed point.

Alternatively, we can compute the eigenvalues in the more “classical” way, i.e. by solving:

$$\begin{aligned} \det(J(u_1^*, u_2^*) - \lambda \mathbb{I}) = 0 &\Rightarrow \det \begin{pmatrix} -\frac{r_1(1+b)}{1+ab} - \lambda & \frac{r_1b(1+b)}{1+ab} \\ -\frac{r_2a(1-a)}{1+ab} & -\frac{r_2(1-a)}{1+ab} - \lambda \end{pmatrix} = 0 \Rightarrow \\ &\Rightarrow \lambda^2 + \lambda \frac{r_1(1+b) + r_2(1-a)}{1+ab} + \frac{r_1r_2(1+b)(1-a)}{1+ab} = 0 \Rightarrow \\ &\Rightarrow \lambda_{\pm} = \frac{1}{2} \left(-\frac{r_1(1+b) + r_2(1-a)}{1+ab} \pm \sqrt{\Delta} \right) \end{aligned}$$

where the discriminant Δ is:

$$\Delta = \frac{(r_1(1+b) + r_2(1-a))^2}{(1+ab)^2} - 4 \frac{r_1r_2(1+b)(1-a)}{1+ab}$$

which can be rewritten as:

$$\Delta = \frac{r_1^2(1+b)^2 + r_2^2(1-a)^2 - 2r_1r_2(1-a)(1+b)(1+2ab)}{(1+ab)^2}$$

Now, the real part of the eigenvalues is:

$$\text{Re } \lambda_{\pm} = -\frac{r_1(1+b) + r_2(1-a)}{2(1+ab)} < 0$$

because $a < 1$. Therefore, both eigenvalues have negative real part, and the fixed point is stable.

- (c) Next examine the discriminant Δ of the analysis in (b), which depends on the parameters a , b and $r := r_2/r_1$. 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) .

Solution

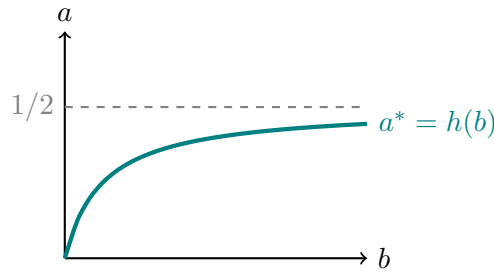
If we plug $r_1 = r_2 := r$ in Δ , we get:

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

Since Δ is the square of an expression, it will *never* be negative, and can only be zero when:

$$a^* - b + 2a^*b = 0 \Rightarrow a^* = \frac{b}{1+2b} := h(b)$$

Since $\Delta = 0$ is the smallest value that the discriminant can take, the points on this line are all minima of Δ . The plot of $h(b)$ is:



Alternatively, if we wanted to use the “brute force” approach to show that those are the minima, we first must show where the derivatives of Δ with respect to a and b are null:

$$\begin{cases} \frac{\partial \Delta}{\partial a} = 0 \\ \frac{\partial \Delta}{\partial b} = 0 \end{cases} \Rightarrow \begin{cases} 2r^2 \frac{(1+b)^2}{(1+ab)^3} (a-b+2ab) = 0 \\ -2r^2 \frac{(1-a)^2}{(1+ab)^3} (a-b+2ab) = 0 \end{cases} \Rightarrow a-b+2ab=0 \Rightarrow a = \frac{b}{1+2b}$$

In order to show that these points are minima, we have to compute the Hessian matrix of the system:

$$\begin{aligned} H(a, b) &= \begin{pmatrix} \frac{\partial^2 \Delta}{\partial a^2} & \frac{\partial^2 \Delta}{\partial a \partial b} \\ \frac{\partial^2 \Delta}{\partial b \partial a} & \frac{\partial^2 \Delta}{\partial b^2} \end{pmatrix} = \\ &= \begin{pmatrix} 2r^2 \frac{(1+b)^2}{(1+ab)^4} [1+2b-2ab+3b^2-4ab^2] & 2r^2 \frac{(1-a)(1+b)}{(1+ab)^4} (-1-3b+3a+5ab) \\ 2r^2 \frac{(1-a)(1+b)}{(1+ab)^4} (-1-3b+3a+5ab) & 2r^2 \frac{(1-a)^2}{(1+ab)^4} (1-2a+3a^2-2ab+4a^2b) \end{pmatrix} \end{aligned}$$

and then evaluate it along the curve $a = b/(1 + 2b)$:

$$H^* = H(b/(1 + 2b), b) = \begin{pmatrix} 2r^2 \frac{(1+2b)^4}{(1+b)^4} & -2r^2 \frac{(1+2b)^2}{(1+b)^4} \\ -2r^2 \frac{(1+2b)^2}{(1+b)^4} & \frac{2r^2}{(1+b)^4} \end{pmatrix}$$

In order to show that the points in $a = b/(1 + 2b)$ are minima, we have to show that H^* is *positive semi-definite*, i.e. that the real parts of its eigenvalues are either positive or null.

