Equilibrium points

week 3

1. Equilibrium points in 1D

1. Equilibrium points in 1D

Logistic equation

$$\boxed{\frac{dX}{dt} = rX(1 - \frac{X}{k})}$$

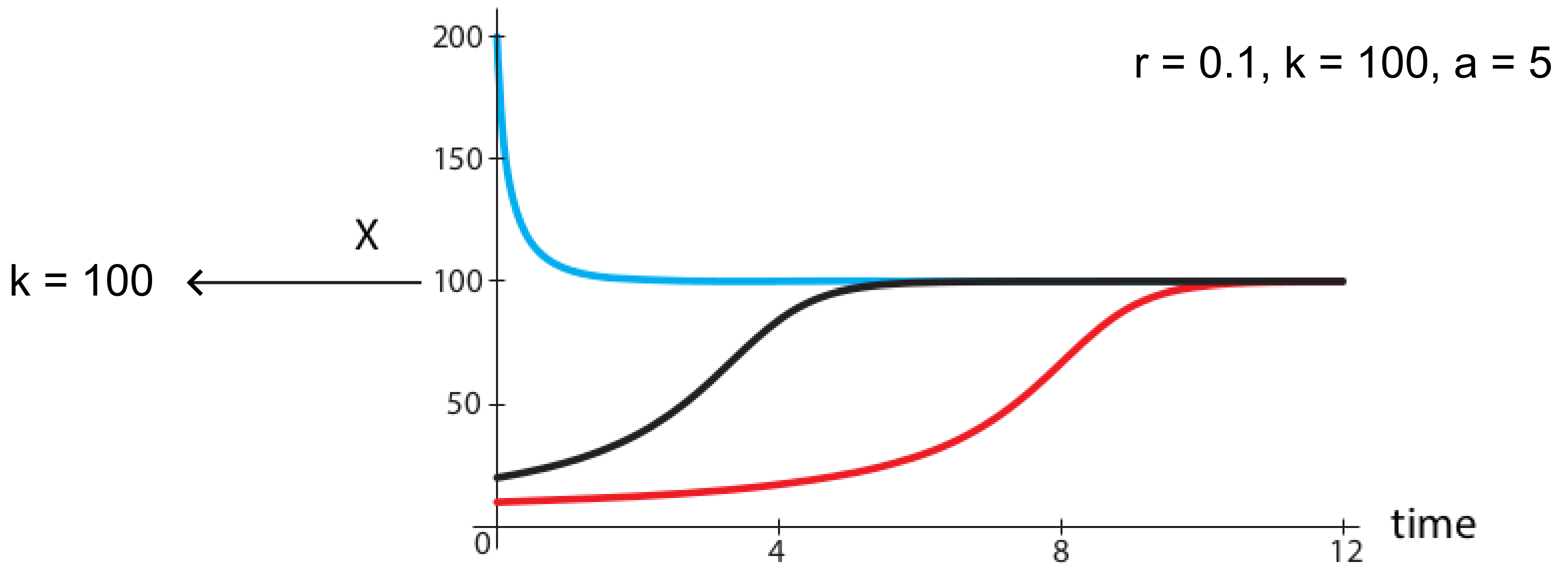
- In some species, a minimal number of animals is necessary to ensure the survival of the group
- For example, African hunting dogs, require the help of others to bring up their young. As a result, their reproductive success declines at low population levels, and a population that’s too small may go extinct
- This decline in per capita population growth rates at low population sizes is called the Allee effect

