PHYSICS 282 Spatiotemporal Biodynamics
Spatiotemporal Dynamics in Biological Systems
Fall 2024

Solution of Homework #1

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

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1. **Phase diagram and phase transitions in dynamical systems**
In class, we studied a model of growth and predation. Let the density of an organism be $\rho(t)$. If the growth of the organism is described by a logistic term and the effect of predation by a hyperbolic term, then the dynamics is given by the following ODE:

$$\frac{d\rho}{dt} = r\rho \cdot \left(1 - \frac{\rho}{\tilde{\rho}}\right) - \frac{\delta \cdot \rho}{1 + \frac{\rho}{\rho_K}}$$

where r is the maximal replication rate and δ is the maximal predation rate. Of the two remaining parameters, $\tilde{\rho}$ describes the carrying capacity and ρ_K describes the saturating density for predation.

Upon introducing dimensionless variables, $u := \rho/\tilde{\rho}$, $\tau := rt$, the above equation becomes

$$\frac{du}{d\tau} = u(1-u) - \frac{\alpha u}{1 + \frac{u}{\kappa}}$$

with two dimensionless parameters $\alpha := \delta/r$ and $\kappa = \rho_K/\tilde{\rho}$.

(a) *Write a general expression for the fixed point $u^*(\kappa, \alpha)$ at which $du/d\tau = 0$, and show that the nature of the solution u^* depends importantly on whether the relative predation rate α is smaller or larger than*

$$\alpha_c(\kappa) = \frac{1}{2} + \frac{\kappa}{4} + \frac{1}{4\kappa}$$

Show that $\alpha_c(\kappa)$ has a single minimum at $\kappa = 1$. The point $(\kappa = 1, \alpha = \alpha_c(1)$ is called the "critical point" due to the special behavior exhibited by the system in the vicinity of this point as we will see below.

Solution
The value u^* at which $du/d\tau = 0$ is obtained by solving:

$$0 = u^*(1-u^*) - \frac{\alpha u^*}{1 + \frac{u^*}{\kappa}} \quad \Rightarrow \quad u^*(1-u^*) = \frac{\alpha u^*}{1 + \frac{u^*}{\kappa}}$$

One solution is $u^* = 0$. Assuming $u^* \neq 0$ and dividing by u^* on both sides we get:

$$1 - u^* = \frac{\alpha}{1 + \frac{u^*}{\kappa}} \;\Rightarrow\; (1-u)\left(1 + \frac{u^*}{\kappa}\right) = \alpha \;\Rightarrow\; 1 + \frac{u^*}{\kappa} - u^* - \frac{(u^*)^2}{\kappa} = \alpha \;\Rightarrow$$

$$\Rightarrow\; \frac{(u^*)^2}{\kappa} + u^*\left(1 - \frac{1}{\kappa}\right) + (\alpha - 1) = 0 \;\Rightarrow\; (u^*)^2 + u^*(\kappa - 1) + \kappa(\alpha - 1) = 0$$

and the solution of this quadratic equation is:

$$u^*_\pm = \frac{-(\kappa-1) \pm \sqrt{(\kappa-1)^2 - 4\kappa(\alpha-1)}}{2} = \frac{(1-\kappa) \pm \sqrt{\kappa^2 + 1 - 2\kappa - 4\kappa\alpha + 4\kappa}}{2} =$$

$$= \frac{(1-\kappa) \pm \sqrt{\kappa^2 + 2\kappa - 4\kappa\alpha}}{2} = \frac{(1-\kappa) \pm \sqrt{(\kappa+1)^2 - 4\kappa\alpha}}{2}$$

So, values u^* at which $du/d\tau = 0$ are:

$$u^*_0 = 0 \qquad\qquad u^*_\pm = \frac{(1-\kappa) \pm \sqrt{(\kappa+1)^2 - 4\kappa\alpha}}{2} \tag{1}$$

Let's consider the expression of $u^*_\pm$: depending on the sign of $(\kappa+1)^2 - 4\kappa\alpha$, we might have two distinct real solution (> 0), one degenerate[1] real solution ($= 0$) or two complex conjugate solutions (< 0). The only physically acceptable solutions in our systems are $u^* \geq 0$: in fact, $u = \rho/\tilde{\rho}$ where $\tilde{\rho}$ is a positive parameter and ρ is the population density, which by definition cannot be negative.
Therefore, if $(\kappa+1)^2 - 4\kappa\alpha < 0$ the only physically acceptable solution will be $u^* = 0$. This happens when:

$$(\kappa+1)^2 - 4\kappa\alpha < 0 \;\Rightarrow\; 4\kappa\alpha > (\kappa+1)^2 \;\Rightarrow\; \alpha > \frac{2\kappa + \kappa^2 + 1}{4\kappa} \;\Rightarrow$$

$$\Rightarrow\; \alpha > \frac{1}{2} + \frac{\kappa}{4} + \frac{1}{4\kappa} = \alpha_c(\kappa)$$

The physical meaning of this result is that when the predation rate is sufficiently larger than the replication rate (remember that $\alpha = \delta/r$), then the population will not survive (i.e., the only possible equilibrium is $u^* = 0$, which is extinction). In other words, the replication rate must be sufficiently larger than the predation rate for the system to be able to sustain a non-zero population.
Let us now find the minima of $\alpha_c(\kappa)$:

$$\frac{d\alpha_c}{d\kappa} = 0 \;\Rightarrow\; \frac{d}{d\kappa}\left(\frac{1}{2} + \frac{\kappa}{4} + \frac{1}{4\kappa}\right) = 0 \;\Rightarrow$$

$$\Rightarrow\; \frac{1}{4} - \frac{1}{4\kappa^2} = 0 \;\Rightarrow$$

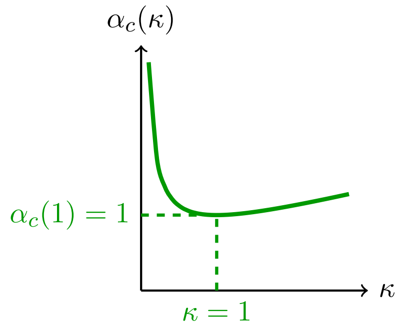
$$\Rightarrow\; \frac{1}{4\kappa^2} = \frac{1}{4} \;\Rightarrow\; \kappa^2 = 1 \;\Rightarrow\; \kappa = \pm 1$$

However, κ is a positive parameter ($\kappa = \rho_K/\tilde{\rho}$, with both ρ_K and $\tilde{\rho}$ positive parameters), so the only acceptable solution is $\kappa = 1$. To check that this is indeed a minimum, we evaluate the second derivative of $\alpha_c(\kappa)$ in $\kappa = 1$:

$$\left.\frac{d^2\alpha_c}{d\kappa^2}\right|_{\kappa=1} = \left.\frac{d}{d\kappa}\left(\frac{1}{4} - \frac{1}{4\kappa^2}\right)\right|_{\kappa=1} = -\left.\frac{1}{4}\cdot\frac{-2}{\kappa^3}\right|_{\kappa=1} = -\frac{1}{4}\cdot\frac{-2}{(1)^3} = \frac{2}{4} = \frac{1}{2} > 0$$

[1] This is just the mathematical term to indicate two solutions of a quadratic equation with the same value.

Here is a plot of $\alpha_c(\kappa)$:



(b) *For $\kappa = 1$, find $u^*(\alpha)$ vs α. [Hint: there are two non-negative real values for $u^*(\alpha)$ for $\alpha < \alpha_c$, and only one for $\alpha > \alpha_c$. Ignore any imaginary solutions which are irrelevant.] To see which of the fixed points is stable/unstable, plot $du/d\tau$ vs u for $\kappa = 1$ and the following values of α: (i) $\alpha \lesssim \alpha_c(1)$, (ii) $\alpha = \alpha_c(1)$, (iii) $\alpha \gtrsim \alpha_c(1)$. For each case, plot the "flow", i.e. the direction of $du/d\tau$ as arrows for different regions of u. The type of* phase transition *which occurs at the critical point here is called a "supercritical bifurcation".*

Solution

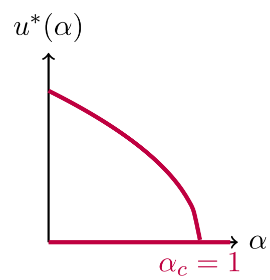
For $\kappa = 1$, the expression of the equilibria u^* become (from Eq (1)):

$$u_0^* = 0 \qquad\qquad u_\pm^* = \pm\sqrt{1-\alpha}$$

We can reject the negative solution ($u^* \geq 0$) and the complex solution ($\alpha > 1 = \alpha_c(1)$), so in the end we have:

$$u_0^* = 0 \qquad\qquad u^* = \sqrt{1-\alpha} \quad \text{with} \quad \alpha \leq 1$$

This is the plot of $u^*(\alpha)$:

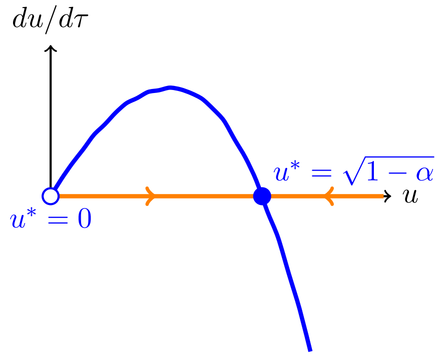


If we now set $\kappa = 1$ in the equation of our system we get:

$$\frac{du}{d\tau} = u(1-u) - \frac{\alpha u}{1+u}$$

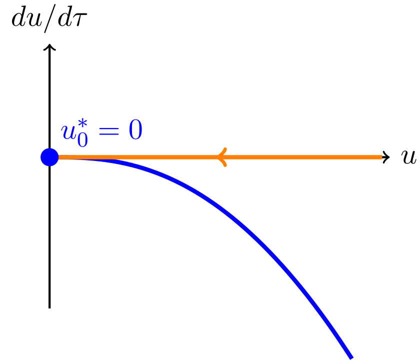
Let's now plot $du/d\tau$ for three values of α as required and determine the stability of the equilibria with a streamplot (i.e., a plot of the "flow"):

i. $\boldsymbol{\alpha \lesssim \alpha_c}$: we choose $\alpha = 0.95$. The streamplot we obtain is the following:



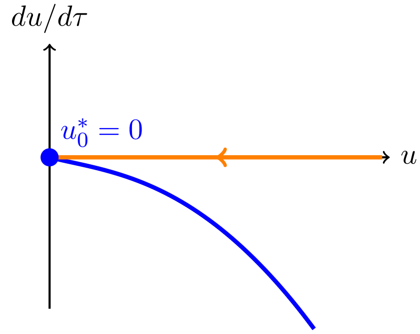
Therefore, $u_0^* = 0$ is an unstable equilibrium, while $u^* = \sqrt{1-\alpha}$ is stable. As soon as the initial condition is larger than 0, the population will always tend towards $u^* = \sqrt{1-\alpha}$

ii. $\boldsymbol{\alpha = \alpha_c}$: we have $\alpha = 1$. The streamplot we obtain is the following:



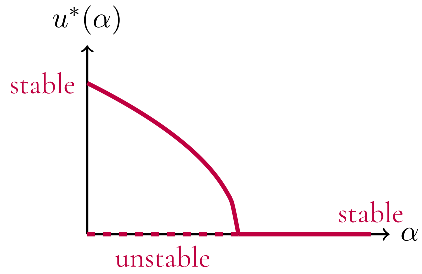
Therefore, the only equilibrium $u_0^* = 0$ is stable ($u^* = \sqrt{1-\alpha} = \sqrt{1-1} = 0$). Whatever the initial condition, the population will always tend towards 0 (i.e., the populaton will ultimately always go to extinction).

iii. $\boldsymbol{\alpha \gtrsim \alpha_c}$: we choose $\alpha = 1.1$. The streamplot we obtain is the following:



Therefore, also in this case the only equilibrium $u_0^* = 0$ is stable ($u^* = \sqrt{1-\alpha}$ is not an acceptable equilibrium in this case).