The trace and determinant of H^* are:

$$\text{tr } H^* = \frac{2r^2[1 + (1 + 2b)^4]}{(1 + b)^4} > 0 \quad \det H^* = 0$$

Since $\det H^* = 0$ one of the eigenvalues is null, and because $\text{tr } H^* > 0$ the other one is positive. Therefore, H^* is indeed positive semi-definite, and so all the points on the curve $a^* = b/(1 + 2b)$ are minima of Δ . If we substitute $a = b/(1 + 2b)$ in the expression of Δ we have $\Delta = 0$, and so the minimum value of Δ is zero.

- (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 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.

Solution

Since $r_2/r_1 = 1 + \epsilon$, we can substitute $r_2 = r + r\epsilon$ (where we have called $r_1 = r$) in the expression of Δ and then neglect all terms beyond the first order in ϵ :

$$\begin{aligned} \Delta(1 + ab)^2 &= r^2(1 + b)^2 + (r + r\epsilon)^2(1 - a)^2 - 2r(r + r\epsilon)(1 - a)(1 + b)(1 + 2ab) = \\ &= r^2(1 + b)^2 + r^2(1 - a)^2 - 2r^2(1 - a)(1 + b)(1 + 2ab) + 2r^2\epsilon(1 - a)^2 - 2r^2\epsilon(1 - a)(1 + b)(1 + 2ab) = \\ &= r^2(1 + b)^2 + r^2(1 - a)^2 - 2r^2(1 - a)(1 + b)(1 + 2ab) + 2r^2\epsilon [(1 - a)^2 - (1 - a)(1 + b)(1 + 2ab)] \\ &\Rightarrow \Delta = \underbrace{\frac{r^2(1 + b)^2 + r^2(1 - a)^2 - 2r^2(1 - a)(1 + b)(1 + 2ab)}{(1 + ab)^2}}_{\Delta_{r=1}} + \\ &\quad + \frac{2r^2\epsilon}{(1 + ab)^2} [(1 - a)^2 - (1 - a)(1 + b)(1 + 2ab)] \Rightarrow \\ &\Rightarrow \Delta = \Delta_{r=1} + 2\epsilon \left(\frac{r}{1 + ab} \right)^2 (a - 1)(a + b + 2ab + 2ab^2) \end{aligned}$$

where we have called $\Delta_{r=1}$ the expression of Δ found in (c). If we now substitute $a = b/(1 + 2b)$:

$$\Delta = \underbrace{\Delta_{r=1}(b/(1 + 2b), b)}_{=0} + 2\epsilon \frac{r^2}{\left(1 + \frac{b}{1+2b}b\right)^2} \left(\frac{b}{1 + 2b} - 1\right) \left(\frac{b}{1 + 2b} + b + 2\frac{b}{1 + 2b}b + 2\frac{b}{1 + 2b}b^2\right) \Rightarrow$$

$$\Rightarrow \Delta = -\epsilon \frac{4br^2}{1+b}$$

Therefore, we will have $\Delta < 0$ if $\epsilon > 0$. To find the width $\delta(b)$, we can Taylor expand the original expression of Δ around the points $(a = b/(1+2b), r = 1)$ and see when $\Delta < 0$. Therefore, if we call $r = 1 + \epsilon$ and $a = \frac{b}{1+2b} + \delta$, we want to compute the following Taylor expansion:

$$\Delta = \delta \left. \frac{\partial \Delta}{\partial a} \right|_{a=\frac{b}{1+2b}, r=1} + \epsilon \left. \frac{\partial \Delta}{\partial r} \right|_{a=\frac{b}{1+2b}, r=1} + \dots$$

From what we have shown before, the derivative of Δ with respect to a will always be null⁴ when $a = b/(1+2b)$ (since all the points on this line are minima):

$$\left. \frac{\partial \Delta}{\partial a} \right|_{a=\frac{b}{1+2b}, r=1} = 0$$

Therefore, we have to go to the second order in the Taylor expansion:

$$\begin{aligned} \left. \frac{\partial^2 \Delta}{\partial a^2} \right|_{a=\frac{b}{1+2b}, r=1} &= \frac{2(1+b)}{(1+b)^2} r_1^2 [3b^2(1+b) + 2b^2r(1-3a-2ab) + r^2(1+3b-2ab)] \Big|_{a=\frac{b}{1+2b}, r=1} = \\ &= 2 \frac{(1+2b)^3}{(1+b)^6} r_1^2 [r^2(1+4b) + 2rb^2(1-2b) + 3b^2(1+2b)] \Big|_{r=1} = 2r_1^2 \frac{(1+2b)^4}{(1+b)^4} \end{aligned}$$

