LECTURE 9

Interacting Species

Having spent several lectures on solving linear systems of ODEs, it's about time we discussed a prototypical situation in which they arise.

The situations we shall now try to model will involve multiple species - which will be either competing for the same food supply or in a predator-prey relationship.

1. Single Species

Let's begin by modeling a single species in isolation. We wish to obtain a function that describes the population P of a species as a function of time. The simplest model would be to simply say that the growth rate of a species should be proportional to the size of the populations. A little more explicitly, in the situation where the birth and death rates of the species are constants (respectively, r_b and r_d), then

$$\frac{dP}{dt} = (r_b - r_d)\,P \qquad \Longrightarrow \qquad P = P_0 e^{(r_b - r_d)t} \tag{1}$$

This simple model obviously only allows for only exponential growth or extinction.

A slightly more realistic model would include a term that would slow the rate of growth until it reached a certain size (perhaps corresponding to a saturation of the available food supply). So we might try adding a term to the right hand side of (1) that is positive when P is small, decreasing as P grows, and eventually negative when P gets too large. The simplest kind of term with these properties would be a term of the form

$$(\lambda - aP)\,P$$

with λ and a positive. Thus, we are lead to an ODE of the form

$$\frac{dP}{dt} = (\lambda - aP)\,P \qquad \lambda, a > 0 \tag{2}$$

The constant λ can be thought of as accounting for *intrinsic* growth rate and the constant a as somehow reflecting the effect of the population size has its the food supply.

In fact, notice that when

$$\lambda - aP = 0$$

the rate of population growth will be zero. Thus,

$$P = \lambda / a$$

is a critical point for the ODE. In fact, it is a stable and asymptotical stable critcal point. To see this, let's examine the linearization of $P(t)$ about λ/a.

If we set

$$u(t) = P(t) - \frac{\lambda}{a} \qquad \Rightarrow \qquad P(t) = u(t) + \frac{\lambda}{\alpha}$$

then

$$\frac{du}{dt} = \left(\lambda - \alpha\left(u + \frac{\lambda}{\alpha}\right)\right)\left(u + \frac{\lambda}{\alpha}\right) = -\alpha\mu\left(u + \frac{\lambda}{\alpha}\right) = -\lambda u - \alpha u^2$$

Note that for small u,

$$\frac{du}{dt} \approx -\lambda u$$

which implies $u(t) = 0$ is a stable and asymptotically stable node, which implies $P(t) = \frac{\lambda}{\alpha}$ is a stable and asysympotically stable critical point. .

corresponds to a steady state population. Let us denote this steady state population by P_s. Then in terms of the intrinsic growth rate λ and the steady state population P_s

$$P_s = \frac{\lambda}{a} \quad \Longrightarrow \quad a = \frac{P_s}{\lambda}$$

we have

$$\frac{dP}{dt} = \left(\lambda - \frac{\lambda}{P_s}P\right)P = \lambda\left(1 - \frac{P}{P_s}\right)P$$

Let's go ahead and solve and see if its solution matches our intuition. Equation (2) is separable, and so we can determine its general solution as follows

$$\begin{aligned}
\frac{dP}{dt} = \lambda(1 - P/P_s)P \quad &\Longrightarrow \quad \frac{1}{(1 - P/P_s)P}\frac{dP}{dt} = \lambda \\
&\Longrightarrow \quad \int \frac{1}{(1 - P/P_s)P}dP = \int \lambda dt + C \\
&\Longrightarrow \quad -\ln(P_s - P) + \ln P := \lambda t + C \\
&\Longrightarrow \quad \ln(P/(P_s - P)) = \lambda(t + C) \\
&\Longrightarrow \quad \frac{P}{P_s - P} = e^{\lambda(t+C)} = e^C e^{\lambda t} \\
&\Longrightarrow \quad \frac{P}{1 - (P/P_s)} = Ae^{\lambda t}
\end{aligned}$$

: The constant A can be chosen so that when $t = 0$ the population is P_0.

