Continuous modelling by ODEs

Qualitative behaviour of a system of ODEs

Computational Biology

Adérito Araújo (alma@mat.uc.pt)
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Qualitative analysis: scalar case

- What is the long time behaviour? $x(\infty) = ?$

$$\frac{dx}{dt} = f(x)$$

- If we are lucky, it coincides with the steady state solution.
- Steady state solution of the ODE: the values x^* of x for which

$$\frac{dx}{dt} = 0 \quad \Leftrightarrow \quad f(x) = 0.$$

- Since $dx/dt = 0$, the rate does not change, the ODE "stays there" forever.
- The steady states are also called fixed points or equilibria.
- A steady state is stable if a solution which starts nearby stays nearby; a steady state which is not stable is unstable.
- A steady state is asymptotically stable if all solutions which start nearby converge to it.

Stability analysis: Malthus law

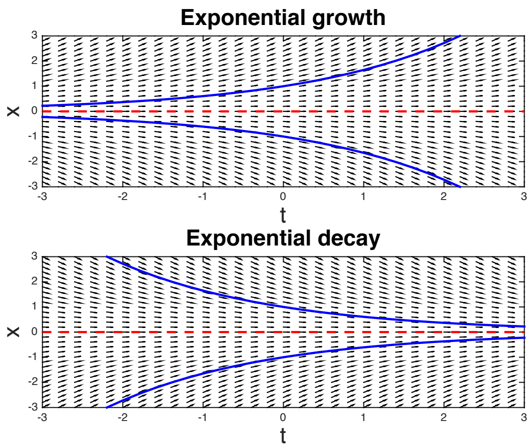
Malthus law:

$$f(x) = rx \quad \Rightarrow \quad x^* = 0.$$

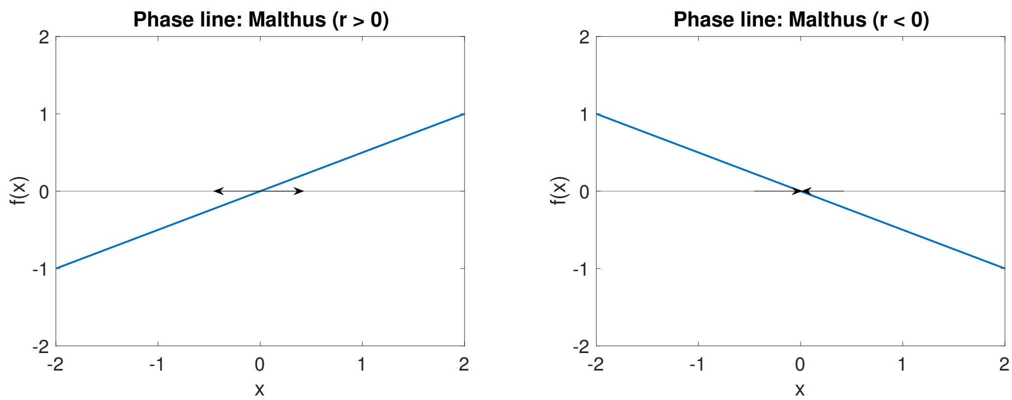
What is the behaviour of $x(t)$ in a small neighbourhood of x^* (of size $\epsilon > 0$)?

1. $r > 0$:
$$\begin{cases} x = x^* - \epsilon & \Rightarrow \quad f(x) < 0 \\ x = x^* + \epsilon & \Rightarrow \quad f(x) > 0 \end{cases}$$
Then $x^* = 0$ is unstable

2. $r < 0$:
$$\begin{cases} x = x^* - \epsilon & \Rightarrow \quad f(x) > 0 \\ x = x^* + \epsilon & \Rightarrow \quad f(x) < 0 \end{cases}$$
Then $x^* = 0$ is stable