On the other hand, we have already Taylor expanded Δ on $a = b/(1+2b)$ around $r = 1$ so we already know that:

$$\left. \frac{\partial \Delta}{\partial r} \right|_{a=\frac{b}{1+2b}, r=1} = -\frac{4br_1^2}{1+b}$$

Thus, the full Taylor expansion of Δ around $(a = b/(1+2b), r = 1)$ is:

$$\Delta \approx \frac{\delta^2}{2} \left. \frac{\partial^2 \Delta}{\partial a^2} \right|_{a=\frac{b}{1+2b}, r=1} + \epsilon \left. \frac{\partial \Delta}{\partial r} \right|_{a=\frac{b}{1+2b}, r=1} = \frac{\delta^2}{2} \cdot r_1^2 \frac{(1+2b)^4}{(1+b)^4} - \epsilon \cdot \frac{4br_1^2}{1+b}$$

Therefore, we will have $\Delta < 0$ when:

$$\begin{aligned} \frac{\delta^2}{2} r_1^2 \frac{(1+2b)^4}{(1+b)^4} < \epsilon \frac{4br_1^2}{1+b} &\Rightarrow \delta^2 < \epsilon \cdot 8b \frac{(1+b)^3}{(1+2b)^4} \Rightarrow \\ &\Rightarrow -\frac{\sqrt{8b(1+b)^3}}{(1+2b)^2} \cdot \sqrt{\epsilon} < \delta < \frac{\sqrt{8b(1+b)^3}}{(1+2b)^2} \cdot \sqrt{\epsilon} \end{aligned}$$

⁴We can also show this explicitly:

$$\begin{aligned} \left. \frac{\partial \Delta}{\partial a} \right|_{a=\frac{b}{1+2b}, r=1} &= -\frac{2(1+b)}{(1+ab)^3} r_1^2 [b(1+b) + r(1+3ab+2ab^2) - r^2(1-a)] \Big|_{a=\frac{b}{1+2b}, r=1} = \\ &= -2r_1^2 \frac{(1+2b)^2}{(1+b)^4} (1-r)(b+2b^2-r) \Big|_{r=1} = 0 \end{aligned}$$

Now, if b is small we have:

$$\frac{\sqrt{8b(1+b)^3}}{(1+2b)^2} \approx \sqrt{8b} + \dots$$

and so $\Delta < 0$ when:

$$-\sqrt{8b} \cdot \sqrt{\epsilon} < \delta < \sqrt{8b} \cdot \sqrt{\epsilon}$$

When ϵ is small, this range will also be small. On the other hand, as $b \rightarrow \infty$ we have:

$$\frac{\sqrt{8b(1+b)^3}}{(1+2b)^2} \xrightarrow{b \rightarrow \infty} \frac{1}{\sqrt{2}}$$

and thus $\Delta < 0$ when:

$$-\sqrt{\frac{\epsilon}{2}} < \delta < \sqrt{\frac{\epsilon}{2}}$$

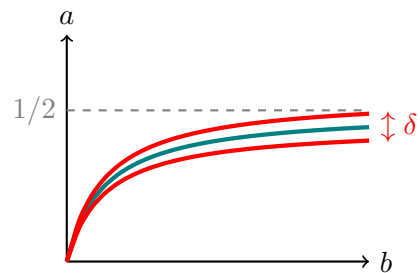
Therefore, also when b is very large the range within which $\Delta < 0$ is narrow if ϵ is small.

- (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 $r = 2$.