$$A = Ae^{\lambda 0} = \frac{P(0)}{1 - P(0)/P_s} = \frac{P_0}{1 - P_0/P_s}$$

Incorporating this initial condition we now have

$$\frac{P}{1 - P/P_s} = \frac{P_0}{1 - P_0/P_s}e^{\lambda t}$$

or

$$P = \frac{P_0(1 - P/P_s)}{1 - P_0/P_s}e^{\lambda t}$$

or

$$P\left(1 + \frac{P_0/P_s}{1 - P_0/P_s}e^{\lambda t}\right) = \frac{P_0}{(1 - P_0/P_s)}e^{\lambda t}$$

or

$$P\left(1 - P_0/P_s + P_0/P_s e^{\lambda t}\right) = P_0 e^{\lambda t}$$

or

$$P(t) = \frac{P_0 e^{\lambda t}}{1 - P_0/P_s + P_0/P_s e^{\lambda t}}$$

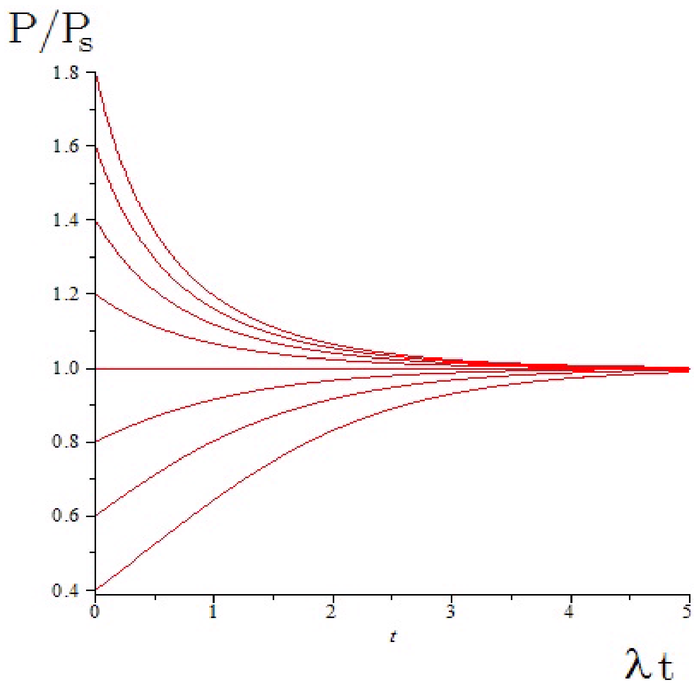
To make this result a bit more understandable, let

$$\beta(t) = \frac{P(t)}{P_s}$$

be the ratio of the population size at time t to the steady state population, and let $\beta_0 := P_0/P_s$ be the initial ratio. We have

$$\beta(t) = \frac{\beta_0 e^{\lambda t}}{1 - \beta_0 + \beta_0 e^{\lambda t}}$$

Plotting $\beta(t)$ as a function of t gives us a picture of the possible scenarios (by varying β_0).



2. Competing Species

Let us now consider a situation where there are two species competing for the same food supply. Let $x(t)$ and $y(t)$ denote the populations of species 1 and 2 at time t. In the absence of competition, we would expect these functions to be governed by differential equations of the form

$$\begin{aligned} \frac{dx}{dt} &= x(\varepsilon_1 - \sigma_1 x) \\ \frac{dy}{dt} &= y(\varepsilon_2 - \sigma_2 y) \end{aligned}$$

The competition between the specifies is to be reflected as a negative contribution to the growth rate of one species that is proportional to to population of the other species. Thus, we consider systems of the form

$$\begin{aligned} \frac{dx}{dt} &= x(\varepsilon_1 - \sigma_1 x - \alpha_1 y) \\ \frac{dx_2}{dt} &= y(\varepsilon_2 - \sigma_2 y - \alpha_2 x) \end{aligned}$$

To get some idea of what can happen let's look at a particular example:

2.1. Example 1:

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - y) \\ \frac{dy}{dt} &= y(3/4 - y - x/2) \end{aligned}$$