Phase line: Malthus law



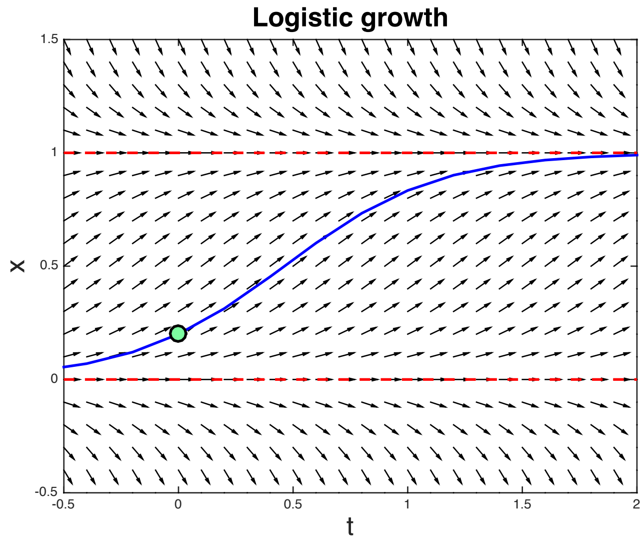
For $r > 0$: $\frac{df}{dx}(x^*) = r > 0$ and so x^* is unstable.

For $r < 0$: $\frac{df}{dx}(x^*) = r < 0$ and so x^* is (asymptotically) stable.

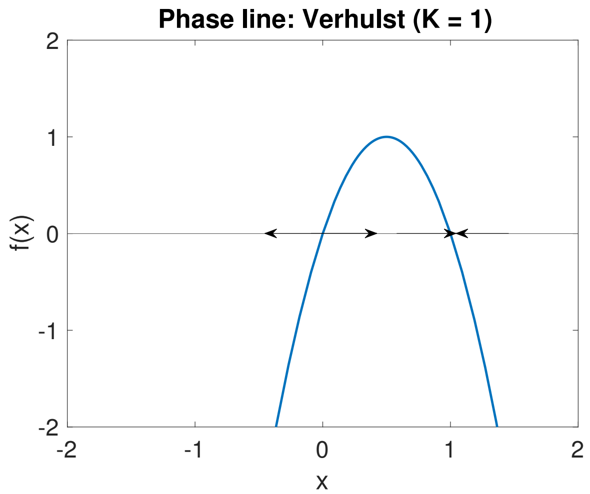
Stability analysis: Verhulst law

Verhulst law:

$$f(x) = rx\left(1 - \frac{x}{K}\right) \quad \Rightarrow \quad x_1^* = 0 \quad \text{and} \quad x_1^* = K.$$



Phase line: Verhulst law



For $x_1^* = 0$:

$$\frac{df}{dx}(x_1^*) = r - 2rx_1^*/K = r > 0 \quad \Rightarrow \quad x_1^* = 0 \ \text{unstable}.$$

For $x_2^* = K$:

$$\frac{df}{dx}(x_2^*) = r - 2rx_2^*/K = -r < 0 \quad \Rightarrow \quad x_2^* = 0 \ \text{stable}.$$

Qualitative analysis: general 2×2 system

$$\begin{cases} \frac{dx_1}{dt} & = & f_1(x_1, x_2) \\ \frac{dx_2}{dt} & = & f_2(x_1, x_2) \end{cases}$$

- At each $x = (x_1, x_2)$, the vector field $f(x) = (f_1(x), f_2(x))$ gives a good representation of the overall dynamics.
- A solution $x(t)$ is a parametric curve in the x_1x_2-plane, is called the trajectory or an orbit whose tangent vector is specified by the vector field.
- The sketch of the x_1x_2-plane with a number of typical solutions is called the phase space.
- The x_j-nullcline n_j is the set of points (x_1, x_2) such that

$$\frac{dx_j}{dt} = f_j(x_1, x_2) = 0, \qquad j = 1, 2.$$

- In general, equilibria or steady state of the system are the solutions of

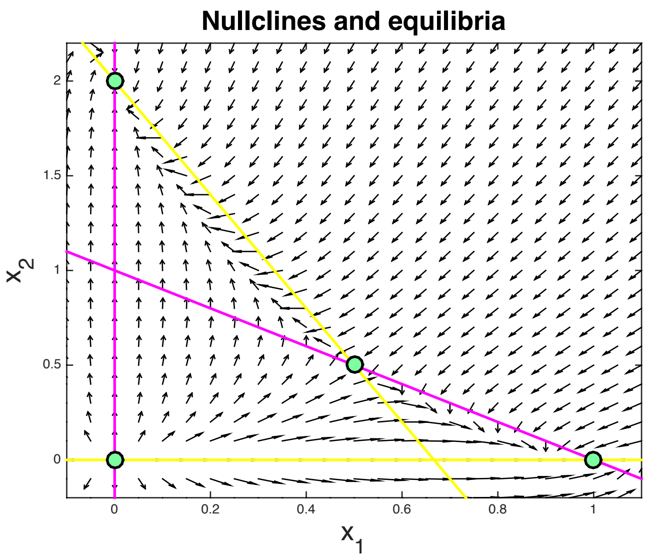
$$f_1(x_1, x_2) = 0, \qquad f_2(x_1, x_2) = 0.$$