$$\boxed{X' = rX(1 - \frac{X}{k})(\frac{X}{a} - 1)}$$

1. Equilibrium points in 1D

Logistic equation with Allee effect

$$X' = rX(1 - \frac{X}{k})(\frac{X}{a} - 1)$$



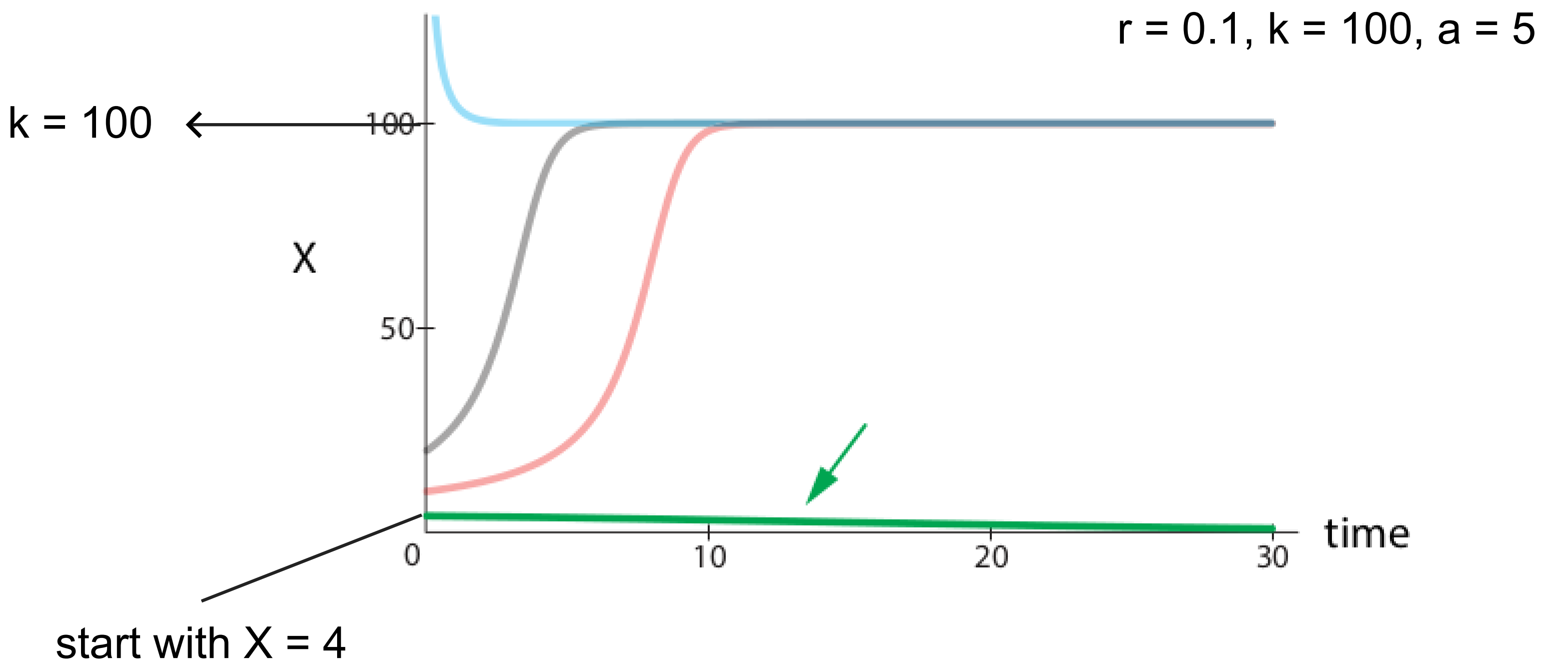
Where is the equilibrium?

Is this the only equilibrium?

1. Equilibrium points in 1D

Logistic equation with Allee effect

$$X' = rX(1 - \frac{X}{k})(\frac{X}{a} - 1)$$



1. Equilibrium points in 1D

More simple: logistic equation

$$\boxed{\frac{dX}{dt} = rX(1 - \frac{X}{k})}$$

What are the equilibrium points?

X = 0 and X = k

What is the stability of the equilibria?