This is a *supercritical pitchfork bifurcation*. The bifurcation diagram is:



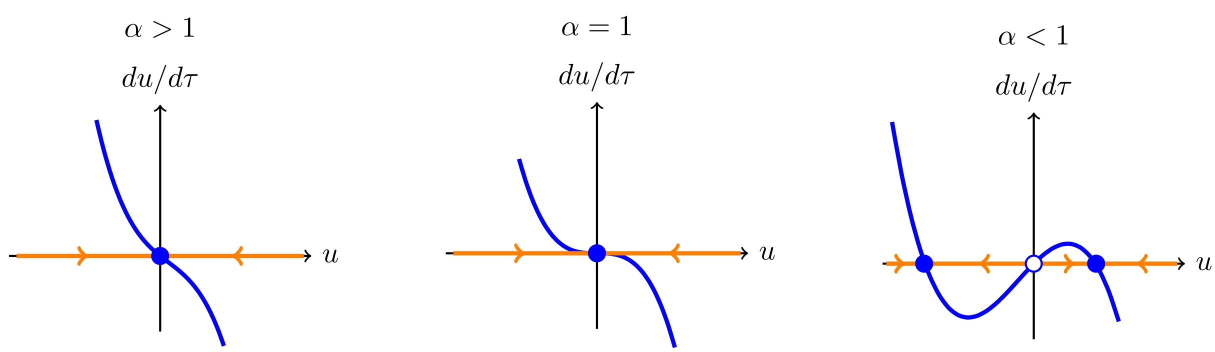
We can't see the full "pitchfork" because we are restricting u^* to non-negative values. To show that this is indeed a supercritical bifurcation, we can expand the equation of the system around $u^* = 0$:

$$\frac{du}{dt} = u(1-u) - \alpha u \left(1 - \frac{u}{\kappa} + \frac{u^2}{\kappa^2} + \cdots\right) =$$
$$= u - u^2 - \alpha u + \frac{\alpha}{\kappa}u^2 - \frac{\alpha}{\kappa^2}u^3 + \cdots =$$
$$= u(1-\alpha) - u^2\left(\frac{\alpha}{\kappa} - 1\right) - \frac{\alpha}{\kappa^2}u^3 + \cdots$$

If we now set $\kappa = 1$ we are left with:

$$\frac{du}{d\tau} \approx u(1-\alpha) + u^2(\alpha - 1) - \alpha u^3 \tag{2}$$

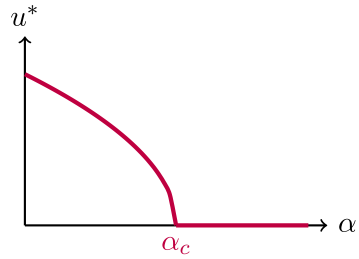
Despite not having the same form of the "prototypical" example of supercritical bifurcation (i.e., $\dot{x} = rx - x^3$), the behavior of this system is qualitatively the same:



(c) *Sketch (i.e., plot the approximate dependence by hand, not by computer) the dependence of the stable fixed point u^* in the vicinity of the* critical point $\alpha_c(1)$*. The robustness of the system can be characterized by the sensitvity of the density u^* to small changes in the environment. Let $S := du^*/d\alpha$ be a measure of the change in population density when the predation rate changes. Sketch $S(\alpha)$ in the vicinity (i.e., on both sides) of the critical point, and describe the behavior in words.*

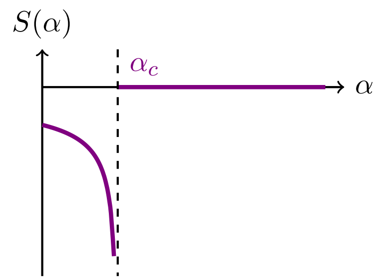
Solution

The dependence of the stable fixed point u^* around α_c is taken simply from the bifurcation diagram shown above:



Where the curve on the left of α_c is $\sqrt{1-\alpha}$. Notice that $u^*(\alpha)$ is continuous but not smooth (i.e., not differentiable) in α_c.

The sensitivity $S(\alpha) = du^*/d\alpha$ will surely be equal to 0 for $\alpha > \alpha_c$ (since $u^*(\alpha)$ is constant for $\alpha > \alpha_c$). For $\alpha < \alpha_c$, $S(\alpha)$ will always be negative (u^* decreases as α increases), and will decrease tending to[2] $-\infty$ for $\alpha \to \alpha_c$:



Therefore, the sensitivity $S(\alpha)$ undergoes an abrupt, discontinuous change in $\alpha = \alpha_c$.

(d) *For $\kappa = 1/2$, show that there are three solutions for $u^*(\alpha)$ for a range of α at $\alpha_0 \leq \alpha \leq \alpha_c(1/2)$, where α_0 is a positive number you need to determine. To see which of the solutions are stable/unstable, plot $du/d\tau$ vs u for $\kappa = 1/2$ and the following values of α: (i) $\alpha \lesssim \alpha_c(1/2)$, (ii) $\alpha = \alpha_c(1/2)$, (iii) $\alpha \gtrsim \alpha_c(1/2)$, (iv) $\alpha \lesssim \alpha_0$, (v) $\alpha = \alpha_0$, (vi) $\alpha \gtrsim \alpha_0$. For each case, plot the "flow" as in **(b)**. Indicate the stable and unstable fixed points which arise in each case. In cases where there are multiple stable fixed points for the same value of α, what determines the value of u^*, the steady-state density?*

Solution

The general expression of the equilibria of the system is given by Eq (1):

$$u_0^* = 0 \qquad\qquad u_\pm^* = \frac{(1-\kappa) \pm \sqrt{(\kappa+1)^2 - 4\kappa\alpha}}{2}$$

We will have three solutions if i) the two solutions $u_\pm^*$ are real (i.e. $\alpha < \alpha_c$) and if ii) they are both non-negative.

[2] In fact, the derivative of $\sqrt{1-\alpha}$ is $-(2\sqrt{1-\alpha})^{-1}$, which tends to $-\infty$ for $\alpha \to 1$

This happens when the smaller solution, u^*_-, is non-negative, i.e.:

$$\frac{(1-\kappa)-\sqrt{(\kappa+1)^2-4\kappa\alpha}}{2} \geq 0 \;\Rightarrow\; \frac{(1-\kappa)}{2} \geq \frac{\sqrt{(\kappa+1)^2-4\kappa\alpha}}{2} \;\Rightarrow$$

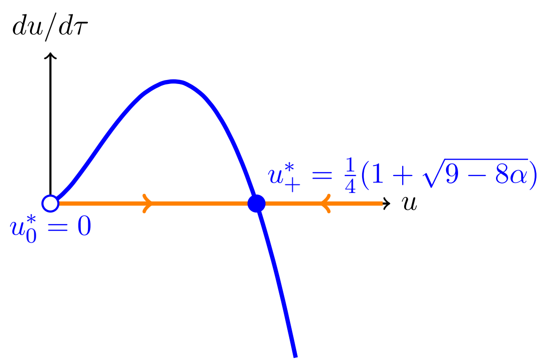
$$\Rightarrow\; (1-\kappa) \geq \sqrt{(\kappa+1)^2-4\kappa\alpha} \;\Rightarrow\; (1-\kappa)^2 \geq (k+1)^2-4\kappa\alpha \;\Rightarrow$$

$$\Rightarrow\; 1+\kappa^2-2\kappa \geq 1+\kappa^2+2\kappa-4\kappa\alpha \;\Rightarrow\; 4\kappa\alpha \geq 4\kappa \;\Rightarrow\; \alpha \geq 1 := \alpha_0$$

Therefore, we will have three distinct solutions for $1 \leq \alpha \leq \alpha_c(1/2) = 9/8 = 1.125$.

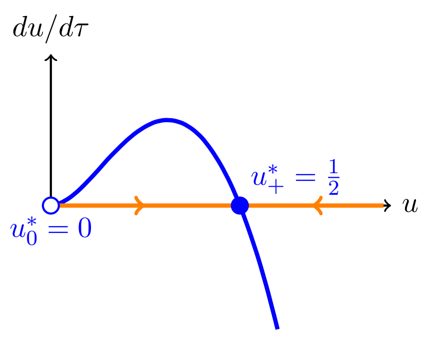
Let's now plot $du/d\tau$ for $\kappa = 1/2$ and the required values of α to determine the stability of the equilibria with a streamplot:

i. $\boldsymbol{\alpha \lesssim \alpha_0}$: we choose $\alpha = 0.95$. The streamplot we obtain is the following:



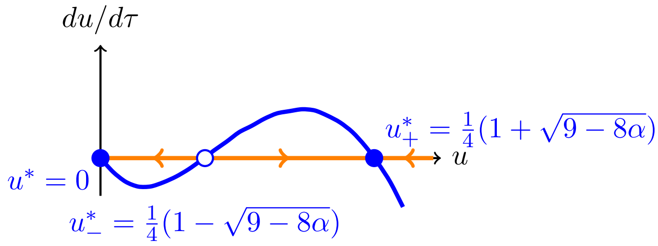
so we have one unstable equilibrium at $u^* = 0$ and one stable one at $u^*_+ > 0$. As soon as the initial condition is larger than 0, the population will tend towards u^*_+.

ii. $\boldsymbol{\alpha = \alpha_0}$: we have $\alpha = 1$. The streamplot we obtain is the following:



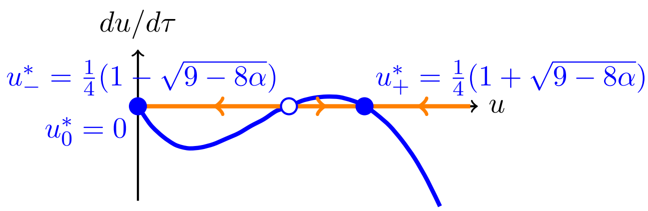
and so the situation is the same as the previous point.

iii. $\boldsymbol{\alpha \gtrsim \alpha_0}$: we choose $\alpha = 1.05$. The streamplot we obtain is the following:



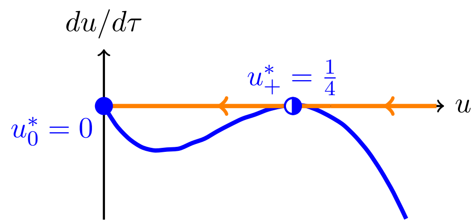
Now a new equilibrium has emerged, and $u^* = 0$ is now stable. Therefore, if the initial condition is $0 < u(0) < u^*_-$, the system will end up in $u^* = 0$; in other words, if the initial population is smaller than a threshold (u^*_-), the population will die out. On the other hand, if $u(0) > u^*_-$, the population will always tend towards u^*_+. This population size effect (i.e., the fact that in order to have a non-zero stationary population the initial population must be larger than a threshold) is known as the Allee effect.

iv. $\boldsymbol{\alpha \lesssim \alpha_c(1/2)}$: we choose $\alpha = 1.12$. The streamplot we obtain is the following:



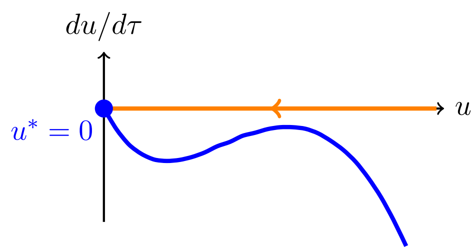
The situation is the same as before; the two equilibria $u^*_\pm > 0$ are approaching each other.

v. $\boldsymbol{\alpha = \alpha_c(1/2)}$: we have $\alpha = 1.125$. The streamplot we obtain is the following:



The two equilibria $u^* > 0$ have now merged into a saddle point. If the initial population is $u(0) > u^*_+$, the system will slowly tend towards u^*_+, but as soon as the population is pushed below u^*_+ it will go to extinction.

vi. $\boldsymbol{\alpha \gtrsim \alpha_c(1/2)}$: we choose $\alpha = 1.13$. The streamplot we obtain is the following:



Now the only possible equilibrium is $u^* = 0$, and so the population will go to extinction independently of the initial condition.

(e) *For the nonzero stable fixed point u^* obtained in **(d)**, use Taylor expansion to obtain the leading dependence on α in the vicinity of $\alpha_c(1/2)$ and in the vicinity of α_0. From these results, obtain the sensitivity $S(\alpha)$ of this fixed point and sketch both $u^*(\alpha)$ and $S(\alpha)$ in the vicinity of α_0. The type of* phase transition *which occurs at $\alpha_c(1/2)$ is called a "saddle-point bifurcation", while the phase transition which occurs at α_0 is called a "subcritical bifurcation". Describe in words how they are different from each other and from the supercritical bifurcation encountered in **(b)**.*

Solution

The expression of the non-zero fixed point is:

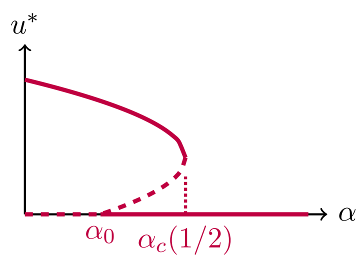
$$u^*_\pm = \frac{(1-\kappa) \pm \sqrt{(\kappa+1)^2 - 4\kappa\alpha}}{2}$$

By plugging $\kappa = 1/2$ we get:

$$u^*_\pm = \frac{1 - 1/2 \pm \sqrt{(1/2+1)^2 - 4\alpha \cdot 1/2}}{2} = \frac{1/2 \pm \sqrt{(3/2)^2 - 2\alpha}}{2} = \frac{1}{4} \pm \frac{1}{2}\sqrt{\frac{9}{4} - 2\alpha} =$$

$$= \frac{1}{4} \pm \frac{1}{2}\sqrt{\frac{9-8\alpha}{4}} = \frac{1}{4} \pm \frac{1}{2}\cdot\frac{1}{2}\sqrt{9-8\alpha} = \frac{1}{4}(1 \pm \sqrt{9-8\alpha})$$

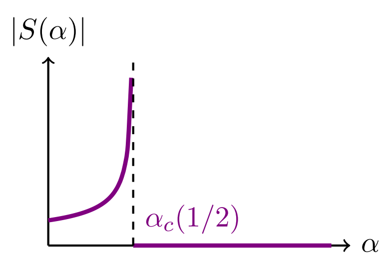
The bifurcation diagram (i.e., the plot of the dependence of u^* on α) is the following:



Therefore, at $\alpha_c(1/2)$ a new fixed point emerges, and splits into two fixed points for $\alpha \lesssim \alpha_c(1/2)$. Furthermore, the absolute value of the derivative $S(\alpha) = du^*/d\alpha$ diverges to ∞ for[3] $\alpha \to \alpha_c(1/2)^-$:

$$|S(\alpha)| = \left|\frac{du^*}{d\alpha}\right| = \left|\frac{1}{4}(1+\sqrt{9-8\alpha})\right| = \left|-\frac{1}{\sqrt{9-8\alpha}}\right| = \frac{1}{\sqrt{9-8\alpha}} \xrightarrow{\alpha\to\alpha_c(1/2)^-} +\infty \tag{3}$$

and so a Taylor expansion around $\alpha_c(1/2)$ is *not* possible. The plot of $|S(\alpha)|$ is the following:



[3]The expression "$\alpha \to \alpha_c(1/2)^-$" means that α is approaching $\alpha_c(1/2)$ "from below", i.e. from values smaller than $\alpha_c(1/2)$.