Two species competing for the same prey

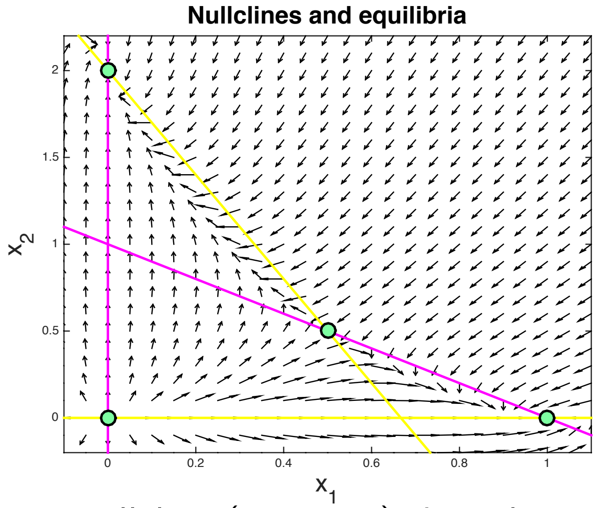
$$\begin{cases} \frac{dx_1}{dt} & = & x_1(1 - x_1) - x_1x_2 \\ \frac{dx_2}{dt} & = & 2x_2(1 - x_2/2) - 3x_1x_2 \end{cases}$$

The equilibrium points are given by

$$\begin{cases} x_1(1 - x_1) - x_1x_2 & = & 0 \\ 2x_2(1 - x_2/2) - 3x_1x_2 & = & 0 \end{cases} \Rightarrow \begin{cases} x_1 = 0 & \text{or} & 1 - x_1 - x_2 = 0 \\ x_2 = 0 & \text{or} & 2 - 3x_1 - x_2 = 0 \end{cases}$$

