



CHALMERS
UNIVERSITY OF TECHNOLOGY

Assignment #1

MVE 162 Ordinary differential equations and mathematical modelling

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Introduction

This report is done within the course of Ordinary differential equation and mathematical modelling (MVE162). It consists of studying the evolution of the population within the same specie and then between two species living together and expose to a finite amount of resource.

At first, we will start by studying the case when we have only one specie and analysing the long term results. Then, we will study the long term result of two competing species by first analysing the model, then computing different kind of equilibrium points and finally make conclusions about their stability.

Competition Model within the same specie

Malthusian growth model

We consider a population of a certain specie, with a growth rate r .

The Malthusian law of growth suggests that : a specie that has a population x with a constant growth rate $r > 0$ tends to infinity when $t \rightarrow \infty$.

This model suggests, that resources are infinite, or else, overpopulation will end up by exhausting all the resources at some point and the population would be extinct. It is represented by the following equation :

$$x'_i = r_i x_i \quad (1)$$

Note: Although the resources are infinite, we can see on the figure below that resources increase at an arithmetic rate, as for the population, the evolution is exponential. That being said, we can conclude that when the population becomes large, resources are actually limited and an inevitable competition is taking place.

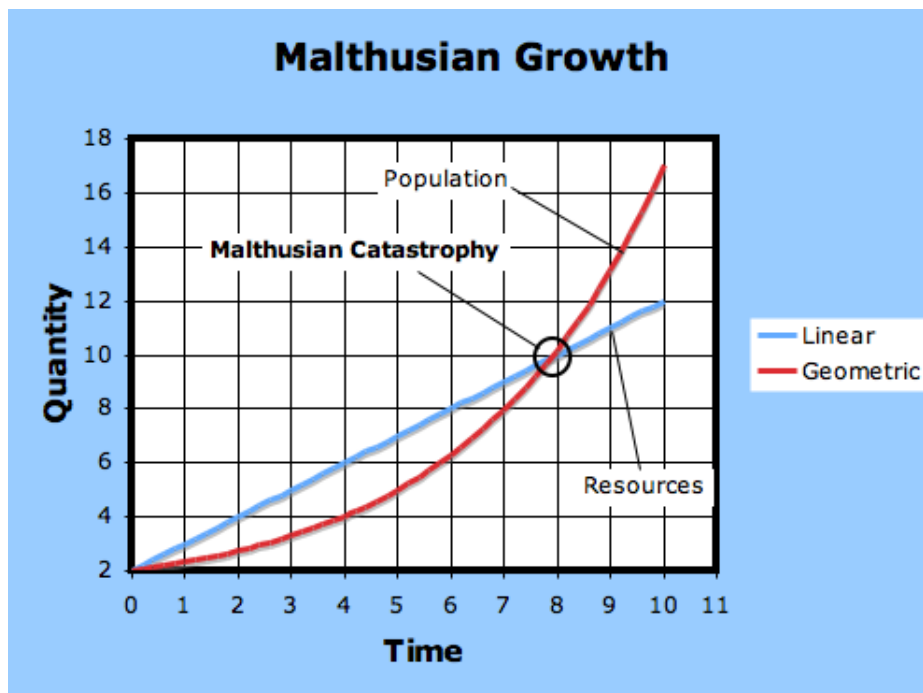


Figure 1: Malthusian growth model

Verhulst Model

We can now try to draw a new model that takes into consideration competition within the specie.

This model is called the logistic or Verhulst model that can be modelled as following:

$$x'_i = r_i x_i \left(1 - \frac{x_i}{K_i}\right) \quad (2)$$

1. K_i is the carrying capacity¹

¹"The carrying capacity of a biological species in an environment is the maximum population size of the species that the environment can sustain indefinitely, given the food, habitat, water, and other necessities available in the environment. In population biology, carrying capacity is defined as the environment's maximal load, which is different from the concept of population equilibrium"^[4]

2. r_i is the growth rate
3. x_i is the population size

Let's write $\alpha = (1 - \frac{x_i}{K_i})$, we have 3 different possible values for α :

1. Population exceeds carrying capacity: $\frac{x_i}{K_i} > 1$ and $\alpha < 0$, in this case we can say that there is an overpopulation and the resources will be exhausted at some point, which will lead to a decrease in the population until it reaches the carrying capacity again.
2. Population is inferior to carrying capacity, therefore the growth $\frac{x_i}{K_i} < 1$ and $\alpha > 0$, and the population would increase until it reaches the carrying capacity at a speed that is exponentially relative to the growth rate r_i
3. Population is equal to the carrying capacity, in this case we will be at the stable point from the initial starting point and the population will keep a constant population equal to its carrying capacity

We can verify our assumption by using MATLAB, the following code can be used for this purpose :

```

r = 1 ;
xdif = @(t,x,k) r*x*(1 - x/k );
k = 3;
time=[0 20];
figure()
for x_0 = 1 : 5;
hold on
[t,x] = ode45( @(t,y) xdif(t,y,k),time,x_0);
plot (t,x,'LineWidth',1.5);
title('x_0 variation');
set(gca,'LineWidth',1)
xlabel('t(time)')
ylabel('population size x_i')
legend('x_0=1','x_0=2','x_0=3','x_0=4','x_0=5')
end ;
hold off
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
k = 3 ;
xdif = @(t,x,r) r*x*(1 - x/k );
x_0 = 1;
time=[0 100];
figure()
for r =[0.01 0.1 1 5 10];
hold on
[t,x] = ode45( @(t,y) xdif(t,y,r),time,x_0);
plot (t,x,'LineWidth',1.5);
set(gca,'LineWidth',1)
title('r variation');
xlabel('t(time)')
ylabel('population size x_i')
legend('r=0.01','r=0.1','r=1','r=5','r=10');
end ; hold off
%%