The critical points for this system occur when

$$0 = x\,(1 - x - y)$$
$$0 = y\,(3/4 - y - x/2)$$

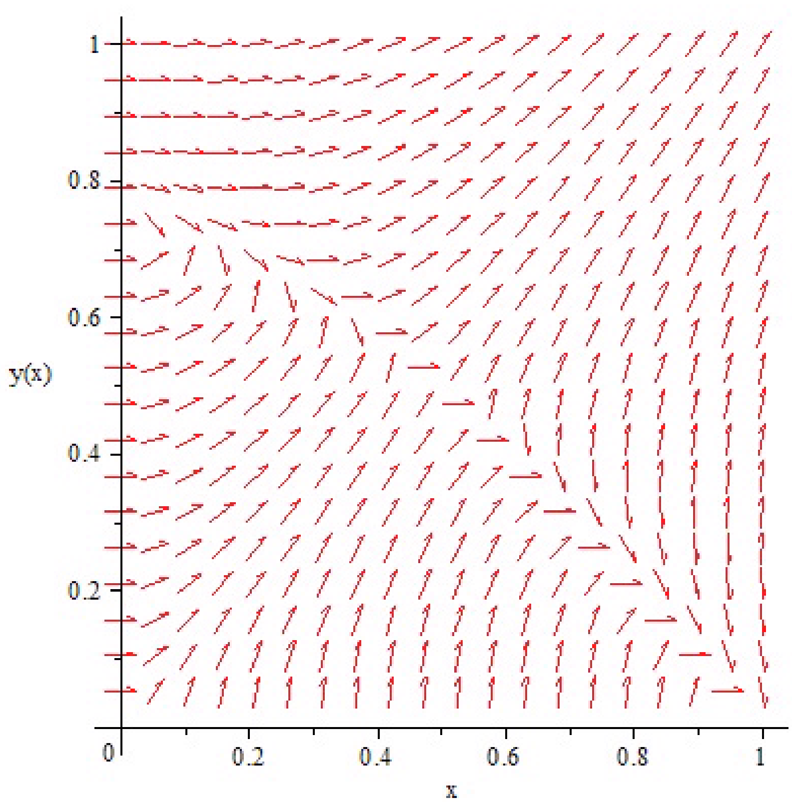
or

$$x = 0\ ,\ \ y = 0$$
$$x = 0\ ,\ \ y = 3/4$$
$$x = 1\ ,\ \ y = 0$$
$$x = 1/2\ ,\ \ y = 1/2$$

This seems easy enough to understand: there a basically four different possibilities for the evolution of these species, depending on the initial state.

(i) If neither species is present at $t = 0$, then they both stay dead (the solution $\mathbf{x}\,(t) = (0, 0)$).
(ii) If one species is not present at $t = 0$ (that is, we start off on one of the coordinate axes), then the other species grows (or shrinks) to its stable population (corresponding to the constant accompanying the quadratic term x_i^2 in its differential equation).
(iii) If both species are present at $t = 0$, then the two populations will eventually evolve to the stable critical point $(0.5, 0, 5)$

However, a closer analysis will reveal some troubles with this interpretation. For starts, consider the plot of the direction field for this system



Note that the critical points at $(0, 0)$, (1.0) and $(0, 3/4)$ do not look at all like nodes.

2.2. Behavior near critical points. As plot above shows, a computer generated direction field plot doesn't necessarily make it clear whether a critical point is stable, asympotically stable or unstable. To get a much clearer idea as to what is going on near a critical point, a good strategy is to "linearize" the system near the critical point, and infer from the behavior of the resulting linear system the stability properties of a critical point.

Here's how this works. Suppose $\mathbf{c}$ is a critical point of an autonomous system

$$\mathbf{x}' = \mathbf{F}(\mathbf{x})$$

Taylor expanding the vector valued function $\mathbf{F}$ about the critical point we get

$$\mathbf{x}' = \mathbf{F}(\mathbf{c}) + \begin{pmatrix} \left.\frac{\partial F_1}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_1}{\partial x_n}\right|_{\mathbf{c}} \\ \cdots & & \\ \left.\frac{\partial F_n}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_n}{\partial x_n}\right|_{\mathbf{c}} \end{pmatrix} \begin{bmatrix} x_1 - c_1 \\ \vdots \\ x_n - c_n \end{bmatrix} + \text{higher order terms}$$