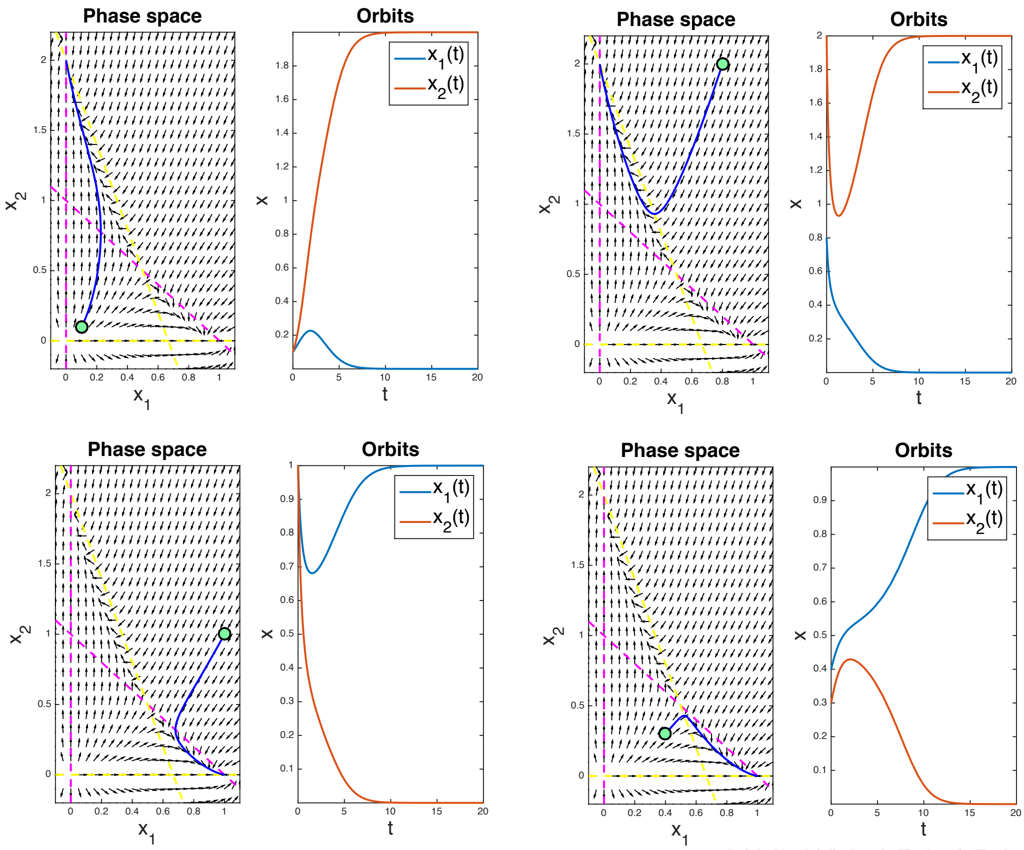


Two species competing for the same prey



- Along the x_1−nullcline (magenta) the velocity vectors are vertical while along the x_2−nullcline (yellow) the velocity vectors are horizontal.
- As long as we are traveling along a nullcline without crossing an equilibrium point, then the direction of the velocity vector must be the same; once we cross an equilibrium point, then we may have a change in the direction.

Two species competing for the same prey



Linearization

We can determine the stability of a steady state by linearizing the system around the steady state $x^* = (x_1^*, x_2^*)$. Using Taylor expansion

$$f(x^* + z) = f(x^*) + Df(x^*)z + \text{ higher-order terms},$$

where

$$Df(x^*) = \begin{bmatrix} a & b \\ c & d \end{bmatrix} = \begin{bmatrix} \frac{\partial f_1}{\partial x_1}(x^*) & \frac{\partial f_1}{\partial x_2}(x^*) \\ \frac{\partial f_2}{\partial x_1}(x^*) & \frac{\partial f_2}{\partial x_2}(x^*) \end{bmatrix}$$

is the Jacobian matrix of f at x^*. Replacing in the equation and dropping the higher-order terms, since $f(x^*) = 0$ we obtain a linear system for the dependent variable z

$$\frac{d}{dt}\begin{bmatrix} z_1 \\ z_2 \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}\begin{bmatrix} z_1 \\ z_2 \end{bmatrix}$$

For most (but not all) steady states, conclusions obtained for the linearized system indeed carry over to the original nonlinear system.

Some theoretical results

- A steady state x^* is called hyperbolic if all eigenvalues of the Jacobian $Df(x^*)$ have nonzero real part.
- (Hartman-Grobman Theorem) Assume that x^* is a hyperbolic equilibrium. Then, in a small neighbourhood of x^*, the phase portrait of the nonlinear system is the same as that of the linearized system.

Remarks:

- At a hyperbolic equilibrium x^*, stability properties are determined by the eigenvalues of the Jacobian matrix, $Df(x^*)$ (see next slides). This method of linearization may fail for nonhyperbolic equilibria.
- The phrase “the same as” in the above theorem refers to topological equivalence of vector fields.

Stability for linear systems

$$\frac{d}{dt}\begin{bmatrix} z_1 \\ z_2 \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}\begin{bmatrix} z_1 \\ z_2 \end{bmatrix}$$

- First case: real eigenvalues $\lambda_1 = a$, $\lambda_2 = b$

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix}$$

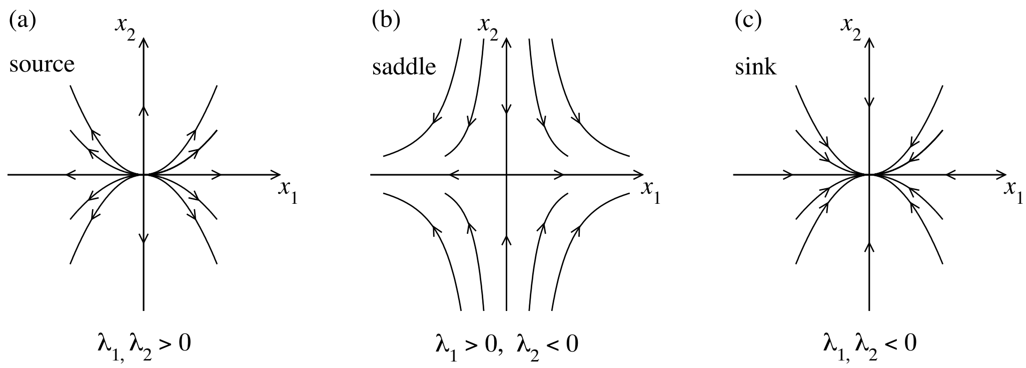
- Second case: complex eigenvalues $\alpha \pm i\beta$