- X = 0: unstable
- X = k: stable

1. Equilibrium points in 1D

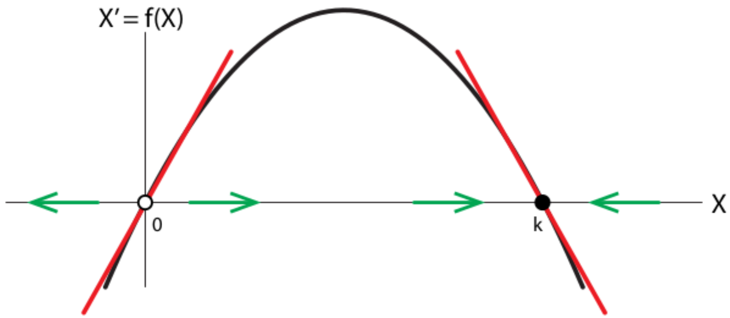
Different methods to test the stability

$$\boxed{\frac{dX}{dt} = rX\left(1 - \frac{X}{k}\right)}$$

1. Test points or analyze the equation

2. Linear stability analysis

$$f(X) = X\left(1 - \frac{X}{k}\right)$$



Compute derivatives in the points

$$\frac{df(X)}{dX} = 1 - \frac{2X}{k}$$

$$\left.\frac{df(X)}{dX}\right|_{X=0} = +1 \quad > 0 \text{ unstable}$$

$$\left.\frac{df(X)}{dX}\right|_{X=k} = -1 \quad < 0 \text{ stable}$$

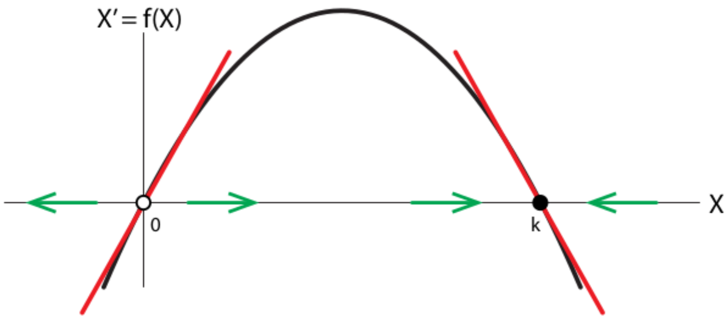
1. Equilibrium points in 1D

Different methods to test the stability

$$\boxed{\frac{dX}{dt} = rX(1 - \frac{X}{k})}$$

2. Linear stability analysis

$$f(X) = X(1 - \frac{X}{k})$$



Compute derivatives in the points

$$\frac{df(X)}{dX} = 1 - \frac{2X}{k}$$

$$\left.\frac{df(X)}{dX}\right|_{X=0} = +1 \quad > 0 \text{ unstable}$$

$$\left.\frac{df(X)}{dX}\right|_{X=k} = -1 \quad < 0 \text{ stable}$$

Deep truth: the stability of an equilibrium point of a vector field is determined by the linear approximation to the vector field at the equilibrium point.

This principle, called the Hartman - Grobman theorem, enables us to use linearization to determine the stability of equilibria.

1. Equilibrium points in 1D

At an equilibrium point X^* (pronounced "X-star," a common notation for equilibria):

(1) If $\frac{df(X)}{dX}\Big|_{X=X^*}$ is positive, then X^* is an **unstable** equilibrium.

(2) If $\frac{df(X)}{dX}\Big|_{X=X^*}$ is negative, then X^* is a **stable** equilibrium.

We will generalize this for higher dimensions!

1. Equilibrium points in 1D

Some exercises:

$$\boxed{X' = rX(1 - \frac{X}{k})(\frac{X}{a} - 1)}$$

1. What are the equilibria?

X = 0; X = k; X = a

1. Equilibrium points in 1D

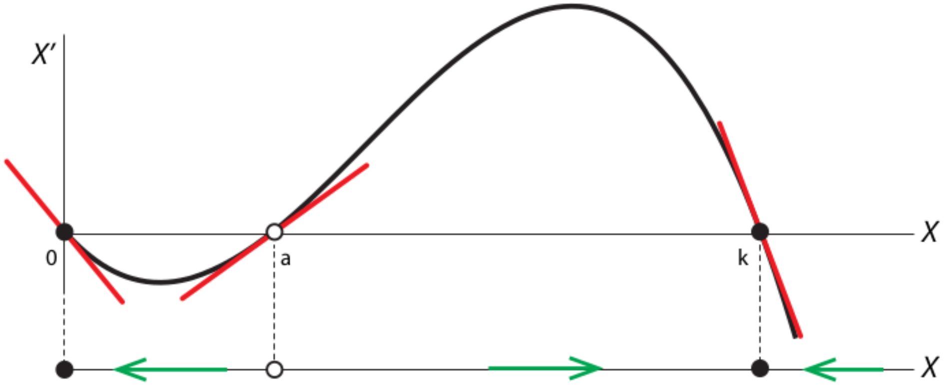
Some exercises:

2. Stability via derivatives? (a < k)

$$X' = rX(1-\frac{X}{k})(\frac{X}{a}-1) = -\frac{r}{ak}X^3 + \frac{r}{a}X^2 + \frac{r}{k}X^2 - rX$$

$$\frac{dX'}{dX} = -\frac{3r}{ak}X^2 + \frac{2r}{a}X + \frac{2r}{k}X - r$$

$$\boxed{\begin{aligned} \frac{dX'}{dX}\Big|_{X=0} &= -r \\ \frac{dX'}{dX}\Big|_{X=a} &= r(1-\frac{a}{k}) \\ \frac{dX'}{dX}\Big|_{X=k} &= r(1-\frac{k}{a}) \end{aligned}}$$

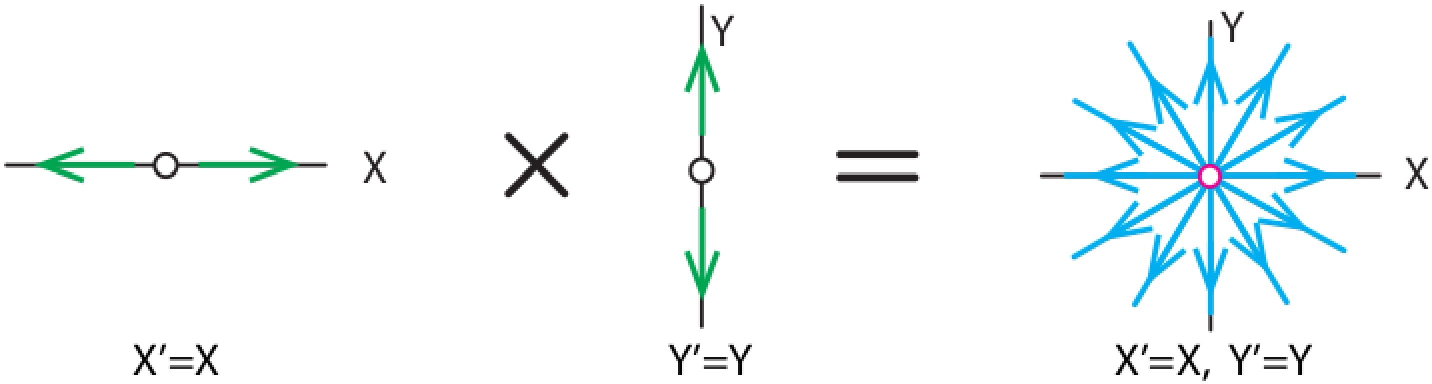


Exercise 3.1.1
3.1.2

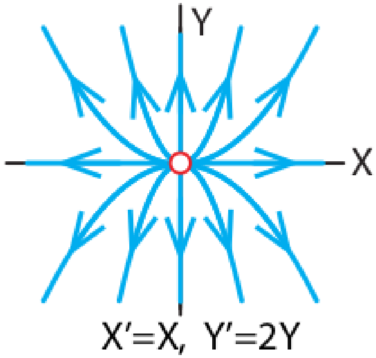
2. Equilibrium points in 2D

2. Equilibrium points in 2D - different types