```

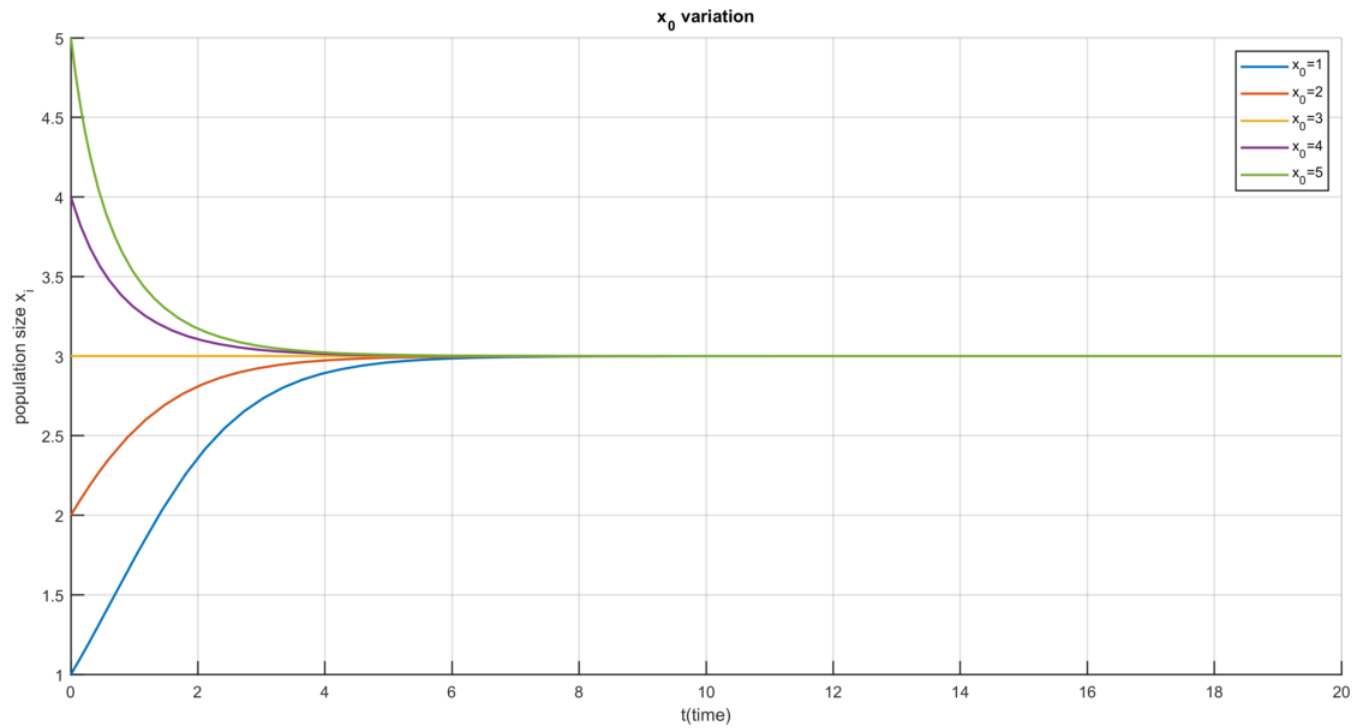


Figure 2: Population growth for different initial population size

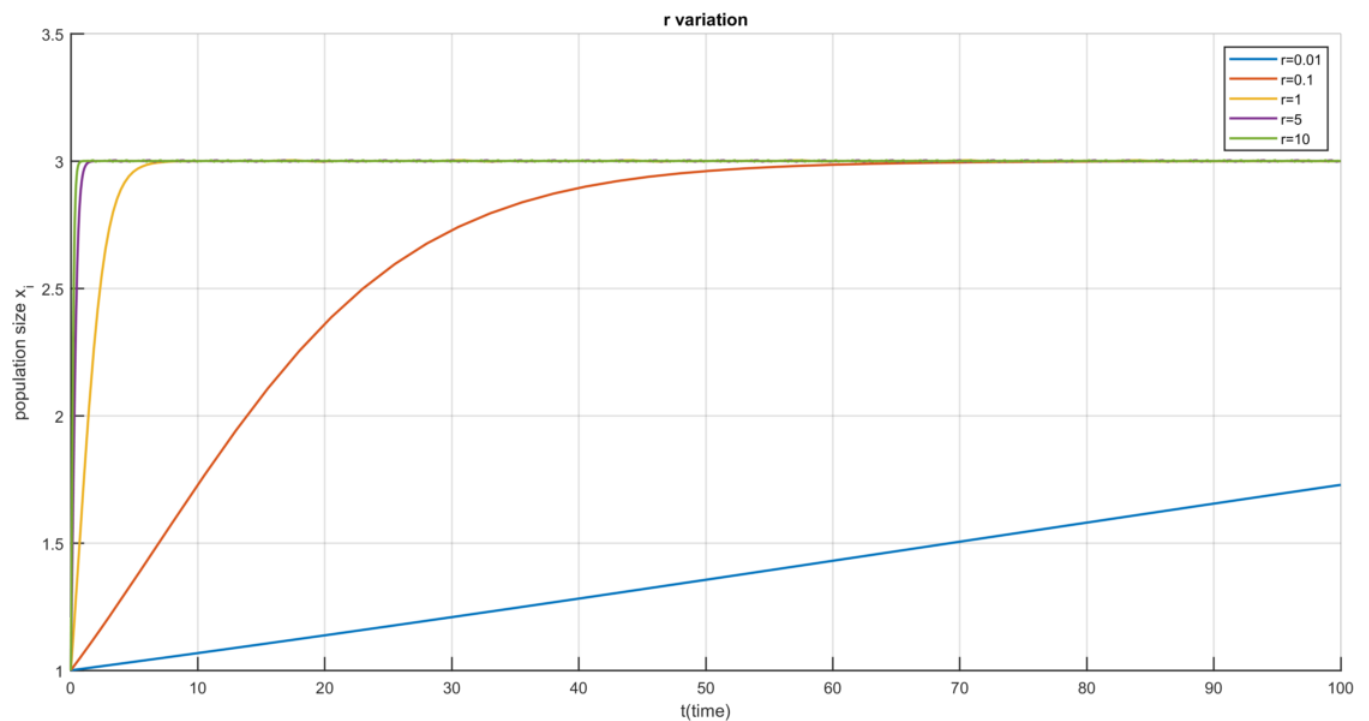


Figure 3: Population growth for different growth rates

Lotka-Volterra Competition Model

The inter-specific competition model was first introduced by Alfred J. Lotka back in 1910 and the same study was followed up by Vito Volterra in 1926. The study aims to analyse the evolution of two different species competing over the same resource based on a couple of nonlinear differential equations² :

$$x'_1 = r_1 x_1 \left(1 - \frac{x_1}{K_1}\right) - \alpha_1 x_1 x_2 \quad (3)$$

$$x'_2 = r_2 x_2 \left(1 - \frac{x_2}{K_2}\right) - \alpha_2 x_2 x_1 \quad (4)$$

Analysis of the model

Useful Theorem:

Let $(\tau, \xi) \in J \times G$ and let $f : J \times G \rightarrow \mathbf{R}^N$ be continuous. Furthermore, let $x : \mathbf{I}_x \rightarrow G$ and $y : \mathbf{I}_y \rightarrow G$ be maximal solutions of (4.1) with $x(\tau) = \xi = y(\tau)$. If f is locally Lipschitz with respect to its second argument, then $x = y$.

$$\begin{aligned} x'(t) &= F(x(t), y(t)) \\ y'(t) &= G(x(t), y(t)) \end{aligned}$$

Let $(x_1(t), y_1(t))$ and $(x_2(t), y_2(t))$ be two trajectories of the system. If times t_1, t_2 exist such that $x_1(t_1) = x_2(t_2)$, $y_1(t_1) = y_2(t_2)$, then for the value $c = t_1 - t_2$ the equations $x_1(t+c) = x_2(t)$ and $y_1(t+c) = y_2(t)$ are valid for all allowed values of t . This means that the two trajectories are on one and the same planar curve, or in the contrapositive, two different trajectories cannot touch or cross in the phase plane.

Using those two theorems, we know that no trajectories can cross each other, so if we take solutions with initial values $x_1 > 0$ and $x_2 = 0$ we have that these will all be somewhere on the positive x-axis. They will in fact fill up the whole axis for different x_1 .

Same applies for $x_2 > 0$ and $x_1 = 0$, we can conclude that any trajectory with $x_1 > 0, x_2 > 0$ cannot cross the x-axis, it can tend to it but never reaches it.

Thus, $x_1(t)$ and $x_2(t)$ always have positive components.

We saw earlier that the solution for (3) will always have a positive component, that means that the solution will always be greater than zero.

Moreover, while analysing the logistic equation, we saw that the solution will always converge to a value K . And, (3) is just a subtraction of the logistic equation (2) by $\alpha_1 x_1 x_2$.

Also, a population cannot be negative, therefore $x_1(t) > 0$ and $x_2(t) > 0, \forall t$, and we have $\alpha_1 > 0$, so $\alpha_1 x_1 x_2 > 0$.

The solution of (3) will then converge to a value between 0 and K_1 , since the solution to the logistic equation converges to K , and the solution to Lotka-Volterra will never be negative.

Now let's prove that the maximal existence interval for solutions to (3) and (4) starting at $t = 0$ with $x_1(0) \geq 0, x_2(0) \geq 0$ is \mathbf{R}_+ .

Useful Theorem: Let $G \subset \mathbf{R}^N$ be a nonempty open subset with $0 \in G$. Consider the differential equation :

$$x'(t) = Ax + h(x)$$

²https://en.wikipedia.org/wiki/Lotka-Volterra_equations

where $A \in \mathbf{R}^{N \times N}$ and $h : G \longrightarrow \mathbf{R}^N$ is a continuous function satisfying :

$$\lim_{z \rightarrow 0} \frac{h(z)}{\|z\|} = 0$$

If A is Hurwitz, that is $\operatorname{Re}(\lambda) < 0 \forall \lambda \in \sigma(A)$, then 0 is an asymptotically stable equilibrium of $x'(t)$. Moreover, there is $\Delta > 0$ and $C > 0$ and $\alpha > 0$ such that for $\|\xi\| < \Delta$ the solution $x(t)$ to the initial value problem with initial data $x(0) = \xi$ satisfies the estimate :

$$\|x(t)\| \leq C\|\xi\|e^{-\alpha t}$$

This estimate implies that the solution must be in \mathbf{R}_+ , because if not, we would have a contradiction, we can prove it using two steps:

1. Our solution is bounded and that was proved earlier, that the maximal solution is a positive finite value, so we can extend $x(t)$ up to an end point t_{max} as
2. By proving that $x(t) > 0 \forall t$, we proved the existence of a solution, so we conclude that there is a solution on the time interval $[t_{max}, t_{max} + \delta)$ with the initial condition t_{max} . This solution is evidently an extension of the original solution $x(t)$ to a larger time interval, that contradicts to our supposition that the solution is not in \mathbf{R}_+ . Thus, the solution $x(t)$ can be extended to the whole \mathbf{R}_+ .

Scenarios of evolution

The analysis of the Lotka-Volterra model can be done by graphs, or at least we can reach many conclusions based on this form of analysis.

With that being said, we will carry out a phase-plane analysis following those steps :

1. Find the isoclines of the system where $x'_1 = 0$ and $x'_2 = 0$
2. Determine the equilibrium points which are the intersection of the isoclines
3. Investigating stability properties of steady points found in step (2)

Determining Isoclines

Let's start by expressing x_2 in function of x_1 in (3) as $x_2 = f(x_1)$ for $x'_1 = 0$:

$$x_2 = \frac{-r_1}{\alpha K_1} x_1 + \frac{r_1}{\alpha_1} \quad (5)$$

Now let's express $x_1 = f(x_2)$:

$$x_1 = \frac{-r_2}{\alpha_2 K_2} x_2 + \frac{r_2}{\alpha_2} \quad (6)$$

Depending on the values of $K_1, K_2, \frac{r_2}{\alpha_2}$ and $\frac{r_1}{\alpha_1}$, we will have different isoclines allures and different equilibrium points :

With this code on MATLAB, we can plot isoclines for each case :

```

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%% % Here, by changing the values we can plot the 4
        different cases
r1=2;
k1=4;
a1=1;
r2=3;
a2=2;
k2=6;
%% %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%Isoclines%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
x1=[k1 0];
y1=[0 r1/a1];
x2=[r2/a2 0];
y2=[0 k2];
%% %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%PLOT%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
hold on
plot(x1,y1,'LineWidth',1.5);

plot(x2,y2,'LineWidth',1.5);
set(gca,'LineWidth',1)
hold off
legend('Species 1','Species 2')
title('Case 4')
xlabel('x1')
ylabel('x2')