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} = \begin{bmatrix} \alpha & \beta \\ -\beta & -\alpha \end{bmatrix}$$

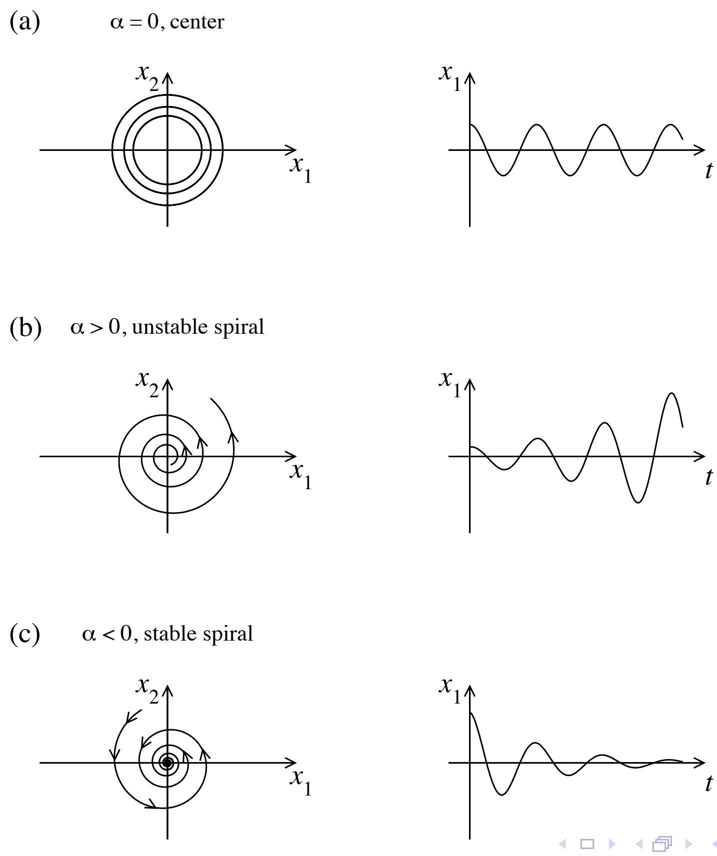
- General case: consider

$$\text{tr}(A) = a + b \quad \text{and} \quad \det(A) = ad - cb$$

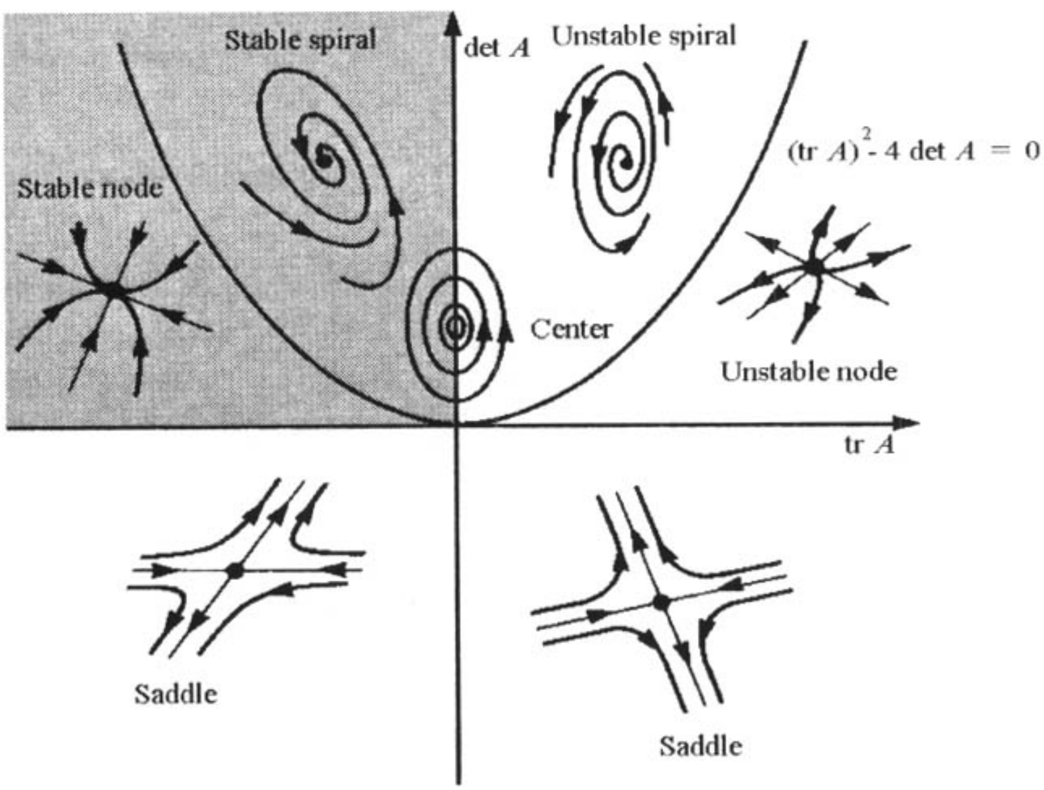
First case: real eigenvalues $\lambda_1 = a$, $\lambda_2 = b$