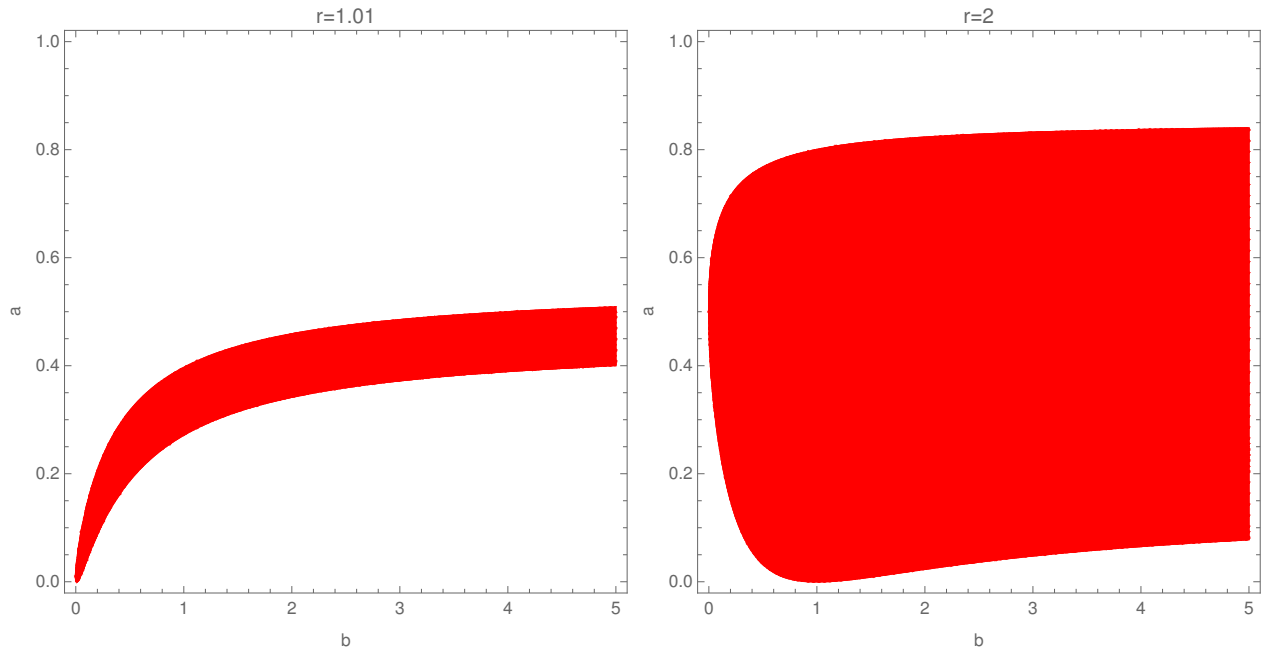
Solution

The region of damped oscillations does *not* occur for $r_1 > r_2$ because species 1 slows down the growth of species 2, and so species 2 cannot help species 1 grows faster. On the other hand, when $r_2 > r_1$ species 2 wants to grow faster than species 1, but as species 2 grows it helps species 1 grow faster, which in turn slows down species 2. Therefore, in this case we can have damped oscillations, where species 2 makes species 1 grow faster until this has a detrimental effect on species 2, and so on until the system reaches a fixed point.

The region where damped oscillations occur makes sense, because it looks like this:



Here is a numerically obtained plot of the region where $\Delta < 0$ for $r = 2$, and for comparison also for $r = 1.01$:



3. Relaxational oscillator

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

$$\dot{v} = f(v) - w + I_a \quad (4)$$

$$\dot{w} = \epsilon(v - w) \quad (5)$$

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

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

- (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).

Solution

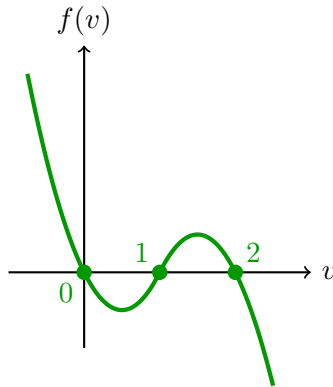
Let's call for simplicity:

$$f_L(v) = v(v - 1) \quad f_R(v) = (2 - v)(v - 1)$$

Then we have:

$$f_L(1) = 0 = f_R(1) \quad \begin{cases} f'_L(1) = 2v - 1|_{v=1} = 1 \\ f'_R(1) = 3 - 2v|_{v=1} = 1 \end{cases} \Rightarrow f'_L(1) = f'_R(1) = 1$$

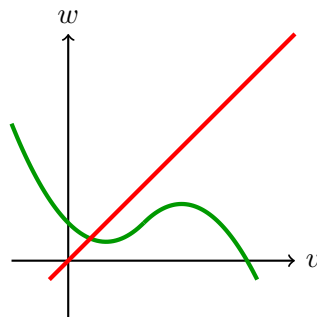
Therefore, $f(v)$ is continuous and differentiable in $v = 1$. This is the plot of the function:



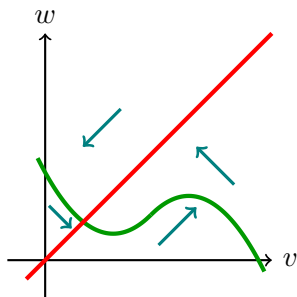
In general, the nullclines of the system are given by:

$$\begin{cases} \dot{v} = 0 \\ \dot{w} = 0 \end{cases} \Rightarrow \begin{cases} w = f(v) + I_a \\ w = v \end{cases}$$

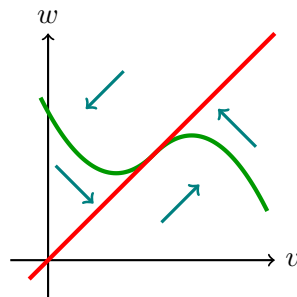
For $I_a = 1/2$, this is how the nullclines look like:



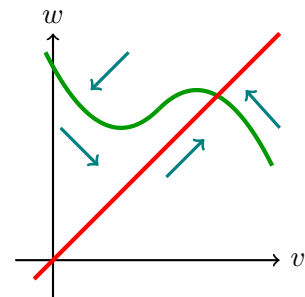
Since $\dot{v} > 0$ when $w < f(v) + I_a$ and $\dot{w} > 0$ when $w < v$, the general behavior of the flow of the system is:



$I_a = 1/2$

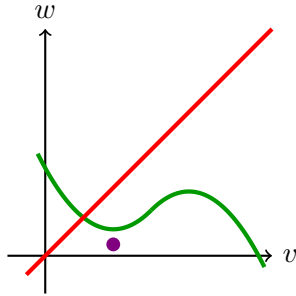


$I_a = 1$

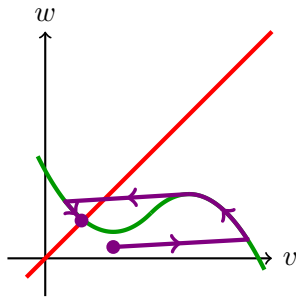


$I_a = 2$

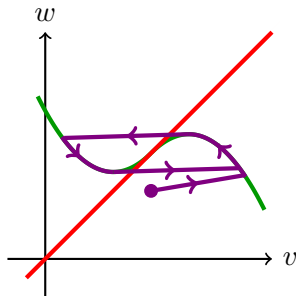
Given what we've seen in class, we can expect the cases $I_a = 1/2$ and $I_a = 2$ to exhibit threshold dynamics, and the trajectories will tend towards the fixed point (i.e., the intersection of the nullclines). For example, if $I_a = 1/2$ and we start from the following point:



We expect the trajectories to look like this:



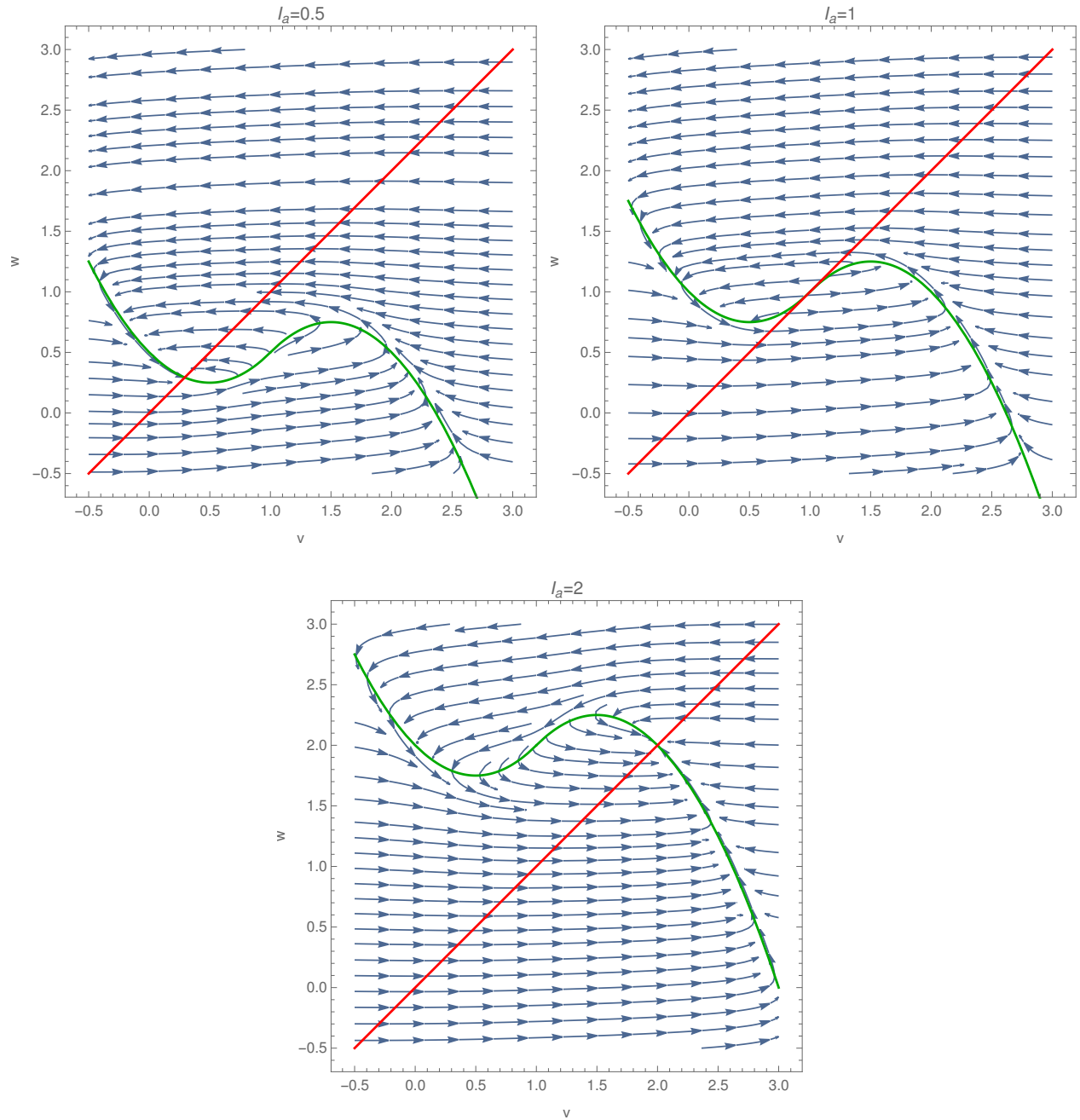
and similarly for $I_a = 2$. However, for $I_a = 1$ the trajectories will look like this:



and so in this case we will *not* have threshold dynamics, but oscillations.

To sum up, the system exhibits threshold dynamics for $I_a = 1/2$ and $I_a = 2$, and oscillations for $I_a = 1$.

These are the *actual* streamplots of the system with $\epsilon = 0.05$ (the nullclines are superimposed for reference):



- (b) Work out the eigenvalues of perturbative dynamics around the nontrivial 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

First, let's write v^* (i.e., the value of v at the fixed point) as a function of I_a :

$$\begin{aligned} \begin{cases} \dot{v} = f(v) - w + I_a = 0 \\ \dot{w} = \epsilon(v - w) = 0 \end{cases} &\Rightarrow \begin{cases} w = f(v) - I_a \\ w = v \end{cases} \Rightarrow f(v) - I_a = v \Rightarrow \\ &\Rightarrow \begin{cases} v^2 - v - I_a = v & v \leq 1 \\ 2v - 2 - v^2 + v - I_a = v & v \geq 1 \end{cases} \Rightarrow \begin{cases} v^2 - 2v + I_a = 0 & v \leq 1 \\ v^2 - 2v - I_a + 2 = 0 & v \geq 1 \end{cases} \Rightarrow \\ &\Rightarrow \begin{cases} v^* = \frac{1}{2}(2 \pm \sqrt{4 - I_a}) & v \leq 1 \\ v^* = \frac{1}{2}(2 \pm 4 - 4(2 - I_a)) & v \geq 1 \end{cases} \Rightarrow \begin{cases} v^* = 1 \pm \sqrt{1 - I_a} & v \leq 1 \\ v^* = 1 \pm \sqrt{I_a - 1} & v \geq 1 \end{cases} \end{aligned}$$

Therefore, the only acceptable solutions are:

$$v^* = 1 - \sqrt{1 - I_a} \quad \text{for } v \leq 1, I_a < 1 \quad v^* = 1 + \sqrt{I_a - 1} \quad \text{for } v \geq 1, I_a > 1$$

In other words, when $I_a < 1$ the only fixed point is $w^* = v^* = 1 - \sqrt{1 - I_a} < 1$, while when $I_a > 1$ it is $w^* = v^* = 1 + \sqrt{I_a - 1} > 1$. Thus, we have:

$$f'(v^*) = \left. \frac{df}{dv} \right|_{v=v^*} = \begin{cases} 2v^* - 1 & v^* \leq 1 \\ 3 - 2v^* & v^* \geq 1 \end{cases} \Rightarrow f'(v^*) = 1 - 2\sqrt{|I_a - 1|}$$

Therefore, the Jacobian matrix of the nontrivial fixed point is:

$$J = \begin{pmatrix} f'(v^*) & -1 \\ \epsilon & -\epsilon \end{pmatrix} = \begin{pmatrix} 1 - 2\sqrt{|I_a - 1|} & -1 \\ \epsilon & -\epsilon \end{pmatrix}$$

The eigenvalues of this matrix are:

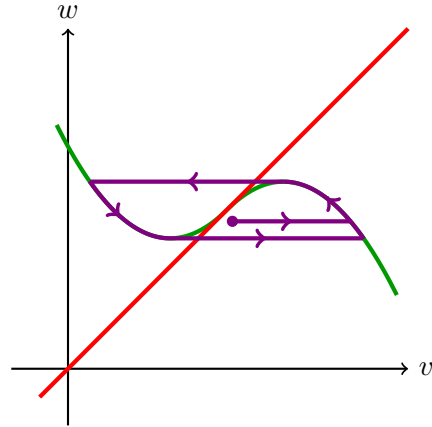
$$\lambda_{\pm} = \frac{1}{2} \left[1 - 2\sqrt{|I_a - 1|} - \epsilon \pm \sqrt{(\epsilon - 1 - 2\sqrt{|I_a - 1|})^2 - 8\epsilon(1 - \sqrt{|I_a - 1|})} \right]$$