```

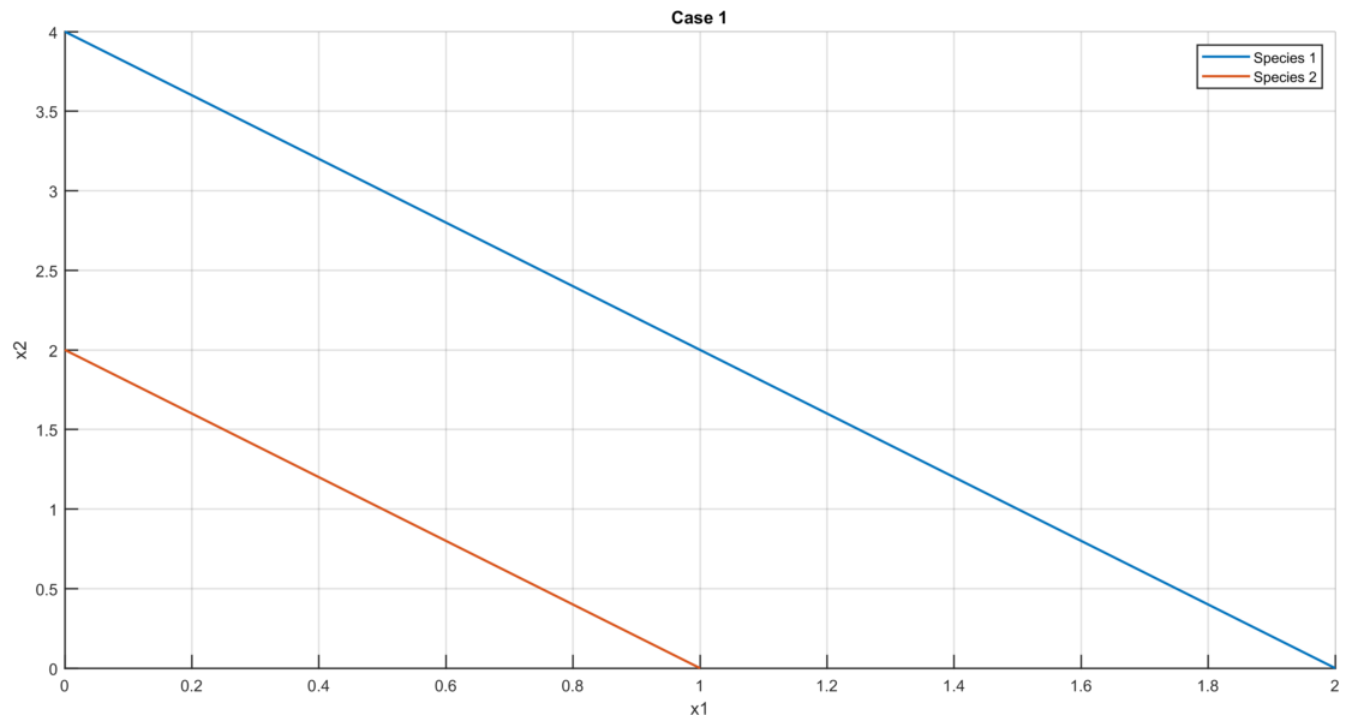


Figure 4: Case 1: $\frac{r_1}{\alpha_1} > K_2$ and $\frac{r_2}{\alpha_2} < K_1$

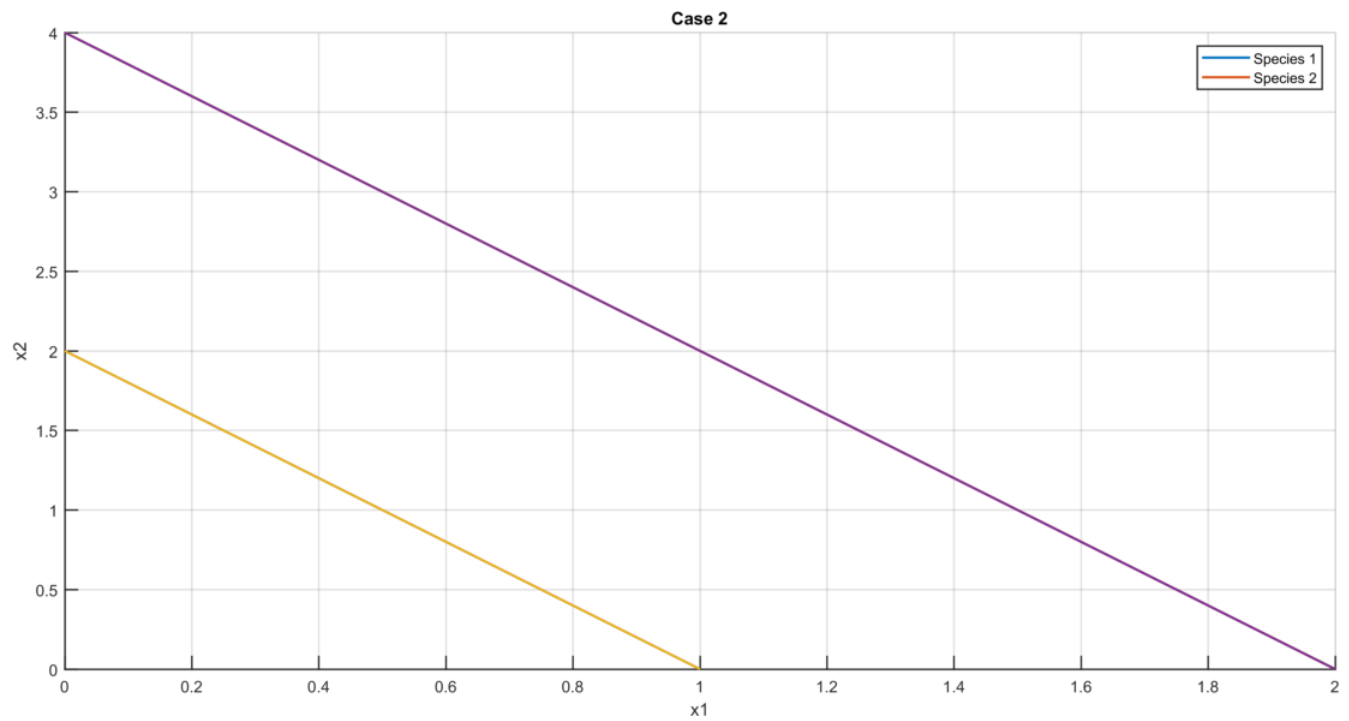


Figure 5: Case 2: $\frac{r_1}{\alpha_1} < K_2$ and $\frac{r_2}{\alpha_2} > K_1$

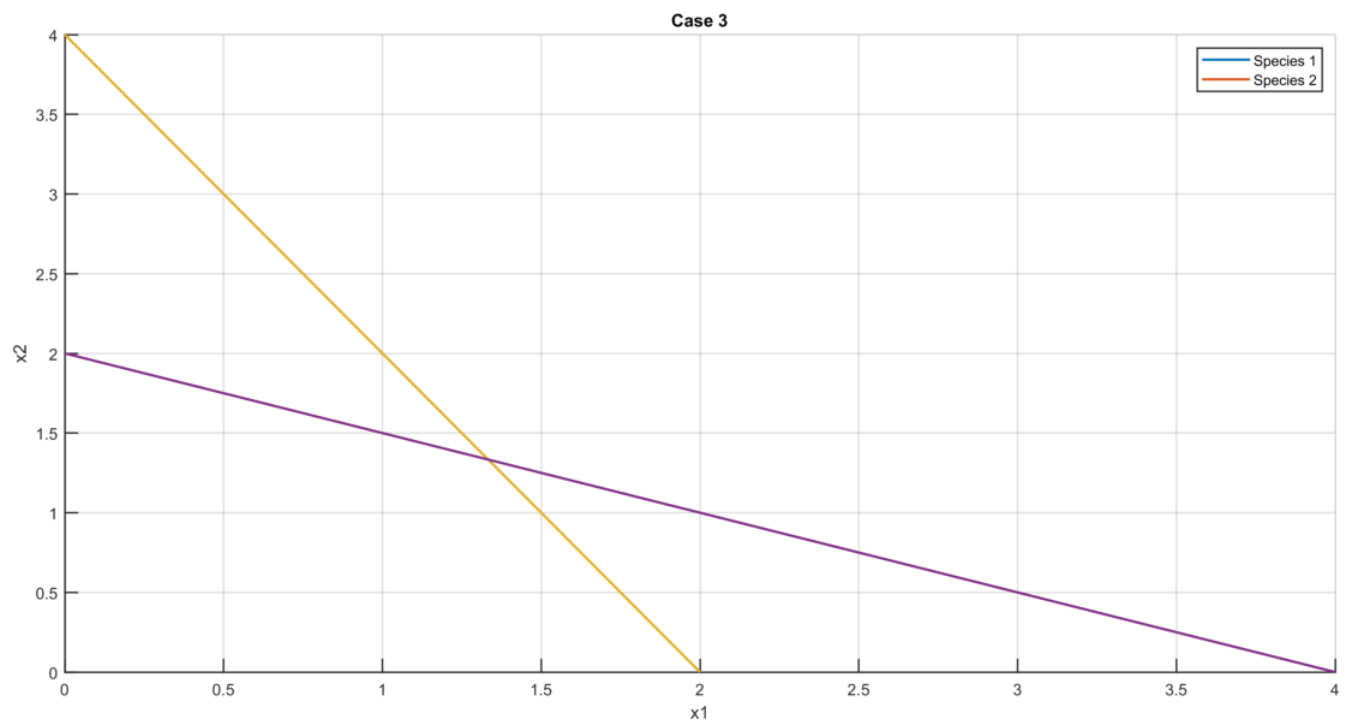


Figure 6: Case 3: $\frac{r_1}{\alpha_1} > K_2$ and $\frac{r_2}{\alpha_2} > K_1$

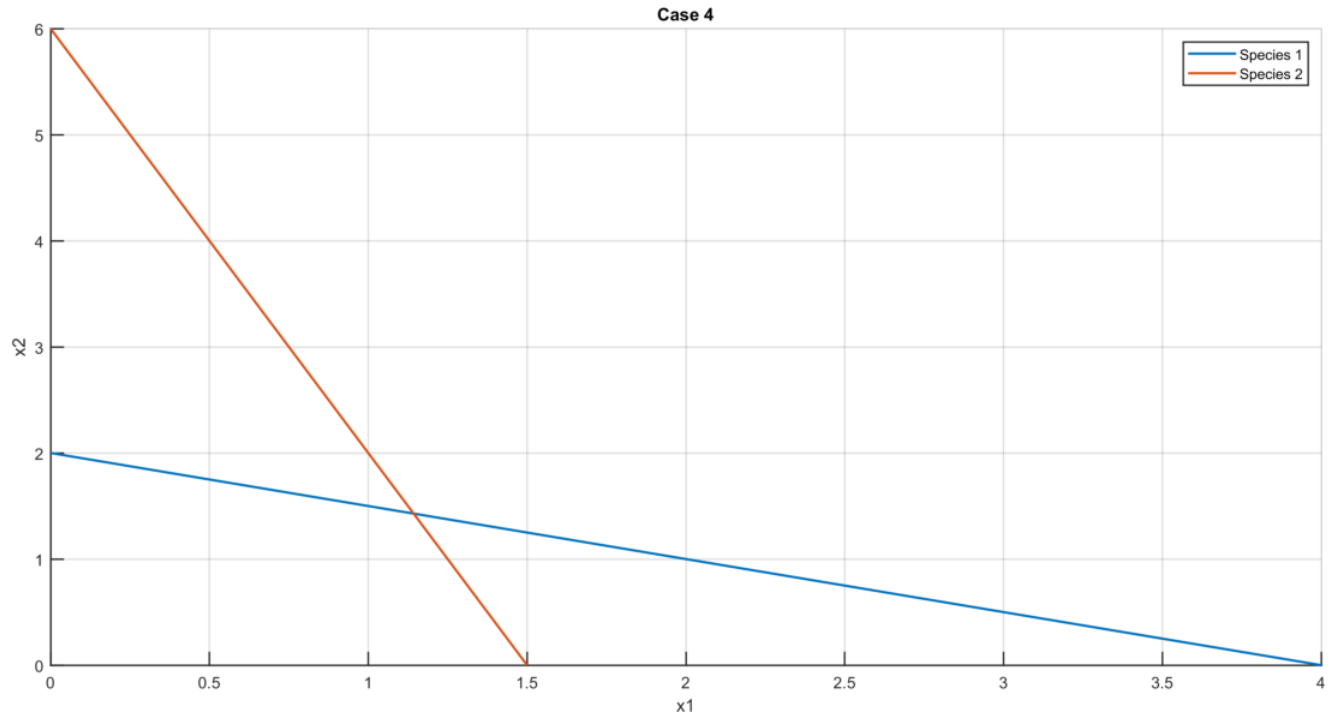


Figure 7: Case 4: $\frac{r_1}{\alpha_1} < K_2$ and $\frac{r_2}{\alpha_2} < K_1$

Finding equilibrium points

We can write (3) as following :

$$\begin{aligned}
 x_1' &= x_1 r_1 - \frac{r_1 x_1^2}{K_1} - \alpha_1 x_1 x_2 \\
 &= x_1 \left(r_1 - \frac{r_1 x_1}{K_1} - \alpha_1 x_2 \right) \\
 &= x_1 \left(K_1 - x_1 - \frac{\alpha_1 K_1}{r_1} x_2 \right) \\
 &= x_1 (K_1 - x_1 - \beta_1 x_2)
 \end{aligned} \tag{7}$$

with $\beta_1 = \frac{\alpha_1 K_1}{r_1}$.