On the other hand, $u_+^*(\alpha)$ and $S(\alpha)$ are continuous and differentiable at $\alpha_0 = 1$, so we can perform a Taylor expansion around that point. Expanding u_+^*:

$$\begin{aligned} u_+^* &= \frac{1}{4}(1+\sqrt{9-8\alpha}) = \\ &= u_+^*(\alpha=1) + \left.\frac{du_+^*}{d\alpha}\right|_{\alpha=1}(\alpha-1) + \frac{1}{2}\left.\frac{d^2u_+^*}{d\alpha^2}\right|_{\alpha=1}(\alpha-1)^2 + \frac{1}{6}\left.\frac{d^3u_+^*}{d\alpha^3}\right|_{\alpha=1}(\alpha-1)^3 + \cdots = \\ &= \left.\frac{1}{4}(1+\sqrt{9-8\alpha})\right|_{\alpha=1} + \left.\left(-\frac{1}{9-8\alpha}\right)\right|_{\alpha=1}(\alpha-1) + \frac{1}{2}\cdot\left.\left[-\frac{4}{(9-8\alpha)^{3/2}}\right]\right|_{\alpha=1}(\alpha-1)^2 + \\ &\qquad + \frac{1}{6}\cdot\left.\left[-\frac{48}{(9-8\alpha)^{5/2}}\right]\right|_{\alpha_1}(\alpha-1)^3 + \cdots = \end{aligned}$$

$$= \frac{1}{2} + (-1)(\alpha-1) + \frac{1}{2}\cdot(-4)(\alpha-1)^2 + \frac{1}{6}\cdot(-48)(\alpha-1)^3 + \cdots = \frac{1}{2} - (\alpha-1) - 2(\alpha-1)^2 - 8(\alpha-1)^3 + \cdots$$

Neglecting all terms beyond leading order in α we get:

$$u^* = \frac{3}{2} - \alpha$$

If we now consider $u_-^*(\alpha)$, this functon will be continuous but not smooth[4] in α_0. The expansion must therefore be written separately for $\alpha \lesssim \alpha_0$ and for $\alpha \gtrsim \alpha_0$:

$$u_-^* \approx \begin{cases} 0 & \alpha < \alpha_0 \\ u_-^*(\alpha=1) + \left.\frac{du_-^*}{d\alpha}\right|_{\alpha=1}(\alpha-1) + \cdots & \alpha > \alpha_0 \end{cases} \quad \Rightarrow \quad u_-^* \approx \begin{cases} 0 & \alpha < \alpha_0 \\ (\alpha-1) & \alpha > \alpha_0 \end{cases}$$

The first important difference between these two transitions is that the transition at α_0 is continuous, while the one at $\alpha_c(1/2)$ is discontinuous.

The difference between the subcritical bifurcation found here and the supercritical bifurcation found in **(b)** is that in this case as the parameter α is changed an unstable equilibrium ($u_0^* = 0$) "splits" into multiple equilibria, while in a supercritical bifurcation it is a *stable* equilibrium that "splits" into more.

(f) *For $\kappa = 2$, show that there are two non-negative solutions $u^*(\alpha)$ for $\alpha < \alpha_1$, where α_1 is a number smaller than $\alpha_c(2)$, and one solution for $\alpha > \alpha_1$. Determine which of the fixed points is stable by plotting $du/d\tau$ vs u for $\kappa = 2$ and the following values of α: (i) $\alpha \lesssim \alpha_1$. (ii) $\alpha = \alpha_1$, (iii) $\alpha \gtrsim \alpha_1$. For each case, plot the "flow" and indicate the stable and unstable fixed points as above. Using Taylor expansion, find the leading dependence of the stable fixed point u^* on α in the vicinity of α_1. From this result, find the sensitivity $S(\alpha)$, and sketch $u^*(\alpha)$, $S(\alpha)$ in the vicinity of α_1. The* phase transition *which occurs at α_1 is called a "transcritical bifurcation". Describe in words again how it is different from the bifurcations encountered in **(b)** and **(e)***

Solution

[4] We are looking at the "merging" of the unstable branch into the equilibrium $u^* = 0$ in the bifurcation diagram above.

For $\kappa = 2$, the expression of the non-zero fixed points is:

$$u^*_\pm = \left.\frac{(1-\kappa) \pm \sqrt{(\kappa+1)^2 - 4\kappa\alpha}}{2}\right|_{\kappa=2} = \frac{-1 \pm \sqrt{3^2 - 4\cdot 2\cdot \alpha}}{2} = \frac{1}{2}(-1 \pm \sqrt{9-8\alpha})$$

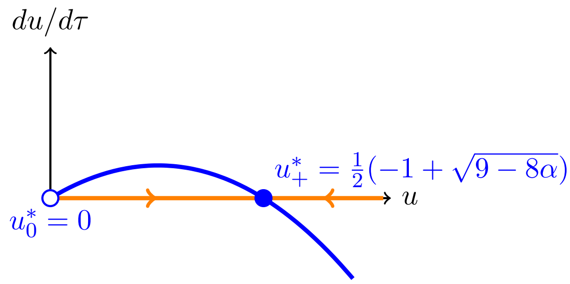
Now, u^*_- is *always* negative and so the only two possible equilibria are $u^*_0 = 0$ and u^*_+. This last fixed point will be non-negative when[5]:

$$\frac{1}{2}(-1+\sqrt{9-8\alpha}) \geq 0 \;\Rightarrow\; \sqrt{9-8\alpha} > 1 \;\Rightarrow\; 9-8\alpha \geq 1 \;\Rightarrow\; -8\alpha \geq -8 \;\Rightarrow\; \alpha \leq 1 := \alpha_1$$

Therefore, we have two non-negative solutions (u^*_0 and u^*_+) for $\alpha < \alpha_1$ and only one solution (u^*_0) for $\alpha > \alpha_1$.

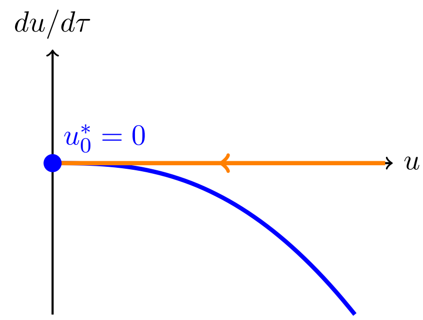
Let's now plot $du/d\tau$ for the three values of α as required and determine the stability of the equilibria with a streamplot:

i. $\boldsymbol{\alpha \lesssim \alpha_1}$: we choose $\alpha = 0.95$. The streamplot we obtain is the following:



Therefore, $u^*_0 = 0$ is an unstable equilibrium, while u^*_+ is stable. As soon as the initial condition is larger than 0, the population will tend towards u^*_+.

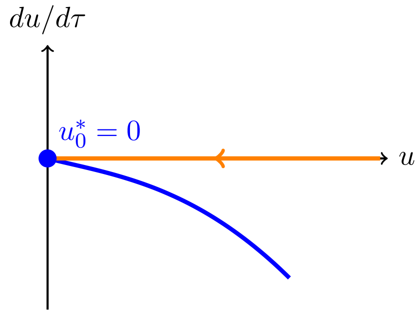
ii. $\boldsymbol{\alpha = \alpha_1}$: we have $\alpha = 1$. The streamplot we obtain is the following:



The only equilibrium, $u^*_0 = 0$ is stable. Whatever the initial condition, the population will always go to extinction.

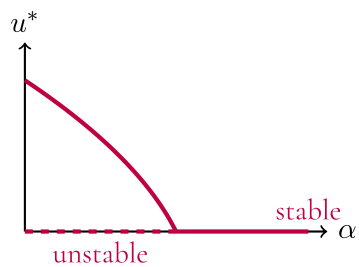
iii. $\boldsymbol{\alpha \gtrsim \alpha_1}$: we choose $\alpha = 1.1$. The streamplot we obtain is the following:

[5]Notice: the fact that $\alpha_1 = \alpha_0$ is just a coincidence.

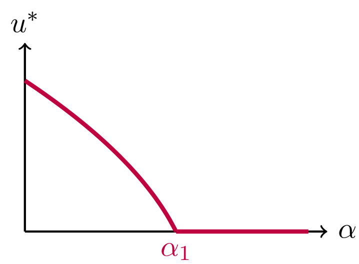


Like in the previous case, the only equilibrium $u_0^* = 0$ is stable.

The bifurcation diagram is the following:



and so the dependence of the stable fixed point u_+^* on α is:

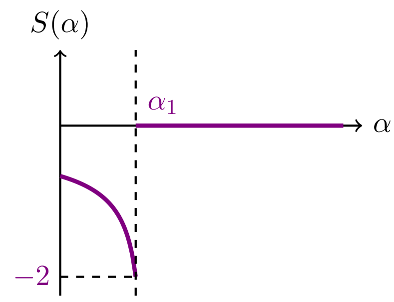


where the curve on the left of α_1 is $\frac{1}{2}(-1+\sqrt{9-8\alpha})$. This curve is not smooth in α_1, so we have again to write the Taylor expansion for $\alpha < \alpha_1$ and $\alpha > \alpha_1$ separately. We get:

$$u_+^* \approx \begin{cases} -2(\alpha - 1) & \alpha < \alpha_1 \\ 0 \quad \alpha > \alpha_1 \end{cases}$$

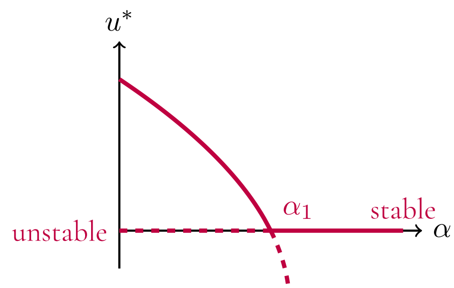
Therefore, in this case the sensitivity $S(\alpha)$, while still being discontinuous, does *not* diverge for $\alpha \to \alpha_1^-$:

$$S = \frac{du^*}{d\alpha} = \frac{d}{d\alpha}\frac{1}{2}(-1+\sqrt{9-8\alpha}) = -\frac{2}{\sqrt{9-8\alpha}} \xrightarrow{\alpha \to \alpha_1^-} -2$$



The difference between this transcritical bifurcation and the subcritical and saddle-point bifurcations encountered before are the following:

- A transcritical bifurcation is continuous, like a subcritical one and unlike a saddle-point bifurcation
- The sensitivity in a transcritical bifurcation is discontinuous but it does not diverge close to the critical point
- Subcritical (and also supercritical) bifurcations and saddle-point bifurcations involve the creation/destruction of fixed points. In a transcritical bifurcation, on the other hand, two fixed points cross each other, "exchanging" their stability. In this particular system we can't see the full picture because $u^* > 0$. If we also allow u^* to be negative, the bifurcation diagram in the vicinity of α_1 looks like this:



(g) *Based on the results obtained in **(a)-(f)** above, sketch the phase diagram in the parameter space $(\kappa.\alpha)$ as follows: draw the line (actually a curve) $\alpha_c(\kappa)$ and put down the special points $(\kappa, \alpha) = (1, \alpha_c(1)), (1/2, \alpha_c(1/2)), (1/2, \alpha_0), (2, \alpha_1)$. With the additional knowledge that the critical values α_0 and α_1 are κ-independent (you don't need to derive this), you can obtain 2 lines that divide the entire parameter space into three distinct regions. Show the two lines in the space of (κ, α) and give a verbal description of the three "phases" separated by these lines. Indicate the nature of phase transitions (bifurcations) upon crossing each line separating the three phases.*

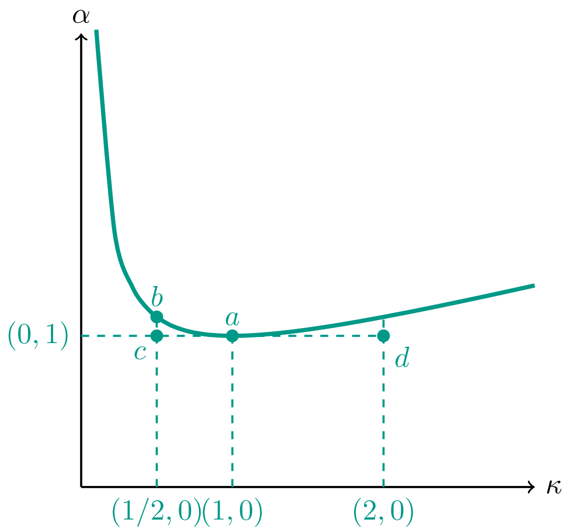
Solution

Let's call the special points:

$$a = (1, \alpha_c(1)) = (1, 1) \qquad b = \left(\frac{1}{2}, \alpha_c\left(\frac{1}{2}\right)\right) = \left(\frac{1}{2}, \frac{9}{8}\right)$$

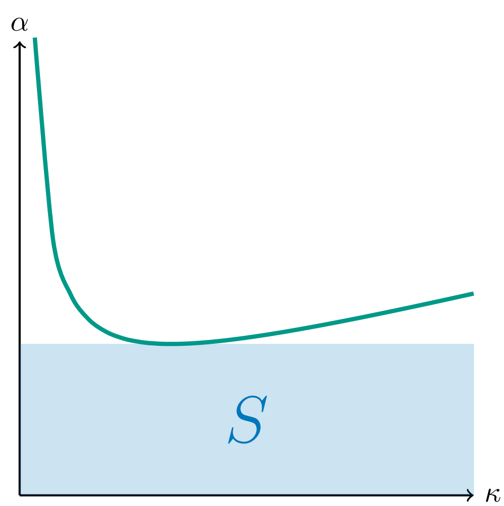
$$c = \left(\frac{1}{2}, \alpha_0\right) = \left(\frac{1}{2}, 1\right) \qquad d = (2, \alpha_1) = (2, 1)$$

and plot them together with $\alpha_c(\kappa)$ (and a few lines for reference):