We will have a stable limit cycle when $\text{Re } \lambda_{\pm} > 0$, i.e. when $1 - 2\sqrt{|I_a - 1|} - \epsilon > 0$ (an equivalent way to get to the same result is to check when $\text{tr } J > 0$):

$$\begin{aligned} 1 - 2\sqrt{|I_a - 1|} - \epsilon > 0 &\Rightarrow \sqrt{|I_a - 1|} < \frac{1 - \epsilon}{2} \Rightarrow |I_a - 1| < \left(\frac{1 - \epsilon}{2}\right)^2 \Rightarrow \\ &\Rightarrow 1 \leq I_a < 1 + \left(\frac{1 - \epsilon}{2}\right)^2 \quad \text{or} \quad 1 - \left(\frac{1 - \epsilon}{2}\right)^2 < I_a \leq 1 \Rightarrow \\ &\Rightarrow 1 - \left(\frac{1 - \epsilon}{2}\right)^2 < I_a < 1 + \left(\frac{1 - \epsilon}{2}\right)^2 \end{aligned}$$

Notice that this is an interval centered around $I_a = 1$, which as we showed above is the only case where the trajectories eventually tend towards the same one, i.e. the system exhibits a stable limit cycle.

Notice also that in this case it is sufficient to show that $\text{tr } J > 0$ for limit cycle to be stable, and we don't need to check the discriminant. In fact, since $\text{tr } J > 0$ at least one of the eigenvalues will be positive and therefore the fixed point will be unstable. This means that, if we start from a point close to the fixed point, the solution will move away from it until it follows the limit cycle:



Therefore, the limit cycle will be stable because the solutions will approach it from both “sides” (i.e., both from the “outside” and the “inside”).

- (c) The stable limit cycles found in (b) becomes relaxational oscillation if the parameter ϵ in Eq. (5) 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.]

Solution

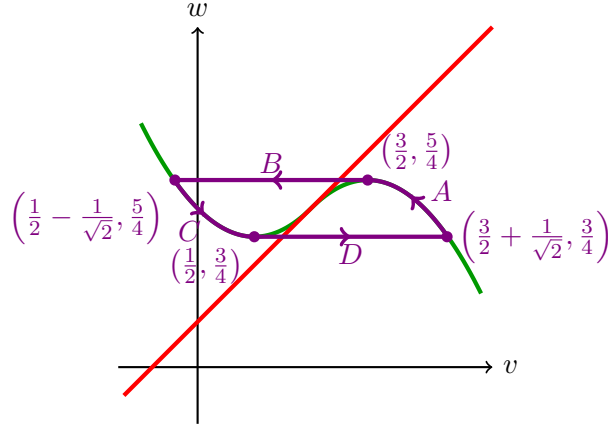
To find the local minimum and maximum of $f(v)$, we have to solve:

$$0 = f'(v) = \begin{cases} 2v - 1 & v \leq 1 \\ 3 - 2v & v \geq 1 \end{cases} \Rightarrow v^* = \frac{1}{2} \quad v^* = \frac{3}{2}$$

and therefore:

$$f_{\min} = f\left(\frac{1}{2}\right) = -\frac{1}{4} \quad f_{\max} = f\left(\frac{3}{2}\right) = \frac{1}{4}$$

As shown above, in this case for $\epsilon \rightarrow 0$ the limit cycle looks like:



where we have called A, B, C, D the four legs of the trajectory.

The slow-legs of the trajectory are A and C , because along them we have $\dot{v} = 0$ (since we are on a nullcline) and \dot{w} is small because $\dot{w} \propto \epsilon$ and ϵ is small. Therefore, B and D are the fast-legs of the trajectory.

Let us write the four legs of the trajectory explicitly. B and D are horizontal lines, so on them we have:

$$B : \quad w = f\left(\frac{3}{2}\right) + 1 = \frac{5}{4} \quad \text{for} \quad \frac{1}{2} - \frac{1}{\sqrt{2}} \leq v \leq \frac{3}{2}$$

$$D : \quad w = f\left(\frac{1}{2}\right) + 1 = \frac{3}{4} \quad \text{for} \quad \frac{1}{2} \leq v \leq \frac{3}{2} + \frac{1}{\sqrt{2}}$$

On the other hand, on A and C we have $\dot{v} = 0$ and so $w = f(v) + I_a$:

$$A : \quad w = (2 - v)(v - 1) + 1 = -v^2 + 3v - 1 \Rightarrow v^2 - 3v + 1 + w = 0 \Rightarrow$$

$$\Rightarrow v = \frac{3 \pm \sqrt{9 - 4(1 + w)}}{2} = \frac{3}{2} \pm \sqrt{\frac{5}{4} - w}$$