Second case: complex eigenvalues $\alpha \pm i\beta$



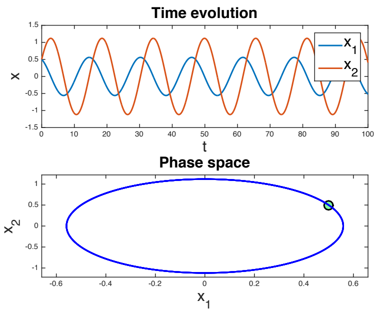
General case: Poincaré diagram $(\det(A), \mathrm{tr}(A))-$plane

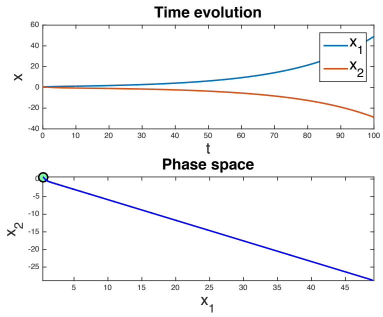


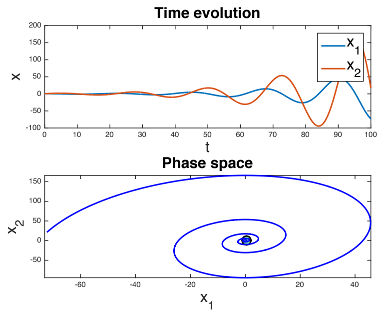
General case: $\tau = \mathrm{tr}(A)$, $\Delta = \det(A)$

$$A_1 = \begin{bmatrix} 0 & -0.2 \\ 0.8 & 0 \end{bmatrix}, \quad A_2 = \begin{bmatrix} 0.1 & 0.1 \\ -0.2 & -0.3 \end{bmatrix}, \quad A_3 = \begin{bmatrix} 0.1 & -0.1 \\ 0.8 & 0 \end{bmatrix}$$

$\mathrm{tr}(A_1) = 0, \det(A_1) = 0.16,$ $\quad$ $\mathrm{tr}(A_2) = -0.2, \det(A_1) = -0.01,$ $\quad$ $\mathrm{tr}(A_3) = 0.1, \det(A_1) = 0.8$







General population interaction model

Consider the general population interaction model

$$\begin{cases} \frac{dx_1}{dt} = \alpha x_1 + \beta x_1 x_2 \\ \frac{dx_2}{dt} = \gamma x_2 + \delta x_1 x_2 \end{cases}$$

and example for predator-prey, one example for mutualism and one example for competition:

α	β	γ	δ	
$-$	$+$	$+$	$-$	Predator (x_1) - prey (x_2) model
$-$	$+$	$-$	$+$	Mutualism of symbiosis model
$+$	$-$	$-$	$-$	Competition model

General population interaction model

1. The equilibrium points are given by

$$\begin{cases} \alpha x_1 + \beta x_1 x_2 &= 0 \\ \gamma x_2 + \delta x_1 x_2 &= 0 \end{cases} \Rightarrow \begin{cases} x_1 = 0 & \text{or} \quad x_2 = -\frac{\alpha}{\beta} \\ x_2 = 0 & \text{or} \quad x_1 = -\frac{\gamma}{\delta} \end{cases}$$

   The equilibrium points are $P_1 = (0,0)$ and $P_2 = \left(-\frac{\gamma}{\delta}, -\frac{\alpha}{\beta}\right)$.