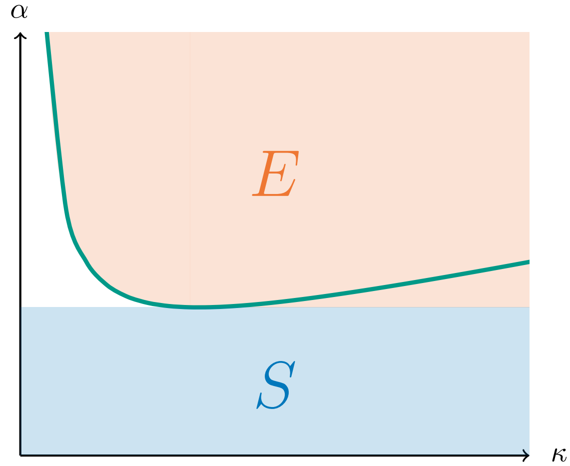


Let's now use all the information we have gathered in the previous points to understand how does the phase diagram look:

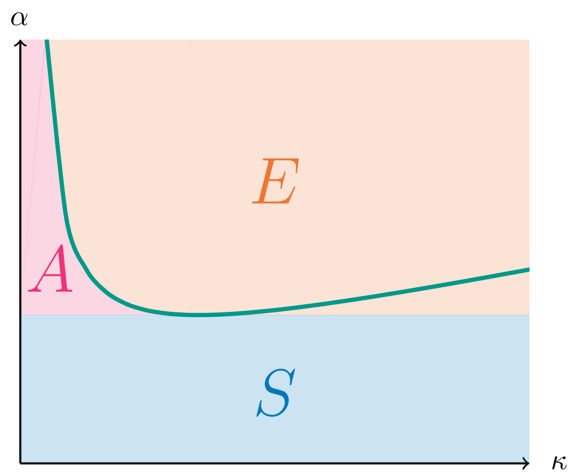
- If we move along any of the the segments $(1/2, 0) \to c$, $(1, 0) \to a$ and $(2, 0) \to d$, we have that the fixed points of the system are u_0^* and u_+^*; we are in the situation where as soon as the initial condition is $u(0) > 0$, the system will tend towards u_+^*. Therefore, we can infer that in the whole region $\alpha < 1$ the system exhibits a nontrivial equilibrium u_+^*, to which the population will always tend to if $u(0) > 0$. We call this phase S for "survival":



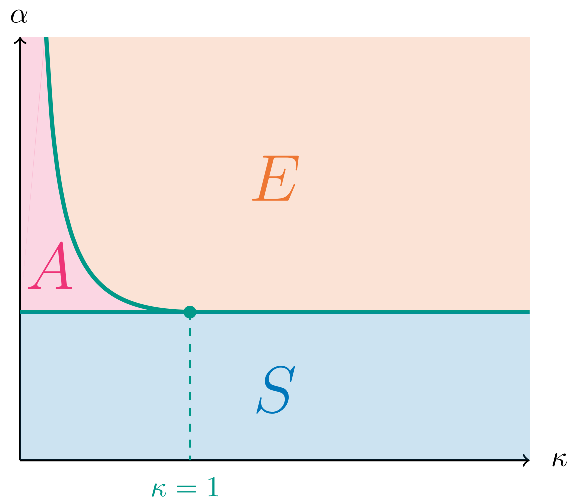
- Above the curve outlined by $\alpha_c(\kappa)$, the only possible fixed point is u_0^*. In this area of the parameter space the population wil always go to extinction, no matter the initial condition. If we move on the segment $(2, 0) \to d$ this is also true between d and the curve $\alpha_c(\kappa)$. Therefore, this will happen in all the area of the parameter space that is between the curve $\alpha_c(\kappa)$ and the region S. We call this phase E for "extinction":



- Finally, if we move along the segment $c \to b$ the system will exhibit the Allee effect (i.e., we need $u(0) > u_-^*$ in order to have a non-zeo stationary population). We call this phase A from “Allee”:



Therefore, the phase diagram of the system (and the two lines that divide it into three regions) are:



The transition $S \longleftrightarrow A$ is a subcritical bifurcation and the transition $A \longleftrightarrow E$ is a saddle-point bifurcation. Finally, the transition $S \longleftrightarrow E$ for $\kappa = 1$ is a supercritical bifurcation while for $\kappa > 1$ is a transcritical bifurcation.

2. Oscillatory genetic circuit

A genetic circuit in a cell involves two transcription factors, an "activator" and a "repressor". The activator activates the expression of itself and the repressor, while the repressor represses the expression of the activator. This circuit is known as the "predator-prey" circuit. Denoting the concentrations of the activator and the repressor by $[A]$ and $[R]$, respectively, we can write down a simple set of equations describing their dynamics:

$$\frac{d[A]}{dt} = \alpha_A \frac{[A]}{[A] + K_A} \cdot \frac{K_R}{[R] + K_R} - \mu[A]$$

$$\frac{d[R]}{dt} = \alpha_R \frac{[A]}{[A] + K_A} - \mu[R]$$

In the above, the parameters K_A and K_R are the dissociation constant for the binding of the activator and the repressor to the promoter regions, respectively, α_A and α_R characterize the activity of the two promoter, and μ is the rate of cell growth (which serves here to dilute the concentrations of the transcription factors). In this problem, you will find conditions under which this circuit sustains oscillation.

(a) *Make these equations dimensionless using $u = [A]/K_A$, $v = [R]/K_R$, and $\tau = \mu t$. Write down the dependences of the two remaining dimensionless parameters, $\sigma_A \propto \alpha_A$ and $\sigma_R \propto \alpha_R$, in terms of the original parameters of the problem.*

Solution

Let's first consider the equation for $[A]$, and plug in it $[A] = uK_A$, $[R] = vK_R$ and $t = \tau/\mu$:

$$\frac{d}{d(\tau/\mu)}(uK_A) = \alpha_A \frac{uK_A}{uK_A + K_A} \cdot \frac{K_R}{vK_R + K_R} - \mu u K_A \quad \Rightarrow$$

$$\Rightarrow \quad \mu K_A \frac{du}{d\tau} = \alpha_A \frac{u}{u+1} \cdot \frac{1}{v+1} - \mu u K_A \quad \Rightarrow$$

$$\Rightarrow \quad \frac{du}{d\tau} = \frac{\alpha_A}{\mu K_A} \cdot \frac{u}{u+1} \cdot \frac{1}{v+1} - u$$

We can therefore define $\sigma_A := \alpha_A/(\mu K_A)$ (note that $\sigma_A \propto \alpha_A$). Similarly, for $[R]$ we get:

$$\frac{d}{d(\tau/\mu)}(vK_R) = \alpha_R \frac{uK_A}{uK_A + K_A} - \mu v K_R \quad \Rightarrow$$

$$\Rightarrow \quad \mu K_R \frac{dv}{dt} = \alpha_R \frac{u}{u+1} - \mu v K_R \quad \Rightarrow$$

$$\Rightarrow \quad \frac{dv}{d\tau} = \frac{\alpha_R}{\mu K_R} \cdot \frac{u}{u+1} - v$$

and we can define $\sigma_R := \alpha_R/(\mu K_R)$ (note that $\sigma_R \propto \alpha_R$). This way, the equations of our system become:

$$\frac{du}{d\tau} = \sigma_A \frac{u}{u+1} \cdot \frac{1}{v+1} - u \qquad\qquad \frac{dv}{d\tau} = \sigma_R \frac{u}{u+1} - v$$

Notice that, by definition, both $\sigma_A > 0$ and $\sigma_R > 0$ (α_A, α_R, K_A, K_R and μ are all positive parameters).

(b) *In (u, v) space, sketch the two null clines (i.e., the relation between u and v that makes $du/d\tau = 0$ or $dv/d\tau = 0$). Indicate each sub-regions of (u, v) space partitioned by the two null clines whether $du/d\tau$ and $dv/d\tau$ are positive or negative. Sketch qualitatively the "flow" of u and v by arrows in the (u, v) space.*

Solution

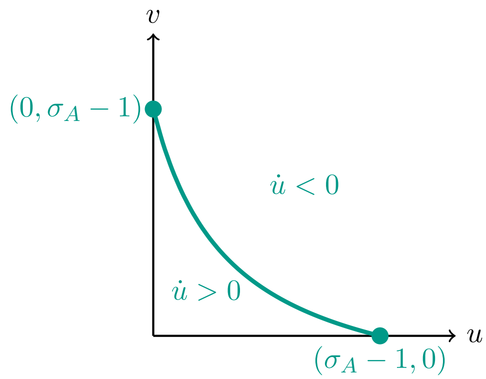
In order to make it easier to plot them, we express the null clines as $v = \cdots$. From the equation for u we obtain:

$$\frac{du}{d\tau} = 0 \quad \Rightarrow \quad \sigma_A \frac{u}{u+1} \cdot \frac{1}{v+1} = u$$

Therefore, one possible solution is $u = 0$. Assuming $u \neq 0$ and dividing by u on both sides:

$$\sigma_A \frac{1}{u+1} = v + 1 \quad \Rightarrow \quad v = \sigma_A \frac{1}{u+1} - 1$$

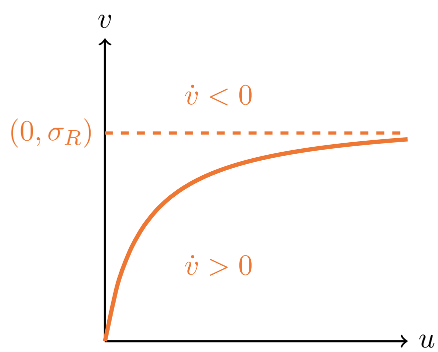
and $du/d\tau$ is positive when v is smaller than this expression. Therefore, the plot of this nulllcline and of the regions where $du/d\tau$ is positive/negative is the following:



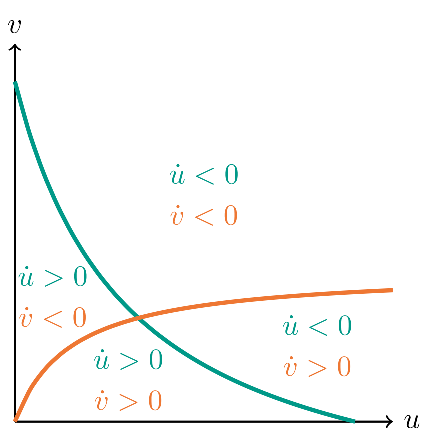
From the equation for v we obtain:

$$\frac{dv}{d\tau} = 0 \quad \Rightarrow \quad \sigma_R \frac{u}{u+1} = v \quad \Rightarrow \quad v = \sigma_R \frac{u}{u+1}$$

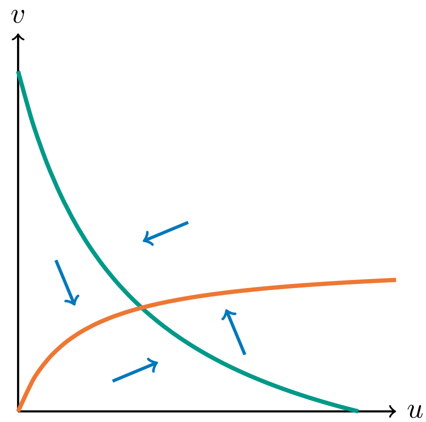
and $dv/d\tau$ is positive when v is smaller than this expression. Therefore, the plot of this nulllcline and of the regions where $dv/d\tau$ is positive/negative is the following:



The combined plot of both null clines is:



Therefore, the qualitative flow of the system is the following:



The solutions of this system will oscillate around the nontrivial fixed point of the system (which is the intersection of the two null clines). It remains to be seen if the solutions spiral *away from* or *towards* this point, or if they go around it in closed orbits (the qualitative analysis we're doing here does not allow us to distinguish between these cases).