Now the leading term $\mathbf{F}(\mathbf{c}) = \mathbf{0}$ since $\mathbf{c}$ is a critical point. Changing variables that that $\mathbf{x} = \mathbf{c}$ corresponds to the origin;

$$\mathbf{y} = \mathbf{x} - \mathbf{c}$$

we get

$$\begin{aligned} \mathbf{y}' = \frac{d}{dt}(\mathbf{x} - \mathbf{c}) = \frac{d}{dt}\mathbf{x} = \mathbf{0} + \begin{pmatrix} \left.\frac{\partial F_1}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_1}{\partial x_n}\right|_{\mathbf{c}} \\ \cdots & & \\ \left.\frac{\partial F_n}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_n}{\partial x_n}\right|_{\mathbf{c}} \end{pmatrix} \begin{bmatrix} x_1 - c_1 \\ \vdots \\ x_n - c_n \end{bmatrix} + ... \\ = \begin{pmatrix} \left.\frac{\partial F_1}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_1}{\partial x_n}\right|_{\mathbf{c}} \\ \cdots & & \\ \left.\frac{\partial F_n}{\partial x_1}\right|_{\mathbf{c}} & \cdots & \left.\frac{\partial F_n}{\partial x_n}\right|_{\mathbf{c}} \end{pmatrix} \mathbf{y} \end{aligned}$$

$\longrightarrow$ a homogeneous linear system whose behavior at the origin should approximate the behavior the original system near the critical point $\mathbf{c}$.

Let's now re-examine the preceding example.

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - y) \\ \frac{dy}{dt} &= y(0.75 - y - 0.5x) \end{aligned} \tag{3}$$

We have

$$\mathbf{F}(x, y) = \begin{bmatrix} x - x^2 - xy \\ 0.75y - y^2 - 0.5xy \end{bmatrix}$$

and so

$$\begin{pmatrix} \frac{\partial F_1}{\partial x} & \frac{\partial F_1}{\partial y} \\ \frac{\partial F_2}{\partial x} & \frac{\partial F_2}{\partial y} \end{pmatrix} = \begin{pmatrix} 1 - 2x - y & -x \\ -0.5y & 0.75 - 2y - 0.5x \end{pmatrix}$$

Let's now see what's happening near each critical point of (3).

- $\mathbf{c} = (0, 0)$

$$\begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}} \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ -0.375 & -0.75 \end{pmatrix}$$

and so near $\mathbf{x} = (0, 0)$ the system (3) behaves like

$$\mathbf{y}' = \begin{pmatrix} 1 & 0 \\ 0 & 0.75 \end{pmatrix} \mathbf{y}$$

This is a decoupled homogenous solution whose general solution is

$$\mathbf{y}(t) = c_1 e^{t} \begin{bmatrix} 1 \\ 0 \end{bmatrix} + c_2 e^{0.75} \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

Evidently, $\mathbf{y} = (0,0)$ is an unstable critical point (both exponential factors are positive so $\lim_{t\longrightarrow\infty} \|\mathbf{y}(t) - \mathbf{0}\| \longrightarrow \infty$).

- $\mathbf{c} = (0, 0.75)$

$$\begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}} \end{pmatrix} = \begin{pmatrix} 0.25 & 0 \\ -0.375 & -0.75 \end{pmatrix}$$

The eigenvalues and eigenvectors of this matrix are

$$r_1 = 0.25 \quad , \quad \xi_1 = \begin{bmatrix} 8 \\ -3 \end{bmatrix}$$

$$r_2 = -0.75 \quad , \quad \xi_2 = \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

and so the general solution of

$$\mathbf{y}' = \begin{pmatrix} 0.25 & 0 \\ -0.375 & -0.75 \end{pmatrix} \mathbf{y}$$

will be

$$\mathbf{y}(t) = c_1 e^{0.25t} \begin{bmatrix} 8 \\ -3 \end{bmatrix} + c_2 e^{-0.75t} \begin{bmatrix} 0 \\ 7 \end{bmatrix}$$

$\mathbf{y} = \mathbf{0}$ (hence, $\mathbf{x} = (0, 0, 75)$ for the original system) is evidently an unstable critical point, where species 1 is growing exponentially and the species to heading for exponential extinction.