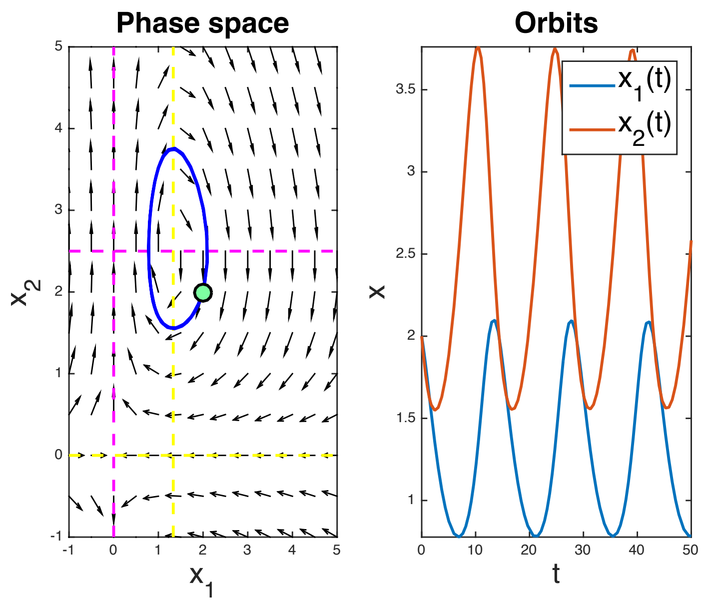
2. The linearization is given by

$$\frac{d}{dt}\begin{bmatrix} z_1 \\ z_2 \end{bmatrix} = \underbrace{\begin{bmatrix} \alpha + \beta x_2^* & \beta x^* \\ \delta x_2^* & \gamma + \delta x_1^* \end{bmatrix}}_{Df(x^*)} \begin{bmatrix} z_1 \\ z_2 \end{bmatrix}.$$

3. The eigenvalues of $Df(P_1)$ are $\lambda_1 = \alpha$ and $\lambda_2 = \gamma$; the eigenvalues of $Df(P_2)$ are $\lambda_j = \pm\sqrt{\alpha\gamma}$, $j = 1, 2$.

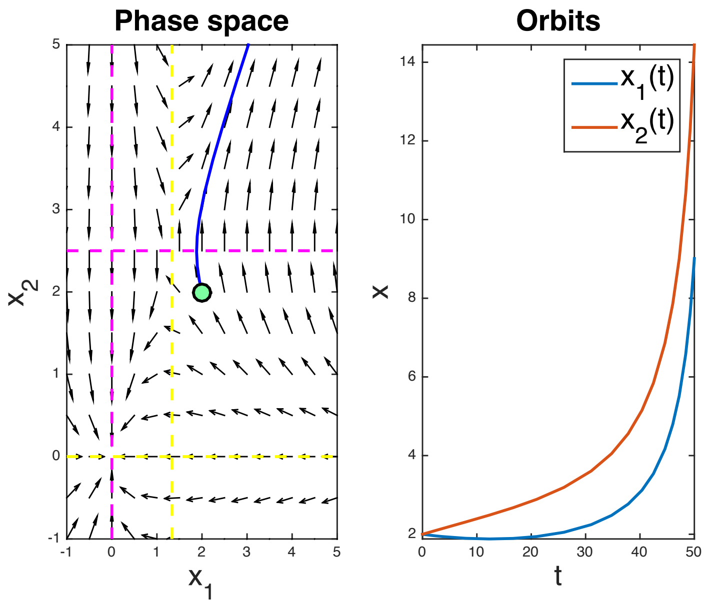
Predator-prey model

- For P_1 the eigenvalues are $\lambda_1 = \alpha < 0$ and $\lambda_2 = \gamma > 0$ which implies that P_1 is a saddle.
- For P_2 (verify that is biological relevant) the eigenvalues are $\lambda_j = \pm i\sqrt{|\alpha\gamma|}$, $j = 1, 2$ which implies that P_2 is a center.