(c) *Find the fixed point(s)* (u^*, v^*) *where* $du/d\tau = 0$ *and* $dv/d\tau = 0$*. Show conditions on the parameters* σ_A *and* σ_R *in order for there to be a "nontrivial" fixed point* $u^* > 0$ *and* $v^* > 0$*. Obtain how the nontrivial fixed point* (u^*, v^*) *depends on the parameters* (σ_A, σ_R)*.*

Solution

In order to find the nontrivial fixed points (i.e., with $u^*, v^* \neq 0$), we must solve:

$$\sigma_A \frac{u^*}{u^*+1} \cdot \frac{1}{v+1} - u^* = 0 \qquad\qquad \sigma_R \frac{u^*}{u^*+1} - v^* = 0 \tag{4}$$

which corresponds to finding the intersection point of the null clines shown above. From the first equation in (4) we get:

$$\sigma_A \frac{u^*}{u^*+1} \cdot \frac{1}{v+1} = u^* \quad \Rightarrow \quad u^* = \frac{\sigma_A}{v^*+1} - 1 \tag{5}$$

where in we have divided by u^* on both sides since we assuming $u^* \neq 0$. From the second equation in (4) we get simply:

$$v^* = \sigma_R \frac{u^*}{u^*+1}$$

Substituting u^* from equation (5) we get:

$$v^* = \sigma_R \left(\frac{\sigma_A}{v^*+1} - 1 \right) \frac{v^*+1}{\sigma_A} = \frac{\sigma_R}{\sigma_A}(\sigma_A - v^* - 1) = \sigma_R - \frac{\sigma_R}{\sigma_A} v^* - \frac{\sigma_R}{\sigma_A} \quad \Rightarrow$$

$$\Rightarrow \quad v^* \left(1 + \frac{\sigma_R}{\sigma_A}\right) = \sigma_R \left(1 - \frac{1}{\sigma_A}\right) \quad \Rightarrow \quad v^*(\sigma_A + \sigma_R) = \sigma_R(\sigma_A - 1) \quad \Rightarrow \quad v^* = \frac{\sigma_R(\sigma_A - 1)}{\sigma_A + \sigma_R}$$

If we now plug this expression of v^* into u^* from equation (5), we get:

$$u^* = \frac{\sigma_A}{\frac{\sigma_R\sigma_A - \sigma_R}{\sigma_A+\sigma_R}+1} - 1 = \frac{\sigma_A}{\sigma_R\sigma_A - \sigma_R + \sigma_A + \sigma_R}(\sigma_A+\sigma_R) - 1 = \frac{\sigma_A}{\sigma_R\sigma_A + \sigma_A}(\sigma_A+\sigma_R) - 1 =$$

$$= \frac{\sigma_A}{\sigma_A(\sigma_R+1)}(\sigma_A+\sigma_R) - 1 = \frac{\sigma_A+\sigma_R}{\sigma_R+1} - 1 = \frac{\sigma_A+\sigma_R-\sigma_R-1}{\sigma_R+1} = \frac{\sigma_A-1}{\sigma_R+1}$$

Therefore, the general expression of the nontrivial fixed point of the system is:

$$(u^*, v^*) = \left(\frac{\sigma_A-1}{\sigma_R+1}, \frac{\sigma_R(\sigma_A-1)}{\sigma_A+\sigma_R}\right)$$

In order for this fixed point to be really nontrivial, we need that the parameters σ_A and σ_R are such that $u^* > 0$ and $v^* > 0$. Therefore, we need:

$$u^* > 0 \quad \Rightarrow \quad \frac{\sigma_A-1}{\sigma_R+1} > 0 \quad \Rightarrow \quad \sigma_A > 1$$

(since $\sigma_R > 0$) and:

$$v^* > 0 \quad \Rightarrow \quad \frac{\sigma_R(\sigma_A-1)}{\sigma_A+\sigma_R} \quad \Rightarrow \quad \sigma_A > 1$$

(since again $\sigma_R > 0$). Therefore, we need $\sigma_A > 1$ in order to have $u^*, v^* > 0$.

(d) *In the vicinity of the nontrivial fixed point obtained in* ***(c)****, use Taylor expansion to linearize the dynamical equations for* $x(t) = u(t) - u^*$, $y(t) = v(t) - v^*$. *Find the two eigenvalues* λ *for the linearized system.*

Solution

First of all, we can rewrite our system as:

$$\frac{d\vec{z}}{d\tau} = f(\vec{z}) \tag{6}$$

where:

$$\vec{z} = \begin{pmatrix} u \\ v \end{pmatrix} \qquad f(\vec{z}) = \begin{pmatrix} f_1(\vec{z}) \\ f_2(\vec{z}) \end{pmatrix} = \begin{pmatrix} \sigma_A \frac{u}{u+1} \cdot \frac{1}{v+1} - u \\ \sigma_R \frac{u}{u+1} - v \end{pmatrix}$$

This way, the linearization of our system around (u^*, v^*) looks like:

$$\frac{d\vec{z}}{d\tau} = f(\vec{z}^*) + J(\vec{z}^*)(\vec{z} - \vec{z}^*)$$

where we are neglecting all terms beyond the first order, and $J(\vec{z}^*)$ is the jacobian matrix of the system computed in $\vec{z}^* = (u^*, v^*)$:

$$J(\vec{z}^*) = \begin{pmatrix} \frac{\partial f_1}{\partial u} & \frac{\partial f_1}{\partial v} \\ \\ \frac{\partial f_2}{\partial u} & \frac{\partial f_2}{\partial v} \end{pmatrix}\Bigg|_{(u^*,v^*)}$$

Let's compute the partial derivatives:

$$\frac{\partial f_1}{\partial u}\bigg|_{(u^*,v^*)} = \frac{\partial}{\partial u}\left(\sigma_A \frac{u}{u+1} \cdot \frac{1}{v+1} - u\right)\bigg|_{(u^*,v^*)} = \sigma_A \left(\frac{1}{u+1} - \frac{u}{(u+1)^2}\right)\frac{1}{v-1} - 1\bigg|_{(u^*,v^*)} =$$

$$= \frac{\sigma_A}{(u^*+1)^2(v^*+1)} - 1 = \cdots = \frac{1-\sigma_A}{\sigma_A+\sigma_R}$$

$$\left.\frac{\partial f_1}{\partial v}\right|_{(u^*,v^*)} = \frac{\partial}{\partial v}\left(\sigma_A \frac{u}{u+1}\cdot\frac{1}{v+1} - u\right)\Bigg|_{(u^*,v^*)} = -\sigma_A \frac{u^*}{u^*+1}\cdot\frac{1}{(v^*+1)^2} - u^* =$$

$$= \cdots = \frac{(\sigma_A+\sigma_R)(1-\sigma_A)}{\sigma_A(\sigma_R+1)^2}$$

$$\left.\frac{\partial f_2}{\partial u}\right|_{(u^*,v^*)} = \frac{\partial}{\partial u}\left(\sigma_R \frac{u}{u+1} - v\right)\Bigg|_{(u^*,v^*)} = \frac{\sigma_R}{(u^*+1)^2} = \cdots = \frac{\sigma_R(\sigma_R+1)^2}{(\sigma_A+\sigma_R)^2}$$

$$\left.\frac{\partial f_2}{\partial v}\right|_{(u^*,v^*)} = \frac{\partial}{\partial v}\left(\sigma_R \frac{u}{u+1} - v\right)\Bigg|_{(u^*,v^*)} = -1$$

Therefore, we have:

$$J(\vec{z}^*) = \begin{pmatrix} \frac{1-\sigma_A}{\sigma_A+\sigma_R} & \frac{(\sigma_A+\sigma_R)(1-\sigma_A)}{\sigma_A(\sigma_R+1)^2} \\ \frac{\sigma_R(\sigma_R+1)^2}{(\sigma_A+\sigma_R)^2} & -1 \end{pmatrix}$$

and we can write the linearization of the system around (u^*, v^*) as:

$$\begin{pmatrix} dx/d\tau \\ dy/d\tau \end{pmatrix} = \begin{pmatrix} \frac{1-\sigma_A}{\sigma_A+\sigma_R} & \frac{(\sigma_A+\sigma_R)(1-\sigma_A)}{\sigma_A(\sigma_R+1)^2} \\ \frac{\sigma_R(\sigma_R+1)^2}{(\sigma_A+\sigma_R)^2} & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

If we call for simplicity:

$$A = \frac{1-\sigma_A}{\sigma_A+\sigma_R} \qquad B = \frac{(\sigma_A+\sigma_R)(1-\sigma_A)}{\sigma_A(\sigma_R+1)^2} \qquad C = \frac{\sigma_R(\sigma_R+1)^2}{(\sigma_A+\sigma_R)^2}$$

the eigenvalues of the linearized system are found by solving:

$$\det\left[\begin{pmatrix} A & B \\ C & -1 \end{pmatrix} - \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix}\right] = 0 \;\Rightarrow\; \det\begin{pmatrix} A-\lambda & B \\ C & -(\lambda+1) \end{pmatrix} = 0 \;\Rightarrow$$

$\Rightarrow -(A-\lambda)(\lambda+1) - BC = 0 \Rightarrow \lambda^2 + \lambda(1-A) - BC - A = 0$ The solution of this quadratic equation is given by:

$$\lambda_\pm = \frac{1}{2}\left[-(1-A) \pm \sqrt{(1-A)^2 - 4(BC-A)}\right] = \cdots$$

$$\cdots = \frac{1}{2(\sigma_A+\sigma_R)}\left[1 - 2\sigma_A - \sigma_R \pm \sqrt{1 + \sigma_R(6-4\sigma_A) + \left(\frac{4}{\sigma_A} - 3\right)\sigma_R^2}\right]$$

(e) *Based on whether the eigenvalues λ found in **(d)** has nonzero imaginary component, and whether the real component of λ is positive or negative, find regions of the parameter space (σ_A, σ_R) where you expect the circuit to exhibit stable oscillation, damped oscillation, or stable coexistence.*

Solution

Let us first determine under which conditions $\operatorname{Re}\lambda_\pm > 0$. This happens when:

$$\frac{1 - 2\sigma_A - \sigma_R}{2(\sigma_A + \sigma_R)} > 0 \ \Rightarrow\ 1 - 2\sigma_A - \sigma_R > 0 \ \Rightarrow\ \sigma_R < 1 - 2\sigma_A$$

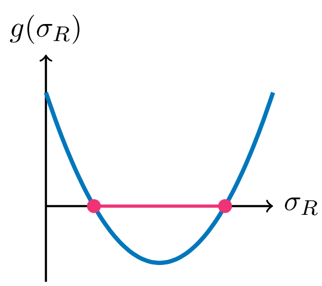
However, we always have $1 - 2\sigma_A < 0$ because $\sigma_A > 1$ (notice that we can't even have $\operatorname{Re}\lambda_\pm = 0$ because of the same reason). Therefore, this inequality can't be solved ($\sigma_R > 0$ by defintion) and we will *always* have $\operatorname{Re}\lambda_\pm < 0$: the nontrivial equilibrium (u^*, v^*) is *always* stable, and all the initial conditions (whether they oscillate or not) will tend towards it.

Let us then determine under which conditions there are oscillations at all. The system will exhibit oscillations if $\operatorname{Im}\lambda_\pm \neq 0$, which happens if[6]:

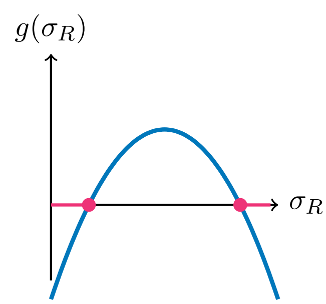
$$g(\sigma_R) := \sigma_R^2\left(\frac{4}{\sigma_A} - 3\right) + \sigma_R(6 - 4\sigma_A) + 1 < 0$$

The function $g(\sigma_R)$ is a parabola, and therefore:

- if it is convex (i.e., the sign of what multiplies σ_R^2 is positive, therefore $3 - 4/\sigma_A > 0 \ \Rightarrow\ \sigma_A < 4/3$), $g(\sigma_R) < 0$ if σ_R is in the region between the two zeroes of the parabola
- if it is concave (i.e., the sign of what multiplies σ_R^2 is negative, therefore $3 - 4/\sigma_A < 0 \ \Rightarrow\ \sigma_A > 4/3$), $g(\sigma_R) < 0$ if σ_R is smaller than the smallest zero or largest than the largest zero of the parabola



The parabola is convex, $\sigma_A < 4/3$



The parabola is concave, $\sigma_A > 4/3$

The zeroes of a parabola described by $g(\sigma_R)$ are:

$$\sigma_R^\pm = \frac{3\sigma_A - 2\sigma_A^2 \pm 2\sqrt{\sigma_A(\sigma_A - 1)^3}}{3\sigma_A - 4}$$

Therefore, for a convex parabola we have:

$$\sigma_A < \frac{4}{3} \qquad\qquad \sigma_R^- < \sigma_R < \sigma_R^+$$

[6] Remember: in order for the eigenvalues $\lambda_\pm$ to have a nonzero imaginary part, the term in their expression under the square root (i.e., the discriminant) must be negative.

while for a concave one:

$$\sigma_A > \frac{4}{3} \qquad \sigma_R < \sigma_R^- \quad \text{and} \quad \sigma_R > \sigma_R^+$$

Looking at, the expression of $\sigma_R^{\pm}$, $\sigma_A(\sigma_A - 1)^3$ is positive for $\sigma_A < 0$ and $\sigma_A > 1$. Since we are assuming $\sigma_A > 1$, the content of the square root is always positive and so $\sigma_R^{\pm}$ are both real. We therefore need to check when $\sigma_R^{\pm}$ are both positive. Since $\sigma_R^- < \sigma_R^+$, we can first check when[7] $\sigma_R^- > 0$:

$$\sigma_R^- \;=\; \frac{3\sigma_A - 2\sigma_A^2 - 2\sqrt{\sigma_A(\sigma_A-1)^3}}{3\sigma_A - 4} \;>\; 0 \quad\Rightarrow\quad \begin{cases} 3\sigma_A - 4 > 0 \\ 3\sigma_A - 2\sigma_A^2 - 2\sqrt{\sigma_A(\sigma_A-1)^3} > 0 \end{cases}$$

The first equation yields $\sigma_A > 4/3$. This means that σ_R^- could be positive only when the parabola is concave. Solving the second equation:

$$3\sigma_A - 2\sigma_A^2 > 2\sqrt{\sigma_A(\sigma_A-1)^3} \;\Rightarrow\; (3\sigma_A - 2\sigma_A^2)^2 > 4\sigma_A(\sigma_A-1)^3 \;\Rightarrow$$

$$\Rightarrow\; 9\sigma_A^2 + 4\sigma_A^4 - 12\sigma_A^3 > 4\sigma_A(\sigma_A^3 - 3\sigma_A^2 + 3\sigma_A - 1) = 4\sigma_A^4 - 12\sigma_A^3 + 12\sigma_A^2 - 4\sigma_A \;\Rightarrow$$

$$\Rightarrow\; 3\sigma_A^2 - 4\sigma_A < 0 \;\Rightarrow\; \sigma_A(3\sigma_A - 4) < 0$$

This last inequality is true if $\sigma_A > 0$ and $3\sigma_A - 4 < 0 \;\Rightarrow\; \sigma_A < 4/3$. Thus:

$$\sigma_R^- > 0 \;\Rightarrow\; \begin{cases} \sigma_A > 4/3 \\ \sigma_A < 4/3 \end{cases}$$

This means that the inequality $\sigma_R^- > 0$ does *not* have any solution: $\sigma_R^- < 0$ for *any* value of σ_A.