For equation (5), we can see that $x_1' = 0$ if :

1. $x_1 = 0$
2. $(K_1 - x_1 - \beta_1 x_2) = 0$

We can extract 2 equilibrium points by replacing $x_1 = 0$ in equation (4), which becomes :

$$x_2' = r_2 x_2 \left(1 - \frac{x_2}{K_2} \right) \tag{8}$$

In (6), $x_2' = 0$ for $x_2 = 0$ or $x_2 = K_2$.

With that being said, we have actually found two equilibrium points : $(0; 0)$ and $(0; K_2)$

We can write (4) as following :

$$\begin{aligned}
 x_2' &= x_2 r_2 - \frac{r_2 x_2^2}{K_2} - \alpha_2 x_2 x_1 \\
 &= x_2 \left(r_2 - \frac{r_2 x_2}{K_2} - \alpha_2 x_1 \right) \\
 &= x_2 \left(K_2 - x_2 - \frac{\alpha_2 K_2}{r_2} x_1 \right) \\
 &= x_2 (K_2 - x_2 - \beta_2 x_1)
 \end{aligned} \tag{9}$$

with $\beta_2 = \frac{\alpha_2 K_2}{r_2}$.

In (7), $x_2' = 0$ if :

1. $x_2 = 0$
2. $K_2 - x_2 - \beta_2 x_1 = 0$

If $x_1 = 0$, then x_1' would be equal to 0 for $x_1 = 0$ and for $x_1 = K_1$.
So we have one new equilibrium point : $(K_1; 0)$

Now, let's go back to case (2) of equation (5) where we had $(K_1 - x_1 - \beta_1 x_2) = 0$. This implies that $x_1' = 0$ if

$$x_1 = K_1 - \frac{\alpha_1 K_1}{r_1} x_2 \tag{10}$$

If we replace value of x_1 by (8) in equation (3), and look for the value of $x_1' = 0$, we would have the following :

$$\begin{aligned}
 x_1' &= r_1 x_1 \left(1 - \frac{x_1}{K_1} \right) - \alpha_1 x_1 (K_2 - \beta_2 x_1) \\
 &= r_1 x_1 - \frac{r_1 x_1^2}{K_1} - \alpha_1 x_1 K_2 + \alpha_1 \beta_2 x_1^2 \\
 &= r_1 x_1 - \frac{r_1 x_1^2}{K_1} - \alpha_1 x_1 K_2 + \frac{\alpha_1 \alpha_2 K_2 x_1^2}{r_2} \\
 &= x_1 \left[r_1 \left(1 - \frac{x_1}{K_1} \right) - \alpha_1 K_2 + \frac{\alpha_1 \alpha_2 K_2 x_1}{r_2} \right] \\
 &\iff r_2 (r_1 K_1 - r_1 x_1 - \alpha_1 K_2 K_1 + \alpha_1 \alpha_2 K_1 K_2 x_1) = 0 \\
 &\iff (\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2) x_1 = -r_2 r_1 K_1 + \alpha_1 K_2 K_1 r_2
 \end{aligned}$$

Finally, for $x_1' = 0$, we have :

$$x_1 = \frac{r_2 K_1 (\alpha_1 K_2 - r_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2} \tag{11}$$

Now, we replace this expression of x_1 in (4) and we get :

$$x_2 = \frac{K_2 r_1 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2} \tag{12}$$

With that being done, we have now the 4th and last equilibrium point : $\left(\frac{r_2 K_1 (\alpha_1 K_2 - r_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2}, \frac{K_2 r_1 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2} \right)$

To sum it up, our four equilibrium points are :

1. $(0;0)$
2. $(K_1;0)$
3. $(0;K_2)$
4. $(\frac{r_2 K_1 (\alpha_1 K_2 - r_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2}; \frac{K_2 r_1 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2})$

Let's explain what does every equilibrium point represent :

1. Both species are extinct, and therefore there is no growth at all
2. Specie 1 growth or decreases (this will be explained in which case it does grow or decrease) until reaching it's carrying capacity and specie 2 is extinct
3. Specie 2 growth or decreases (this will be explained in which case it does grow or decrease) until reaching it's carrying capacity and specie 1 is extinct
4. Both species co-exist, this case is the most critical one and will be discussed further.

Stability of equilibrium points

In order to determine the stability of the equilibrium points, we need to be able to calculate the Jacobi matrices around each of them. For that, we will start by writing down the partial derivative of (3) and (4) to x_1 and x_2 since :

$$J_{\underbrace{(eq_1; eq_2)}_{\text{equilibrium points}}} = \begin{bmatrix} \frac{\partial x'_1}{\partial x_1} & \frac{\partial x'_1}{\partial x_2} \\ \frac{\partial x'_2}{\partial x_1} & \frac{\partial x'_2}{\partial x_2} \end{bmatrix} \quad (13)$$