However, since $v \geq 3/2$ (on leg A we have $3/2 \leq v \leq 2$), the only acceptable solution is:

$$A : \quad v = \frac{3}{2} + \sqrt{\frac{5}{4} - w} \quad \text{for} \quad \frac{3}{2} \leq v \leq 2$$

Similarly, for C :

$$C : \quad w = v(v - 1) + 1 = v^2 - v + 1 \Rightarrow v^2 - v + 1 - w = 0 \Rightarrow v = \frac{1 \pm \sqrt{1 - 4(1 - w)}}{2} = \frac{1}{2} \pm \sqrt{w - \frac{3}{4}}$$

and since now we have $0 \leq v \leq 1/2$, the only acceptable solution is:

$$C : \quad v = \frac{1}{2} - \sqrt{w - \frac{3}{4}} \quad \text{for} \quad 0 \leq v \leq \frac{1}{2}$$

Let's now compute the (approximate) period of the oscillations. We neglect the fast-legs (since the dynamics of the system is much faster there than on the slow-legs), and so we want to determine how long it takes the system to go through A and C . Let's start with A . From the equation for \dot{w} in this case we have:

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

We can solve this equation by separating the variables:

$$\frac{dw}{\frac{3}{2} + \sqrt{\frac{5}{4} - w} - w} = \epsilon dt \Rightarrow \int_{3/4}^{5/4} \frac{dw}{\frac{3}{2} + \sqrt{\frac{5}{4} - w} - w} = \epsilon \int_0^{t_A} dt \Rightarrow t_A = \frac{1}{\epsilon} \int_{3/4}^{5/4} \frac{dw}{\frac{3}{2} + \sqrt{\frac{5}{4} - w} - w}$$

where we have called $t_0 = 0$ and t_A , respectively, the instants at which we start and finish moving on leg A . We can call \mathcal{I}_A the integral, so that $t_A = \mathcal{I}_A/\epsilon$. Let's see however how we can compute it. We can simplify it by defining $s := \frac{5}{4} - w$, so that:

$$t_A = \frac{1}{\epsilon} \int_0^{1/2} \frac{ds}{\frac{1}{4} + s + \sqrt{s}}$$

If we again define $u := \sqrt{s}$, we get:

$$t_A = \frac{1}{\epsilon} \int_0^{1/\sqrt{2}} \frac{2udu}{u^2 + u + \frac{1}{4}} = \frac{1}{\epsilon} \int_0^{1/\sqrt{2}} \frac{2udu}{(u + \frac{1}{2})^2}$$

Again, we substitute $x := u + 1/2$ to obtain:

$$\begin{aligned} t_A &= \frac{1}{\epsilon} \int_{1/2}^{1/2+1/\sqrt{2}} \frac{(2x-1)dx}{x^2} = \int_{1/2}^{1/2+1/\sqrt{2}} \left(\frac{2dx}{x} - \frac{dx}{x^2} \right) = \frac{1}{\epsilon} \left[2 \ln x + \frac{1}{x} \right]_{1/2}^{1/2+1/\sqrt{2}} \Rightarrow \\ &\Rightarrow t_A = \frac{2}{\epsilon} \left(\sqrt{2} - 2 + \ln(1 + \sqrt{2}) \right) \end{aligned}$$

Similarly, on leg C we have:

$$\begin{aligned} \frac{dw}{dt} &= \epsilon \left(\frac{1}{2} - \sqrt{w - \frac{3}{4}} - w \right) \Rightarrow \int_{5/4}^{3/4} \frac{dw}{\frac{1}{2} - \sqrt{w - \frac{3}{4}} - w} = \epsilon \int_0^{t_C} dt \Rightarrow \\ &\Rightarrow t_C = \frac{1}{\epsilon} \int_{5/4}^{3/4} \frac{dw}{\frac{1}{2} - \sqrt{w - \frac{3}{4}} - w} \end{aligned}$$

We call this integral \mathcal{I}_C , so that $t_C = \mathcal{I}_C/\epsilon$. If we want to compute it, we can define $s := w - 3/4$ to obtain:

$$t_C = \frac{1}{\epsilon} \int_0^{1/2} \frac{ds}{\frac{1}{4} + \sqrt{s} + s}$$

The integral that appears here is the same as the one we computed above, so:

$$\mathcal{I} := \mathcal{I}_A = \mathcal{I}_C = 2 \left(\sqrt{2} - 2 + \ln(1 + \sqrt{2}) \right)$$

Therefore, the total period T of the oscillations will be (approximately):

$$T \approx t_A + t_C = \frac{2\mathcal{I}}{\epsilon} = \frac{4}{\epsilon} \left(\sqrt{2} - 2 + \ln(1 + \sqrt{2}) \right)$$