Similarly, we can check when $\sigma_R^+ > 0$:

$$\sigma_R^+ = \frac{3\sigma_A - 2\sigma_A^2 + 2\sqrt{\sigma_A(\sigma_A-1)^3}}{3\sigma_A - 4} > 0 \;\Rightarrow\; \begin{cases} 3\sigma_A - 4 > 0 \\ 3\sigma_A - 2\sigma_A^2 + 2\sqrt{\sigma_A(\sigma_A-1)^3} > 0 \end{cases} \quad\Rightarrow$$

$$\Rightarrow\; \begin{cases} \sigma_A > 4/3 \\ 2\sqrt{\sigma_A(\sigma_A-1)^3} > 2\sigma_A^2 - 3\sigma_A \end{cases}$$

Solving the second equation:

$$4\sigma_A(\sigma_A^3 - 3\sigma_A^2 + 3\sigma_A - 1) = 4\sigma_A^4 - 12\sigma_A^3 + 12\sigma_A^2 - 4\sigma_A > 4\sigma_A^4 + 9\sigma_A^2 - 12\sigma_A^3 \;\Rightarrow$$

$$\Rightarrow\; 3\sigma_A^2 - 4\sigma_A > 0 \;\Rightarrow\; \sigma_A(3\sigma_A - 4) > 0$$

This inequality is true if $\sigma_A > 0$ and $3\sigma_A - 4 > 0 \;\Rightarrow\; \sigma_A > 4/3$, and so:

$$\sigma_R^+ > 0 \;\Rightarrow\; \begin{cases} \sigma_A > 4/3 \\ \sigma_A > 4/3 \end{cases} \quad\Rightarrow\; \sigma_A > \frac{4}{3}$$

Therefore:

[7] Because in that case we know that both $\sigma_R^{\pm} > 0$. If $\sigma_R^- < 0$ we could still have either $\sigma_R^+ > 0$ or $\sigma_R^+ < 0$.

– For $\boldsymbol{\sigma_A < 4/3}$ (i.e., the parabola is convex), $\sigma_R^{\pm} < 0$
– For $\boldsymbol{\sigma_A > 4/3}$ (i.e., the parabola is concave), $\sigma_R^{-} < 0$ and $\sigma_R^{+} > 0$

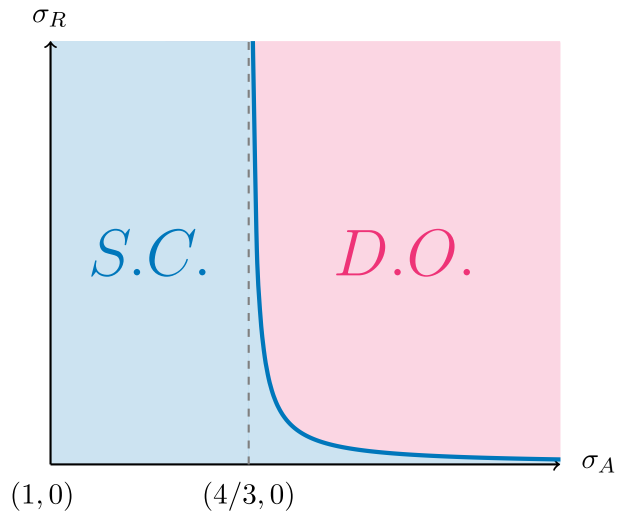
Therefore, the system will exhibit oscillations (i.e., $g(\sigma_R) < 0 \quad \Rightarrow \quad \text{Im}\,\lambda_\pm \neq 0$) *only* when:

$$\sigma_A > \frac{4}{3} \qquad \text{and} \qquad \sigma_R > \sigma_R^+ = \frac{3\sigma_A - 2\sigma_A^2 + 2\sqrt{\sigma_A(\sigma_A-1)^3}}{3\sigma_A - 4}$$

On the other hand, the system will *not* exhibit oscillations (i.e., $g(\sigma_R > 0) \quad \Rightarrow \quad \text{Im}\,\lambda_\pm = 0$) when:

$$\sigma_A < \frac{4}{3} \qquad \text{or} \qquad \sigma_A > \frac{4}{3} \qquad \text{and} \qquad \sigma_R \leq \sigma_R^+ = \frac{3\sigma_A - 2\sigma_A^2 + 2\sqrt{\sigma_A(\sigma_A-1)^3}}{3\sigma_A - 4}$$

The phase diagram of the system is the following:



In phase *S.C.* (which includes the line that separates the two phases) the system exhibits stable coexistence (i.e., $\text{Re}\,\lambda_\pm < 0$, $\text{Im}\,\lambda_\pm = 0$): there are no oscillations and therefore the solutions will simply tend towards the nontrivial fixed point (u^*, v^*). In phase *D.O.*, on the other hand, the solutions will also oscillate and therefore the system will exhibit damped oscillations (i.e., $\text{Re}\,\lambda_\pm < 0, \text{Im}\,\lambda_\pm \neq 0$). There are no regions in the parameter space where the system exhibits stable oscillations (i.e., $\text{Re}\,\lambda_\pm = 0, \text{Im}\,\lambda_\pm \neq 0$).

3. Rock-scissor-paper game

This classic "game" insolves three species R, S and P interacting in a population. S stimulates the growth of R while P stimulates the death of R. Also, P stimulates the growth of S while R stimulates the death of S, and R stimulates the growth of P while S stimulates the death of P. Let p_1, p_2, p_3 denote respectively the frequency of R, S, P in a population, with $p_1 + p_2 + p_3 = 1$. In the simplest case where the gain (cost) of winning (losing) is unity, the dynamics of the system is governed by the following ODES:

$$\frac{dp_1}{dt} = p_1 \cdot (p_2 - p_3)$$

$$\frac{dp_2}{dt} = p_2 \cdot (p_3 - p_1)$$

$$\frac{dp_3}{dt} = p_3 \cdot (p_1 - p_3)$$

In this problem, you will work out the conditions under which the R-S-P game sustains oscillations.

(a) *Show that the above equations admit a* conserved quantity, $p_1p_2p_3 := C$, *where C is a positive constant fixed by the initial condition, i.e. $C = p_1(0) \cdot p_2(0) \cdot p_3(0)$.*

Solution

In order to show that $C = p_1p_2p_3$ is conserved, we simply have to verify that its time derivative is null, i.e. $dC/dt = 0$:

$$\frac{dC}{dt} = \frac{d}{dt}(p_1p_2p_3) = \frac{dp_1}{dt} \cdot p_2p_3 + p_1\frac{d}{dt}(p_2p_3) =$$

$$= \dot{p}_1p_2p_3 + p_1(\dot{p}_2p_3 + p_2\dot{p}_3) = \dot{p}_1p_2p_3 + p_1\dot{p}_2p_3 + p_1p_2\dot{p}_3 =$$

$$= p_1(p_2 - p_3)p_2p_3 + p_1p_2(p_3 - p_1)p_3 + p_1p_2p_3(p_1 - p_2) =$$

$$= (p_1p_2 - p_1p_3)p_2p_3 + p_1p_2(p_3^2 - p_1p_3) + p_1p_2(p_1p_3 - p_2p_3) =$$

$$= \cancel{p_1p_2^2p_3} - \cancel{p_1p_2p_3^2} + \cancel{p_1p_2p_3^2} - \cancel{p_1^2p_2p_3} + \cancel{p_1^2p_2p_3} - \cancel{p_1p_2^2p_3} = 0$$

Since C is constant, its value will be fixed by its initial condition: $C(t) = C(0) = p_1(0) \cdot p_2(0) \cdot p_3(0)$.

(b) *Introducing $x_i = p_1 - 1/3$ to describe the deviation from the symmetric point $p_1 = p_2 = p_3 = 1/3$, write down the two constrains on p_i (on their sum and product) in terms of x_i. Further introducing $y = p_2 - p_3$, write down the constraint $p_1p_2p_3 = C$ in terms of x_1 and y (we will change x_1 to x below to further simplify the notation).*

Solution

From $x_i = p_i - 1/3$ we have $p_i = x_i + 1/3$, and by substituting in the constraint $p_1 + p_2 + p_3 = 1$ we get:

$$1 = p_1 + p_2 + p_3 = x_1 + \frac{1}{3} + x_2 + \frac{1}{3} + x_3 + \frac{1}{3} = x_1 + x_2 + x_3 + 1 \quad \Rightarrow \quad x_1 + x_2 + x_3 = 0$$

On the other hand, substituting in the expression for C:

$$C = p_1p_2p_3 = \left(x_1 + \frac{1}{3}\right)\left(x_2 + \frac{1}{3}\right)\left(x_3 + \frac{1}{3}\right) = \left(x_1x_2 + \frac{x_1}{3} + \frac{x_2}{3} + \frac{1}{9}\right)\left(x_3 + \frac{1}{3}\right) =$$

$$= x_1x_2x_3 + \frac{1}{3}x_1x_2 + \frac{1}{3}x_1x_3 + \frac{1}{9}x_1 + \frac{1}{3}x_2x_3 + \frac{1}{9}x_2 + \frac{1}{9}x_3 + \frac{1}{27} =$$

$$= x_1x_2x_3 + \frac{1}{3}(x_1x_2 + x_2x_3 + x_1x_3) + \frac{1}{9}(\underbrace{x_1 + x_2 + x_3}_{=0}) + \frac{1}{27} =$$

$$= x_1x_2x_3 + \frac{1}{3}(x_1x_2 + x_2x_3 + x_1x_3) + \frac{1}{27}$$

If we now call $x = p_1 - 1/3$ and $y = p_2 - p_3$ we have:

$$p_1 = x + \frac{1}{3} \qquad \begin{cases} p_2 + p_3 = 1 - p_1 = 2/3 - x \\ p_2 - p_3 = y \end{cases}$$

From the second equation in the system we have $p_2 = p_3 + y$, and plugging this expression in the first equation we obtain:

$$p_3 + y + p_3 = \frac{2}{3} - x \;\Rightarrow\; 2p_3 = \frac{2}{3} - x - y \;\Rightarrow\; p_3 = \frac{1}{2}\left(\frac{2}{3} - x - y\right)$$

Plugging this expression for p_3 back in the previous system of equations we get:

$$p_2 = \frac{1}{2}\left(\frac{2}{3} - x - y\right) + y = \frac{1}{2}\left(\frac{2}{3} - x + y\right)$$

We can now use these results to write C in terms of x and y:

$$C = p_1 p_2 p_3 = \left(x + \frac{1}{3}\right)\frac{1}{2}\left(\frac{2}{3} - x - y\right)\frac{1}{2}\left(\frac{2}{3} - x + y\right) =$$

$$= \frac{1}{4}\left(x + \frac{1}{3}\right)\left[\left(\frac{2}{3} - x\right)^2 - y^2\right] = \frac{1}{4}\left(x + \frac{1}{3}\right)\left(\frac{4}{9} + x^2 - \frac{4}{3}x - y^2\right) =$$

$$= \frac{1}{4}\left(\frac{4}{9}x + x^3 - \frac{4}{3}x^2 - xy^2 + \frac{4}{27} + \frac{1}{3}x^2 - \frac{4}{9}x - \frac{1}{3}y^2\right) =$$

$$= \frac{1}{9}x + \frac{1}{4}x^3 - \frac{1}{3}x^2 - \frac{1}{4}xy^2 + \frac{1}{27} + \frac{1}{12}x^2 - \frac{1}{9}x - \frac{1}{12}y^2 =$$

$$= \frac{1}{27} + \frac{1}{4}x^3 - \frac{1}{4}x^2 - \frac{1}{12}y^2(1 + 3x) =$$

$$= \frac{1}{27} - \frac{1}{4}x^2(1 - x) - \frac{1}{12}y^2(3x + 1)$$

(c) *From the constraint on x and y obtained in **(b)**, show that there is a unique maximum for $C(x, y)$ in the allowed space $0 < p_i < 1$. What is the value $C_0 := C(x_0, y_0)$ at the maximum? And what does the location of the maximum (x_0, y_0) corresponds to in terms of the frequencies p_i? Show that for $C \lesssim C_0$ (i.e., for $0 < C_0 - C \ll C_0$), the stable orbits are ellipses centered at (x_0, y_0), i.e. of the form $a(x - x_0)^2 + b(y - y_0)^2 = c$. How does the size of the ellipse depend on the value of $c_0 - C$?*

Solution

To find the maximum of C by "brute force", we have to see where the partial derivatives of C are equal to zero:

$$\frac{\partial C}{\partial x} = -\frac{1}{4}\left(2x(1 - x) + x^2(-1)\right) - \frac{1}{12}y^2 \cdot 3 = -\frac{1}{2}x^2 + \frac{3}{4}x - \frac{1}{4}y^2$$

$$\frac{\partial C}{\partial y} = -\frac{1}{12} \cdot 2y(3x+1) = -\frac{1}{6}y - \frac{1}{2}xy$$

$$\begin{cases} \partial C/\partial x = 0 \\ \partial C/\partial y = 0 \end{cases} \Rightarrow \begin{cases} -\frac{1}{2}x^2 + \frac{3}{4}x - \frac{1}{4}y^2 = 0 \\ -\frac{1}{6}y - \frac{1}{2}xy = 0 \end{cases} \Rightarrow \begin{cases} 3x^2 - 2x - y^2 = 0 \\ y(3x+1) = 0 \end{cases}$$

From the second equation we have either $y = 0$ or $x = -1/3$. If we set $y = 0$ in the first equation we get:

$$3x^2 - 2x = 0 \;\Rightarrow\; x(3x-2) = 0 \;\Rightarrow\; \begin{cases} x = 0 \\ x = 2/3 \end{cases}$$

On the other hand, if we set $x = -1/3$ in the same equation we obtain:

$$3 \cdot \frac{1}{9} + 2\frac{1}{3} - y^2 = 0 \;\Rightarrow\; y^2 = 1 \;\Rightarrow\; y = \pm 1$$

(notice that, from the definitions of x and y and from the fact that $0 \le p_i \le 1$ we have $-1/3 \le x \le 2/3$ and $-1 \le y \le 1$).