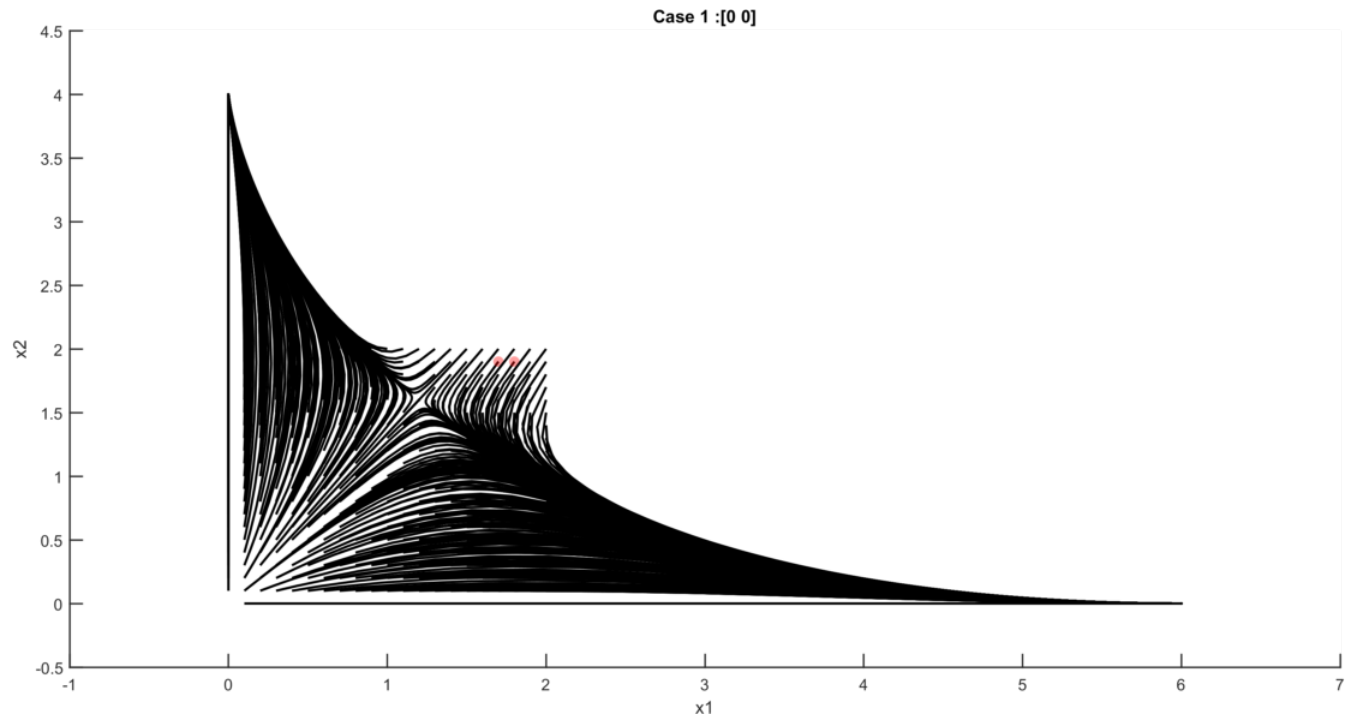
The 4 derivatives are :

$$\left\{ \begin{array}{l} \frac{\partial x'_1}{\partial x_1} = r_1 - \frac{2r_1 x_1}{K_1} - \alpha_1 x_2 \\ \frac{\partial x'_1}{\partial x_2} = -\alpha_1 x_1 \\ \frac{\partial x'_2}{\partial x_1} = -\alpha_2 x_2 \\ \frac{\partial x'_2}{\partial x_2} = r_2 - \frac{2r_2 x_2}{K_2} - \alpha_2 x_1 \end{array} \right.$$

Equilibrium point $(0;0)$:

$$J_{(0;0)} = \begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix} \quad (14)$$

Since this is a diagonal matrix, then the eigenvalues are on its diagonal, and since r_1 and r_2 are always strictly positive then this equilibrium point is unstable.



Equilibrium point $(0; K_2)$:

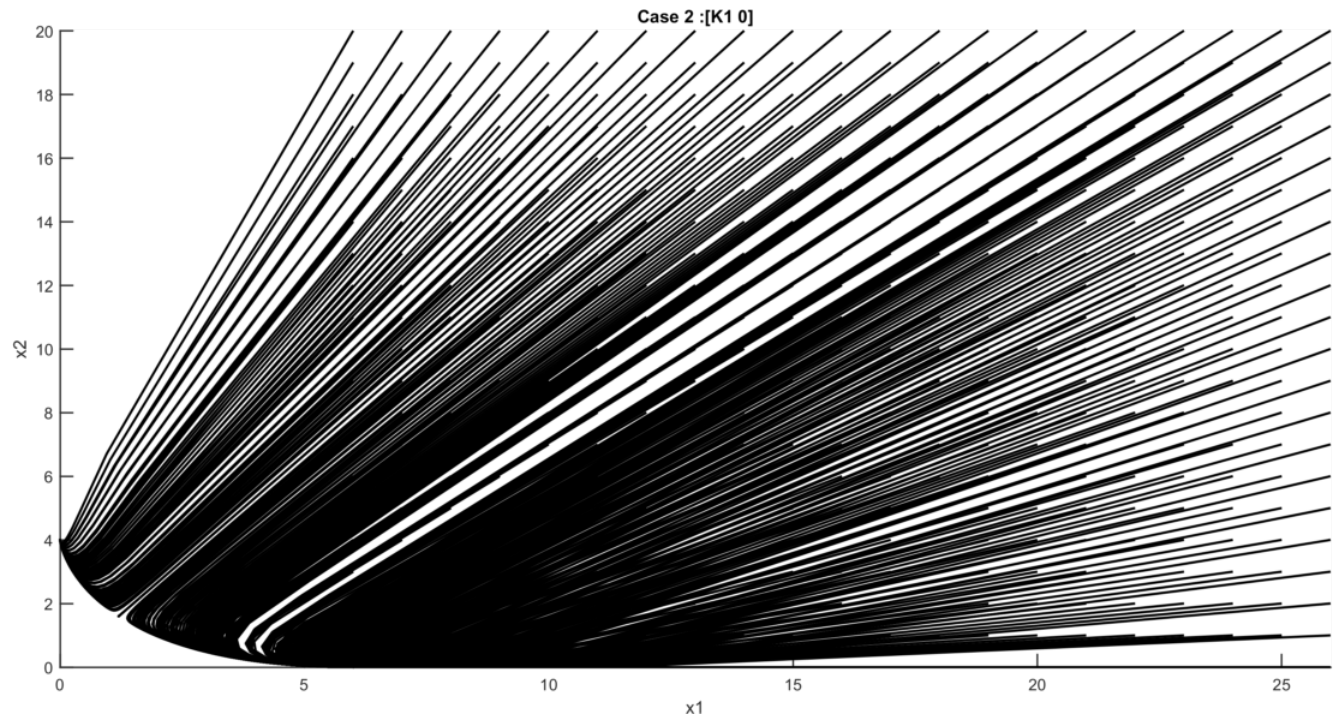
$$J_{(0; K_2)} = \begin{bmatrix} r_1 - \alpha_1 K_2 & 0 \\ -\alpha_1 K_2 & -r_2 \end{bmatrix} \quad (15)$$

This is a triangular matrix, so the eigenvalues are actually on the diagonal.