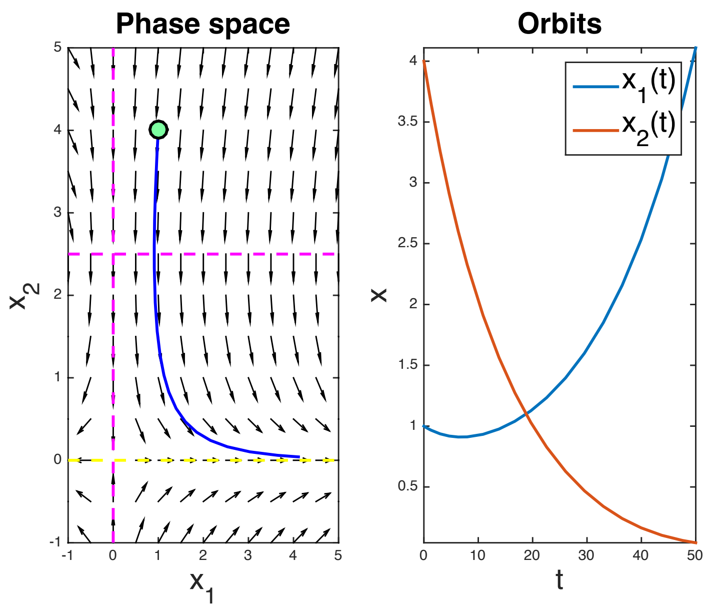
Mutualism model

- For P_1 the eigenvalues are $\lambda_1 = \alpha < 0$ and $\lambda_2 = \gamma < 0$ which implies that P_1 is a stable node.
- For P_2 (verify that is biological relevant) the eigenvalues are $\lambda_j = \pm\sqrt{\alpha\gamma}$, $j = 1, 2$ which implies that P_2 is a saddle.



Competition model

- For P_1 the eigenvalues are $\lambda_1 = \alpha > 0$ and $\lambda_2 = \gamma < 0$ which implies that P_1 is a saddle.
- The equilibrium P_2 is not biological relevant ($-\gamma/\delta < 0$).



Homework %7: Two species competing for the same prey

Exercise 2.18: Consider a model of two species competing for the same resource

$$\begin{cases} \dfrac{dx_1}{dt} = r_1 x_1 \left(1 - \dfrac{x_1}{K_1} - \alpha \dfrac{x_2}{K_1}\right) \\ \dfrac{dx_2}{dt} = r_2 x_2 \left(1 - \dfrac{x_2}{K_2} - \beta \dfrac{x_1}{K_2}\right) \end{cases},$$

where α and β are competition coefficients.

1. Considering

$$u_1 = \frac{x_1}{K_1},\ u_2 = \frac{x_2}{K_2},\ \tau = r_1 t,\ \rho = \frac{r_2}{r_1},\ a = \alpha\frac{K_2}{K_1},\ b = \beta\frac{K_1}{K_2},$$

prove that the system is equivalent to

$$\begin{cases} \dfrac{du_1}{d\tau} = u_1 \left(1 - u_1 - a u_2\right) \\ \dfrac{du_2}{d\tau} = \rho u_2 \left(1 - u_2 - b u_1\right) \end{cases}.$$

Homework %7: Two species competing for the same prey

2. Prove that the previous system has the following equilibria

$$(0,0),\ (1,0),\ (0,1),\ \left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right),$$

assuming that $ab \neq 1$.

Note: The coexistence state is only in the positive quadrant and therefore biologic realistic if either $a < 1$ and $b < 1$, or $a > 1$ and $b > 1$.

3. Prove that the Jacobian matriz for the equilibria (u_1^*, u_2^*) is

$$\begin{bmatrix} 1 - 2u_1^* - a u_2^* & -a u_1^* \\ -\rho b u_2^* & \rho(1 - 2u_2^* - b u_1^*) \end{bmatrix}.$$

Homework %7: Two species competing for the same prey

4. Prove that:
   4.1 $(0,0)$ is unstable (e.v. $\lambda_1 = 1, \lambda_2 = \rho$);
   4.2 $(1,0)$ is stable if $b > 1$ and is unstable if $b < 1$ (e.v. $\lambda_1 = -1, \lambda_2 = \rho(1-b)$); ($x_1$ wins)
   4.3 $(0,1)$ is stable if $a > 1$ and unstable if $a < 1$ (e.v. $\lambda_1 = -1, \lambda_2 = \rho(1-a)$); ($x_2$ wins)
   4.4 The steady state of coexistence is stable if $a < 1$ and $b < 1$ (stable coexistence) and unstable if $a > 1$ and $b > 1$.

Evolutionary point of view: As species x_1, your best evolutionary strategy must be based on increasing $b = \beta\frac{K_1}{K_2}$ or decreasing $a = \alpha\frac{K_2}{K_1}$, i.e. increasing your carrying capacity K_1 relative to your competitors (a so-called $K-$strategy), or increasing your competition coefficient β relative to your competitor's.
There is no advantage in increasing your growth rate r_1 (a so-called $r-$strategy).