Therefore, the points where the derivative of C is null are $(0,0)$, $(2/3,0)$ and $(-1/3,\pm 1)$. In order to check which one of them is a maximum, we have to compute the so-called "hessian matrix" of C, i.e.:

$$H(x,y) = \begin{pmatrix} \frac{\partial^2 C}{\partial x^2} & \frac{\partial^2 C}{\partial x \partial y} \\ \frac{\partial^2 C}{\partial y \partial x} & \frac{\partial^2 C}{\partial y^2} \end{pmatrix}$$

and evaluate it in $(0,0)$, $(2/3,0)$, $(-1/3,-1)$ and $(-1/3,1)$. Remember that a point (x_0,y_0) of a function $f(x,y)$ is a maximum if $H(x_0,y_0)$ is negative definite (i.e., all its eigenvalues are negative).

For our system, we have:

$$\frac{\partial^2 C}{\partial x^2} = -\frac{1}{2} + \frac{3}{2}x$$

$$\frac{\partial^2 C}{\partial x \partial y} = \frac{\partial^2 C}{\partial y \partial x} = -\frac{1}{2}y$$

$$\frac{\partial^2 C}{\partial y^2} = -\frac{1}{2}(3x+1)$$

Therefore:

$$H(x,y) = \begin{pmatrix} -\frac{1}{2} + \frac{3}{2}x & -\frac{1}{2}y \\ -\frac{1}{2}y & -\frac{1}{2}(3x+1) \end{pmatrix}$$

Let's first evaluate it in $(2/3,0)$:

$$H(2/3,0) = \begin{pmatrix} -\frac{1}{2} + \frac{3}{2} \cdot \frac{2}{3} & -\frac{1}{2} \cdot 0 \\ -\frac{1}{2} \cdot 0 & -\frac{1}{2}(3 \cdot \frac{2}{3} + 1) \end{pmatrix} = \begin{pmatrix} \frac{1}{2} & 0 \\ 0 & -\frac{3}{2} \end{pmatrix}$$

The eigenvalues of this matrix are $1/2$ and $-3/2$, so the matrix is neither positive definite nor negative definite.

In $(-1/3,-1)$ we have:

$$H(-1/3,-1) = \begin{pmatrix} -\frac{1}{2} + \frac{3}{2} \cdot \left(-\frac{1}{3}\right) & -\frac{1}{2} \cdot (-1) \\ -\frac{1}{2} \cdot (-1) & -\frac{1}{2}\left[3 \cdot \left(-\frac{1}{3}\right) + 1\right] \end{pmatrix} = \begin{pmatrix} -1 & \frac{1}{2} \\ \frac{1}{2} & 0 \end{pmatrix}$$

The eigenvalues of this matrix are $\lambda_\pm = \frac{1}{2}(-1 \pm \sqrt{2})$, where $\lambda_+ > 0$ and $\lambda_- < 0$ so again the matrix is neither positive definite nor negative definite. Similarly, for $(-1/3, 1)$ we have:

$$H(-1/3,1) = \begin{pmatrix} -\frac{1}{2} + \frac{3}{2} \cdot (-\frac{1}{3}) & -\frac{1}{2} \cdot 1 \\ -\frac{1}{2} \cdot 1 & -\frac{1}{2}\left[3 \cdot (-\frac{1}{3}) + 1\right] \end{pmatrix} = \begin{pmatrix} -1 & \frac{1}{2} \\ \frac{1}{2} & 0 \end{pmatrix}$$

and its eigenvalues are again $\lambda_\pm = \frac{1}{2}(-1 \pm \sqrt{2})$.
Finally, in $(0, 0)$ we have:

$$H(0,0) = \begin{pmatrix} -\frac{1}{2} + \frac{3}{2} \cdot 0 & -\frac{1}{2} \cdot 0 \\ -\frac{1}{2} \cdot 0 & -\frac{1}{2}(3 \cdot 0 + 1) \end{pmatrix} = \begin{pmatrix} -\frac{1}{2} & 0 \\ 0 & -\frac{1}{2} \end{pmatrix}$$

This matrix is indeed negative definite, because its (only) eigenvalue is $-1/2$. Therefore, $(x = 0, y = 0)$ is the maximum of C. From the expression of C we also have $C_0 = C(0, 0) = 1/27$.

There is, however, a smarter way to get to the same conclusions without computing all the derivatives shown above. Let's take a look again at how C is written as a function of x and y:

$$C(x,y) = \frac{1}{27} - \frac{1}{4}x^2(1-x) - \frac{1}{12}y^2(3x+1)$$

Now, from the definitions of x and y we have $-1/3 \leq x \leq 2/3$ and $-1 \leq y \leq 1$, and so x^2, $(1 - x)$, y^2 and $(3x + 1)$ will *always* be positive. Therefore, $C \leq 1/27$ because $-x^2(1 - x)/4 < 0$ and $-y^2(3x + 1)/12 < 0$. Thus, $1/27$ is the maximum value of C. Since $C_0 = C(0, 0) = 1/27$, the point $(0, 0)$ will be its maximum.

From the original expression of our equations, the point $(x_0 = 0, y_0 = 0)$ corresponds to $p_1 = p_2 = p_3 = 1/3$.

To determine the stable orbits around (x_0, y_0), we rewrite the expression of C as:

$$C = C_0 - \frac{1}{4}x^2 + \frac{1}{4}x^3 - \frac{1}{4}xy^2 - \frac{1}{12}y^2$$

If we now call $\delta C = C_0 - C$ and neglect all the terms in the equation beyond the leading order (because x and y will be small, since we are studying the system close to $(x_0 = 0, y_0 = 0)$), we get:

$$-\frac{1}{4}x^2 - \frac{1}{12}y^2 + \delta C = 0$$

and we can rewrite it as:

$$\frac{1}{4}x^2 + \frac{1}{12}y^2 = \delta C \;\;\Rightarrow\;\; \frac{x^2}{4\delta C} + \frac{y^2}{12\delta C} = 1 \;\;\Rightarrow\;\; \left(\frac{x}{2\sqrt{\delta C}}\right)^2 + \left(\frac{y}{2\sqrt{3\delta C}}\right)^2 = 1$$

This is the equation of an ellipse that is centered in $(0, 0)$ and has semiaxes of lengths $2\sqrt{\delta C}$ (along x) and $2\sqrt{3\delta C}$ (along y).

(d) *For an arbitrary value of the constant C in the range $0 < C < C_0$, show that $x(t)$ is bounded in the range $x_{min}(C)$ and $x_{max}(C)$ (in the sense that for the ellipse in* ***(c)****, $x(t)$ is bounded between $\pm\sqrt{c/a}$). Find the values of x_{min} and x_{max} in the limit $C \to 0$ and show that the trajectory is composed of three straight-line segments in this limit. Express these segments in the original variables (p_1, p_2, p_3) and explain in words what is happening along each trajectory. Sketch this trajectory in the (x, y) space, along with the direction of the dynamics. Add to the plot the ellipse in* ***(c)*** *obtained in the limit $C \to C_0$. Finally, sketch your guess of what the trajectories should look like for intermediate values of C.*

Solution

We've just shown that $x_{\min} \le x \le x_{\max}$ when $\delta C \approx 0$, i.e. when $C \approx C_0$. To show that this is true for *any* value of $0 < C < C_0$, let's use the geenral expression of C to write y^2 as a function of x:

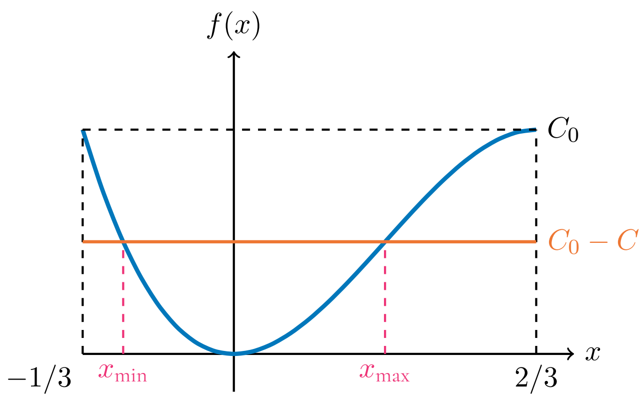
$$C - C_0 = -\frac{1}{4}x^2(1-x) - \frac{1}{12}y^2(3x+1) \;\;\Rightarrow\;\; \frac{1}{12}y^2(3x+1) = C_0 - C - \frac{1}{4}x^2(1-x) \;\;\Rightarrow$$

$$\Rightarrow \;\; y^2 = \frac{12}{3x+1}\left[C_0 - C - \frac{1}{4}x^2(1-x)\right]$$

Since $y^2 \ge 0$, we need this expression to be larger or equal to 0. Since $3x + 1 > 0$ (remember that from the definition of x we have $-1/3 \le x \le 2/3$), we will need:

$$C - C_0 - \frac{1}{4}x^2(1-x) \ge 0 \;\;\Rightarrow\;\; \frac{1}{4}x^2(1-x) \le C_0 - C$$

The term on the left hand side is a cubic function. Therefore, we need to determine when the cubic function assumes values lower or equal to $C_0 - C$. It's not necessary to solve the cubic equation (i.e., the equation with the equality sign "=" instead of "≤"), also because it would be very complicated. We can simply plot $f(x) = x^2(1-x)/4$ and $C_0 - C$ to understand how the system behaves:



Therefore, we immediately see that $x^2(1-x)/4 \le C_0 - C$ when $x_{\min} \le x \le x_{\max}$ for *any* value of $0 < C < C_0$.

If we now take the limit $C \to 0$, we get:

$$\frac{1}{4}x^2(1-x) = C_0 = \frac{1}{27}$$

We could solve the cubic equation, but from the plot above we can see that as $C \to 0$ we will have $C_0 - C \to C_0$ and therefore $x_{\min} \to -1/3$ and $x_{\max} \to 2/3$.

To find the three straight-line segments, we notice that in **(b)** during some calculations we have written C as:

$$C = \frac{1}{4}\left(x+\frac{1}{3}\right)\left[\left(\frac{2}{3}-x\right)^2 - y^2\right]$$

This expression is useful now because in the limit $C \to 0$ we will have:

$$\frac{1}{4}\left(x+\frac{1}{3}\right)\left[\left(\frac{2}{3}-x\right)^2 - y^2\right] = 0$$

This equation has three solutions:

- $x = -1/3$ with any value for y
- $y = 2/3 - x$
- $y = -2/3 + x$

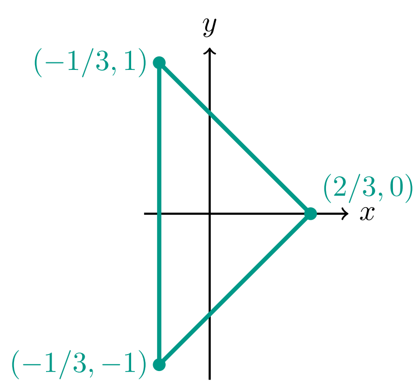
These solutions are represent by three lines in the (x, y) plane. The points in which these three lines intersect are given by:

$$\begin{cases} x = -1/3 \\ y = 2/3 - x \end{cases} \qquad \begin{cases} x = -1/3 \\ y = -2/3 + x \end{cases} \qquad \begin{cases} y = 2/3 - x \\ y = -2/3 + x \end{cases}$$

By solving these simple linear systems we obtain:

$$\begin{cases} x = -1/3 \\ y = 1 \end{cases} \qquad \begin{cases} x = -1/3 \\ y = -1 \end{cases} \qquad \begin{cases} x = 2/3 \\ y = 0 \end{cases}$$

Therefore, this is the plot of the three segments that delineate the orbits of the system in the limit $C \to 0$:



Now, in terms of the original variables (p_1, p_2, p_3) the three points correspond to[8]:

$$\begin{cases} p_1 = 0 \\ p_2 = 1 \\ p_3 = 0 \end{cases} \qquad \begin{cases} p_1 = 0 \\ p_2 = 0 \\ p_3 = 1 \end{cases} \qquad \begin{cases} p_1 = 1 \\ p_2 = 0 \\ p_3 = 0 \end{cases}$$

[8] For example, for the point $(-1/3, 1)$ we have $x = -1/3 \quad \Rightarrow \quad p_1 = 1/3 - 1/3 = 0$ and then:

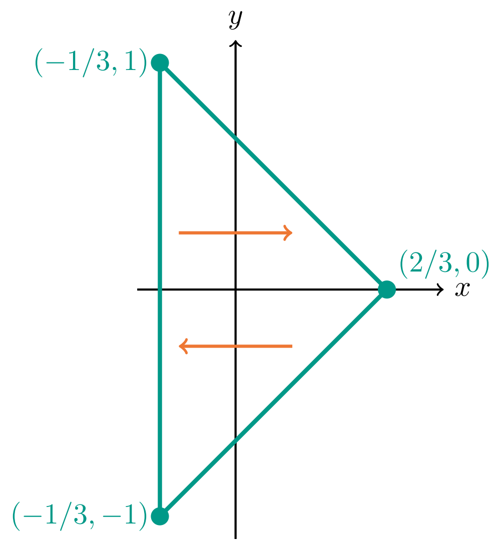
$$\begin{cases} y = p_2 - p_3 = 1 \\ p_1 + p_2 + p_3 = 0 \end{cases} \quad \Rightarrow \quad \begin{cases} p_2 - p_3 = 1 \\ p_2 + p_3 = 0 \end{cases} \quad \Rightarrow \quad \begin{cases} p_2 = 1 \\ p_3 = 0 \end{cases}$$

And similarly for the other points.