$-r_2$ is always negative, so we have to determine the stability on whether $r_1 - \alpha_1 K_2$ is positive or negative.

So,

1. If $r_1 > \alpha_1 K_2$ then the equilibrium point is a saddle point
2. If $r_1 < \alpha_1 K_2$ then the equilibrium point is stable.



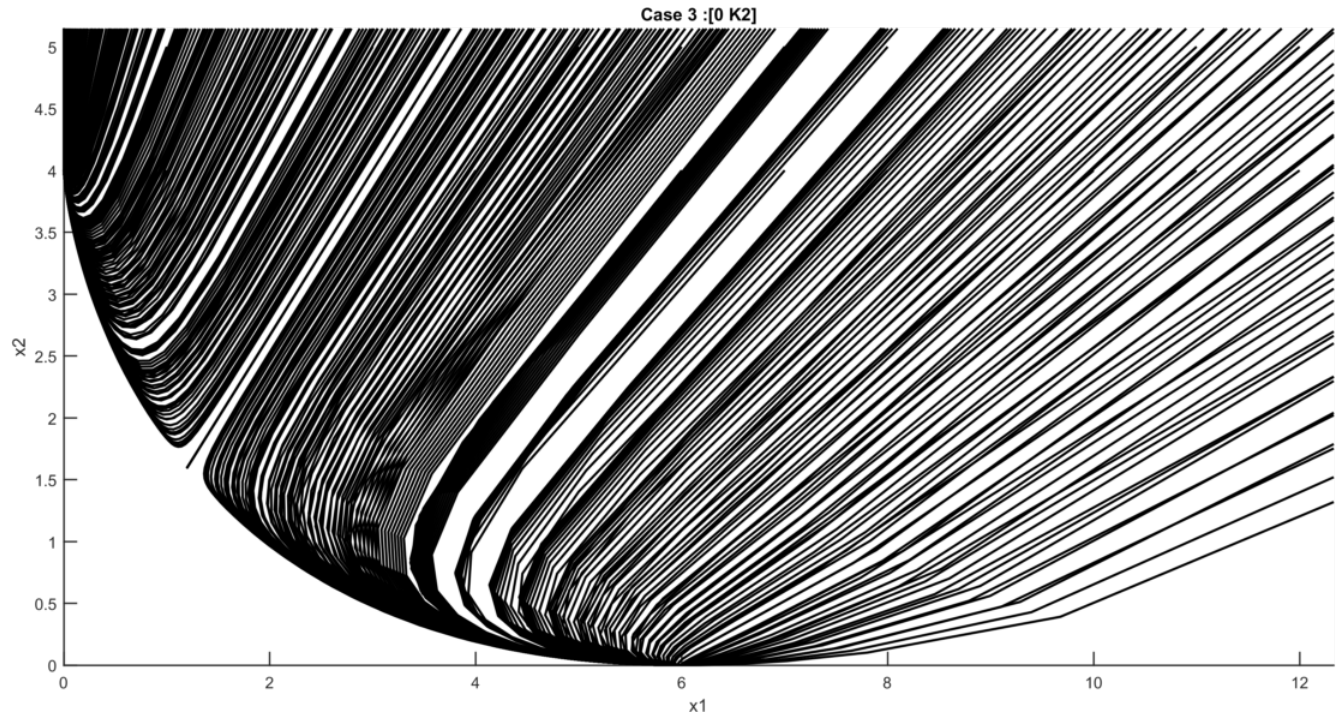
Equilibrium point $(K_1; 0)$:

$$J_{(K_1; 0)} = \begin{bmatrix} -r_1 & -\alpha_1 K_1 \\ 0 & r_2 - \alpha_2 K_1 \end{bmatrix} \quad (16)$$

This is a triangular matrix, so the eigenvalues are actually on the diagonal.

$-r_1$ is always negative, so we have to determine the stability on whether $r_2 - \alpha_2 K_1$ is positive or negative. So,

1. If $\frac{r_2}{\alpha_2} > K_1$ then the equilibrium point is a saddle point
2. If $\frac{r_2}{\alpha_2} < K_1$ then the equilibrium point is stable.



Equilibrium point $\left(\frac{r_2 K_1 (\alpha_1 K_2 - r_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2}; \frac{K_2 r_1 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2} \right)$:

$$J_{(K_1;0)} = \begin{bmatrix} \frac{r_1 r_2 (r_1 - \alpha_1 K_2)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2} & \frac{-\alpha_1 r_2 K_1 (\alpha_1 K_2 - r_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2} \\ \frac{-\alpha_2 r_1 K_2 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2} & \frac{r_1 r_2 (r_2 - \alpha_2 K_1)}{\alpha_1 \alpha_2 K_1 K_2 - r_1 r_2} \end{bmatrix} \quad (17)$$

Calculating eigenvalues was very complicated for this equilibrium point, for that I used an online eigenvalue calculator and I got the following eigenvalues :

$$\lambda_1 = \frac{-\alpha_2 r_1 K_2 (r_2 - \alpha_2 K_1)}{r_1 r_2 - \alpha_1 \alpha_2 K_1 K_2} \quad (18)$$

$$\lambda_2 = \frac{-r_2 (\alpha_1 K_2 - r_1)}{K_2 \alpha_2} \quad (19)$$

For our system to be stable, we need to have the following :

1. $\frac{r_2}{\alpha_2} > K_1$, $\frac{r_1}{\alpha_1} < K_2$ and $\frac{r_1 r_2}{\alpha_1 \alpha_2} > K_1 K_2$
2. $\frac{r_2}{\alpha_2} < K_1$, $\frac{r_1}{\alpha_1} < K_2$ and $K_1 K_2 > \frac{r_1 r_2}{\alpha_1 \alpha_2}$

For the following relations, we would have a saddle point :

1. $\alpha_1 K_2 = r_1$ or;
2. $\alpha_2 K_1 = r_2$

Comparison between logistic equation and Lotka-Volterra equation

Looking back at the two equations, we noticed that both them converge to a positive finite value for large values of t , $t \rightarrow \infty$.

For the logistic equation, the population will converge to K , the carrying capacity.

For the Lotka-Volterra equation, the solution will tend to another value smaller than the carrying capacity K_i depending on the value of α_i . For example, the larger α_1 is the smaller the value of convergence of x_2 will be, and the closer to 0 it will be.

References

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