- $\mathbf{c} = (0, 1)$. In this case we have

$$\begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}} \end{pmatrix} = \begin{pmatrix} -1 & -1 \\ 0 & 0.25 \end{pmatrix}$$

the eigenvalues and eigenvectors of which are

$$r_1 = 0.25 \quad , \quad \xi_1 = \begin{bmatrix} 4 \\ -5 \end{bmatrix}$$

$$r_2 = -1.0 \quad , \quad \xi_2 = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

and so the general solution near the critical point will look like

$$\mathbf{y}(t) = c_1 e^{0.25t} \begin{bmatrix} 4 \\ -5 \end{bmatrix} + c_2 e^{-t} \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

Since the eigenvalues have opposite signs, this critical point will be unstable.

- $\mathbf{c} = (0.5, 0.5)$. In this case, we have

$$\begin{pmatrix} \left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}} \\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}} \end{pmatrix} = \begin{pmatrix} -.5 & -.5 \\ -0.25 & -0.5 \end{pmatrix}$$

with

$$r_1 = -0.146 \quad , \quad \xi_1 = \begin{bmatrix} \sqrt{2} \\ -1 \end{bmatrix}$$

$$r_2 = -0.854 \quad , \quad \xi_2 = \begin{bmatrix} \sqrt{2} \\ 1 \end{bmatrix}$$

and so the general solution near the critical point $(0.5, 0, 5)$ will be

$$\mathbf{y}(t) = c_1 e^{-0.146t} \begin{bmatrix} \sqrt{2} \\ -1 \end{bmatrix} + c_2 e^{-0.854t} \begin{bmatrix} \sqrt{2} \\ 1 \end{bmatrix}$$

In this case, both eigenvalues are negative and so

$$\lim_{t\longrightarrow\infty}\mathbf{y}\left(t\right)=\mathbf{0}$$

implying that for the original system $\mathbf{c}=(0.5,0.5)$ is an asymptotically stable critical point.

In fact, a more detailed examination of the direction field of (3) reveals that all trajectories $\mathbf{x}\left(t\right)$ starting off with $x_1\left(0\right)>0$ and $x_2\left(0\right)>0$ eventually move towards this critical point..

2.3. Example 2: Let's now consider another numerical example:

$$\begin{aligned}\frac{dx}{dt}&=x\left(1-x-y\right)\\ \frac{dy}{dt}&=y\left(0.5-0.25y-0.75x\right)\end{aligned}\tag{4}$$

In this example, we again have four critical points

$$(0,0)\quad,\quad(1,0)\quad,\quad(0,2)\quad,\quad(0.5,0.5)$$

The critical points along the axes again correspond to situations where one or both of the species are not present.

We'll ignore the critical point at $\mathbf{x}=\mathbf{0}$ and try to analyze the behavior of solutions about the other three critical points:

At $\mathbf{c}=(1,0)$, we have

$$\begin{aligned}\frac{\mathbf{dF}}{\mathbf{dx}}(\mathbf{c}):=\left(\begin{array}{cc}\left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}}\\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}}\end{array}\right)&=\left(\begin{array}{cc}\left.1-2x\right|_{(1,0)} & \left.-x\right|_{(1,0)}\\ \left.-0.75y\right|_{(1,0)} & \left.0.5-0.5y-0.75x\right|_{(1,0)}\end{array}\right)\\ &=\left(\begin{array}{cc}-1 & -1\\ 0 & -0.25\end{array}\right)\end{aligned}$$

The eigenvalus of this matrix are

$$r_1=-1\text{ and }r_2=-0.25$$

Since both eigenvalues are negative, $\mathbf{c}=(1,0)$ will be a stable critical point.

At $\mathbf{c}=(0,2)$ we have

$$\begin{aligned}\frac{\mathbf{dF}}{\mathbf{dx}}(\mathbf{c}):=\left(\begin{array}{cc}\left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}}\\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}}\end{array}\right)&=\left(\begin{array}{cc}\left.1-2x\right|_{(0,2)} & \left.-x\right|_{(0,2)}\\ \left.-0.75y\right|_{(0,2)} & \left.0.5-0.5y-0.75x\right|_{(0,2)}\end{array}\right)\\ &=\left(\begin{array}{cc}-1 & 0\\ -1.5 & -0.5\end{array}\right)\end{aligned}$$

The eigenvalues of this matrix are

$$r_1=-1\quad\text{and}\quad r_2=-0.5$$

Since these are both negatives $\mathbf{c}=(0,2)$ will be a stable critical point.