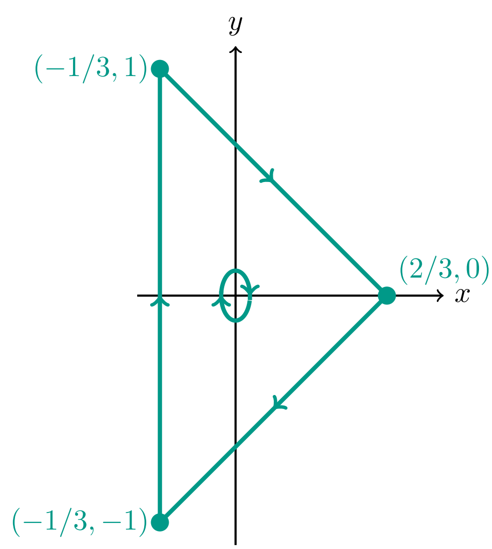
Therefore, the three points correspond to states where only one of the populations is present. When we move from one point to the other along the segment, one population is replacing the other: for example, if we move along the segment $(-1/3, 1) \to (2/3, 0)$ the population p_1 is replacing populations p_2.
To determine the direction of the dynamics (i.e., if the orbits are going clockwise or counterclockwise) we can simply rewrite the equation for p_1 in terms of x and y:

$$\dot{x} = \left(x + \frac{1}{3}\right) y \tag{7}$$

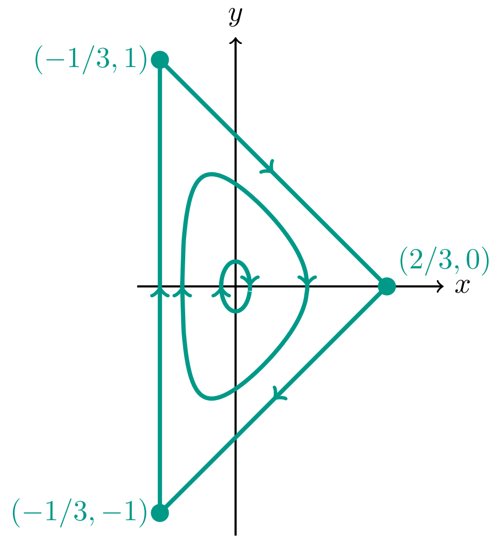
Since $x + 1/3 > 0$, we have that $\dot{x} > 0$ when $y > 0$ and viceversa:



Therefore, the orbits are going clockwise. The stream plot of these orbits and of the ones obtained in **(c)** will be:



The intermediate orbits will have a shape that is something in between the ellipse and the triangle (since C is a continuous function, they will be a continuous deformation from the ellipse to the triangle). For example:



The *actual* streamplot of this system[9], plotted with Mathematica[10], is shown in Figure 1.

(e) *Bonus for the more mathematically inclined: find the period of oscillation for $C \to 0$. You should be able to write your answer in terms of $\ln(1/C)$. [Hint: you will need to obtain deviations of the trajectories from the straight-line segments, and most importantly, the turning points for small but non-zero C. As the three pieces are symmetrical, you just need to work out one of them.]*

[9] It is not required by the homework, but the equations of which I am plotting the streamplot in this figure can be obtained from the original equations by simply plugging the definitions of x and y:

$$\begin{cases} \dot{p}_1 = p_1(p_2 - p_3) \\ \dot{p}_2 = p_2(p_3 - p_1) \\ \dot{p}_3 = p_3(p_1 - p_2) \end{cases} \Rightarrow \begin{cases} \dot{x} = \left(x + \frac{1}{3}\right) y \\ \\ \dot{y} = \frac{d}{dt}(p_2 - p_3) = p_2 p_3 - p_2 p_1 - p_1 p_3 + p_2 p_3 = 2p_2 p_3 - p_1(p_2 + p_3) \end{cases}$$

From the definitions $y = p_2 - p_3$ and $x = p_1 - 1/3$, and from the constraint $p_1 + p_2 + p_3 = 1$ we find $p_2 = 1/3 - x/2 + y/2$ and $p_3 = 1/3 - x/2 - y/2$. Plugging these expressions in the equation for $\dot{y}$, in the end we obtain:

$$\dot{x} = \left(x + \frac{1}{3}\right) y \qquad \dot{y} = \frac{3}{2}x^2 - x - \frac{1}{2}y^2$$

[10] This plot shows the flow for *any* initial condition on x and y, so also for (x, y) outside of the triangle we've studied in this point (which are non-physical solutions of the system).

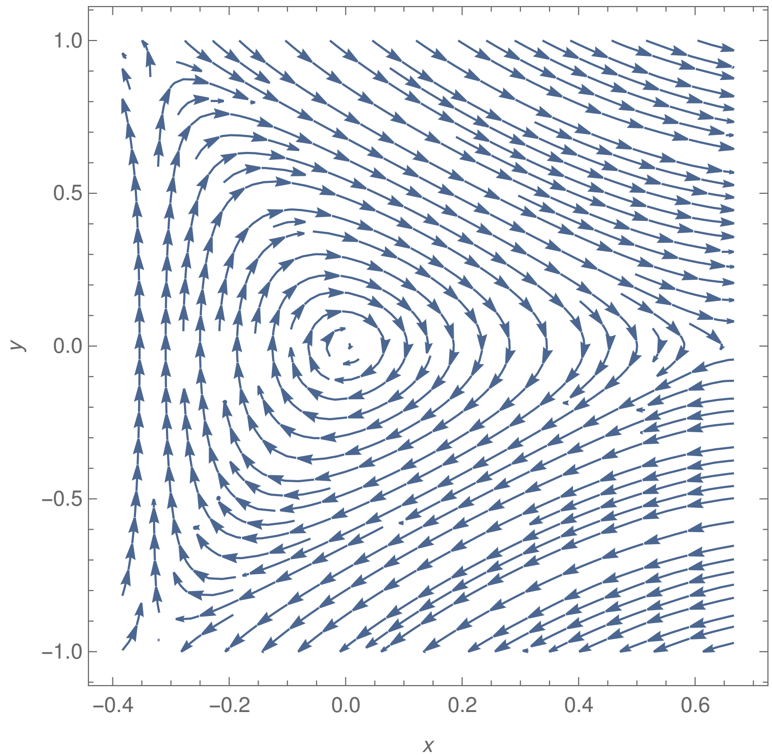
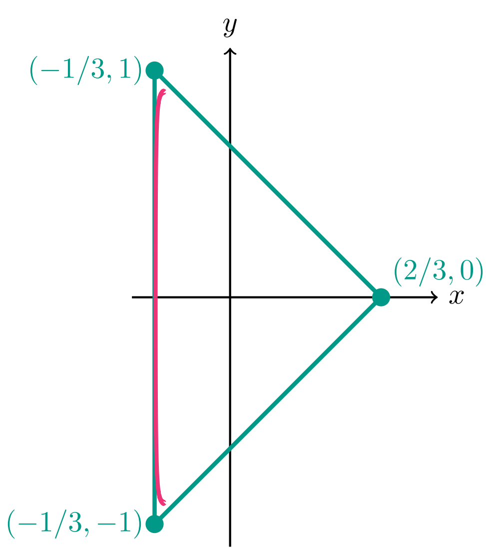


Figure 1: Streamplot of the rock-scissor-paper system.

Solution
The hint suggests us to compute (approximately) the time the system takes to go through a trajectory like this:



In particular, in this trajectory the system is going from one "turning point" to another, where the "turning points" are the points where y is the closest to ± 1 (or in other words, the points where y has the highest/lowest value). Thanks to the symmetry of the problem, once we compute the time t_{segment} that the system takes to go through one of this "pieces" of trajectory, the period T of the complete orbit will be $T = 3t_{\text{segment}}$.

To compute t_{segment}, we solve the equations of the system close to one of the segments, and since the system is symmetrical we can choose any of the three segments. We choose to work near $(-1/3, -1) \to (-1/3, 1)$ (as in the figure above), so we set $x = -1/3 + \epsilon$ (with $\epsilon > 0$ small) in the equations of the system and we get:

$$\begin{cases} \dot{x} = \left(x + \frac{1}{3}\right) y \\ \\ \dot{y} = \frac{3}{2}x^2 - x - \frac{1}{2}y^2 \end{cases} \Rightarrow \begin{cases} \dot{x} = \left(-\frac{1}{3} + \epsilon + \frac{1}{3}\right) y \\ \\ \dot{y} = \frac{3}{2}\left(\frac{1}{9} + \epsilon^2 - \frac{2}{3}\epsilon\right) - \frac{1}{3} + \epsilon - \frac{1}{2}y^2 \end{cases} \Rightarrow$$

$$\Rightarrow \begin{cases} \dot{x} = \epsilon \cdot y \approx 0 \\ \\ \dot{y} = \frac{1}{2} + \frac{3}{2}\epsilon^2 - \frac{1}{2}y^2 \approx \frac{1}{2}(1 - y^2) \end{cases}$$

where we have neglected the terms containing ϵ, since it is small. The first equation expresses the fact that the system remains close to the segment (since $\dot{x} \approx 0$ means that x does not change), while the second one is the equation we have to solve in order to determine t_{segment}. We do so by separating the variables:

$$\frac{dy}{dt} = \frac{1}{2}(1 - y^2) \;\Rightarrow\; 2\frac{dy}{1 - y^2} = dt$$

We now integrate both sides; the right hand side is integrated from $t = 0$ (our initial time) to $t = t_{\text{segment}}$, while since we are moving "up" the segment the left hand side is integrated from $y = -1 + \delta$ to $y = 1 - \delta$, where $\delta > 0$ is small and will depend on ϵ:

$$\int_{-1+\delta}^{1-\delta} 2\frac{dy}{1 - y^2} = \int_0^{t_{\text{segment}}} dt \;\Rightarrow\; \int_{-1+\delta}^{1-\delta} 2dy \left(\frac{1}{1 - y} + \frac{1}{1 - y}\right) = t_{\text{segment}} \;\Rightarrow$$

$$\Rightarrow\; t_{\text{segment}} = 2 \ln\left(\frac{1 + y}{1 - y}\right)\Bigg|_{-1+\delta}^{1-\delta} = 2 \ln \frac{2}{\delta}$$

Now, δ gives a measure of how close y gets to ± 1 at the turning points (as stated above, y goes from $-1 + \delta$ to $1 - \delta$), and we want to express how it depends on C in the limit $C \to 0$. To do this, we start from the expression of C in terms of x and y:

$$C = \frac{1}{4}\left(x + \frac{1}{3}\right)\left[\left(\frac{2}{3} - x\right)^2 - y^2\right]$$

and we set[11] $x = -1/3 + \epsilon$, $y = 1 - \delta$:

$$C = \frac{1}{4}\left(-\frac{1}{3} + \epsilon + \frac{1}{3}\right)\left[\left(\frac{2}{3} + \frac{1}{3} - \epsilon\right)^2 - (1 - \delta)^2\right] = \frac{1}{4}\epsilon\left(1 + \epsilon^2 - 2\epsilon - 1 - \delta^2 + 2\delta\right) \;\Rightarrow$$

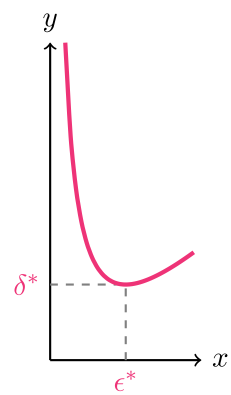
$$\Rightarrow\; 4C = -\epsilon^3 - 2\epsilon^2 - \epsilon\delta^2 + 2\epsilon\delta$$

[11] Notice that our results do not change even if we choose $y = -1 + \delta$, since C depends on y^2.

If we neglet all terms beyond leading orders in δ and ϵ:

$$4C = -2\epsilon^2 + 2\epsilon\delta \;\Rightarrow\; 2C = \epsilon\delta - \epsilon^2 \;\Rightarrow\; \delta = \epsilon + \frac{2C}{\epsilon}$$

The turning point corresponds to the minimum value of δ as a function of ϵ:



$$0 = \frac{\partial}{\partial \epsilon}\delta(\epsilon) = 1 - \frac{2C}{\epsilon^2} \;\Rightarrow\; \epsilon^* = \sqrt{2C} \;\Rightarrow\; \delta^* = 2\sqrt{2C}$$

Therefore, the period of the orbits for $C \to 0$ will be:

$$T = 3t_{\text{segment}} = 3 \cdot 2\ln\frac{2}{\delta^*} = 6\ln\frac{2}{2\sqrt{2C}} = 6\ln\frac{1}{\sqrt{2C}} = 3\ln\frac{1}{2C}$$