Let's look at the nature of solutions near the critical point $\mathbf{c}=(0.5,0.5)$. We have

$$\begin{aligned}\frac{\mathbf{dF}}{\mathbf{dx}}(\mathbf{c}):=\left(\begin{array}{cc}\left.\frac{\partial F_1}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_1}{\partial y}\right|_{\mathbf{c}}\\ \left.\frac{\partial F_2}{\partial x}\right|_{\mathbf{c}} & \left.\frac{\partial F_2}{\partial y}\right|_{\mathbf{c}}\end{array}\right)&=\left(\begin{array}{cc}\left.1-2x\right|_{(0.5,0.5)} & \left.-x\right|_{(0.5,0.5)}\\ \left.-0.75y\right|_{(0.5,0.5)} & \left.0.5-0.5y-0.75x\right|_{(0.5,0.5)}\end{array}\right)\\ &=\left(\begin{array}{cc}-0.5 & -0.5\\ -0.375 & -0.125\end{array}\right)\end{aligned}$$

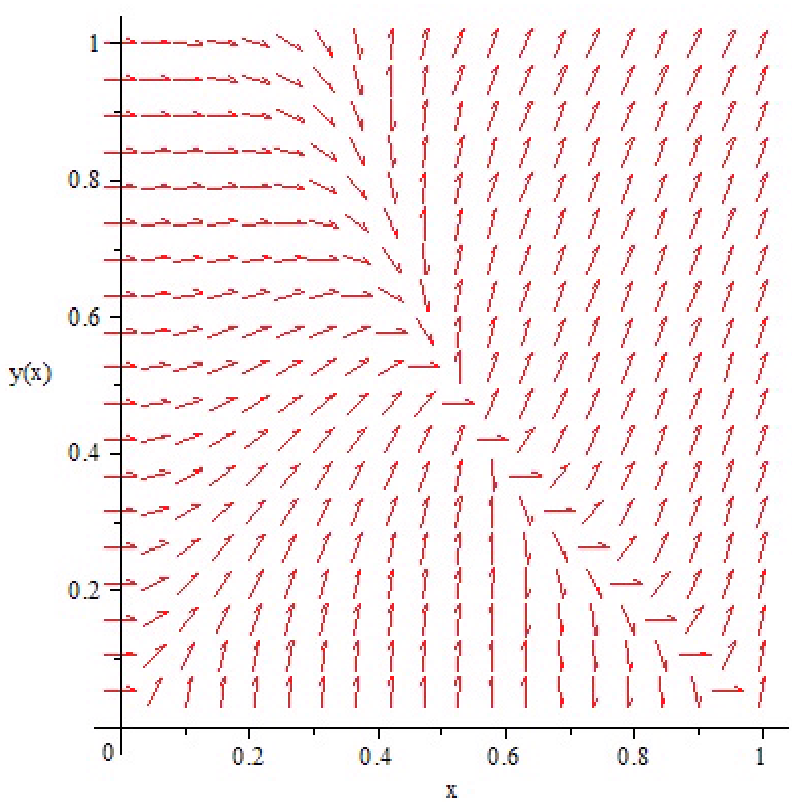
The eigenvectors and eigenvalues of this matrix are

$$r_1 = 0.16 \quad , \quad \xi_1 = \begin{bmatrix} 1 \\ -1.31 \end{bmatrix}$$

$$r_2 = -0.78 \quad , \quad \xi_2 = \begin{bmatrix} 1 \\ 0.57 \end{bmatrix}$$

Thus, this critical point is also unstable.

Below is a plot of the direction field for this system



Apparently, for this ecosystem, except for the (unstable) cases where $\mathbf{x}(0) = (0.5, 0.5)$ or $(0, 0)$, one species will die out while the other will evolve towards its steady state population.