X' = X and Y' = Y



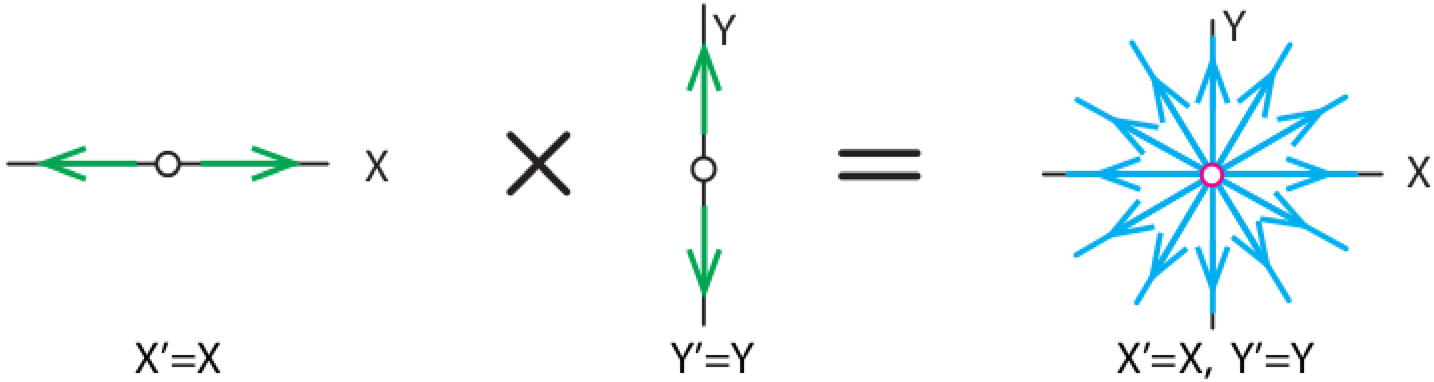
X' = X and Y' = 2Y



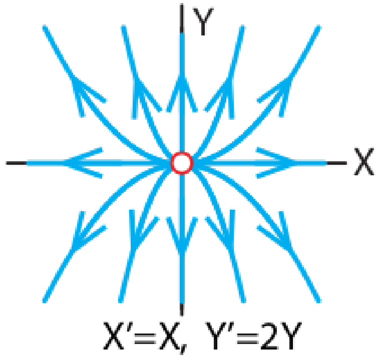
2. Equilibrium points in 2D - different types

X' = X and Y' = Y

unstable node



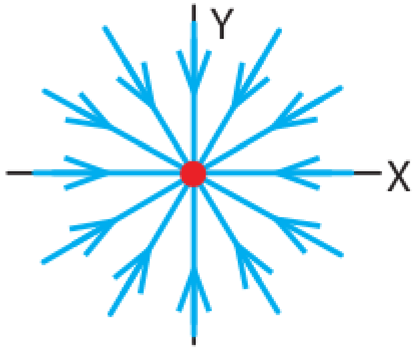
X' = X and Y' = 2Y



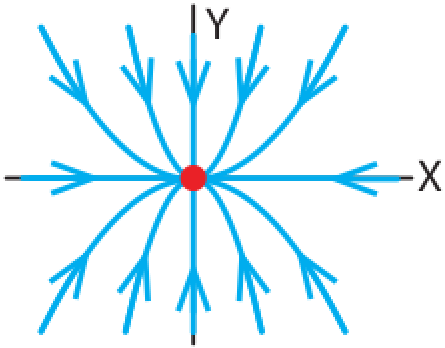
2. Equilibrium points in 2D - different types

X' = -X and Y' = -Y

stable node

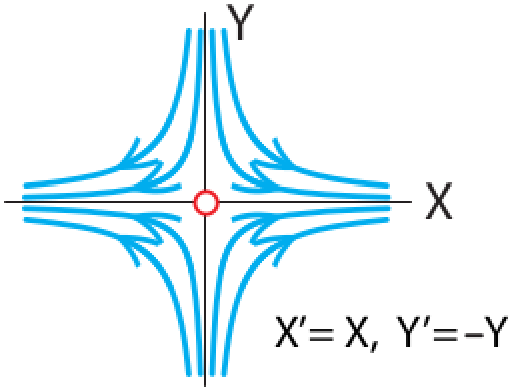


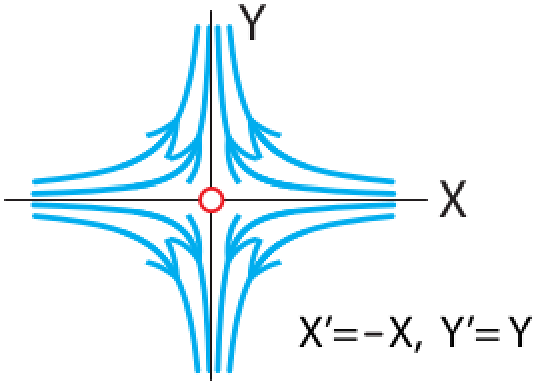
X' = -X and Y' = -2Y



2. Equilibrium points in 2D - different types

saddle point





Stable or unstable?

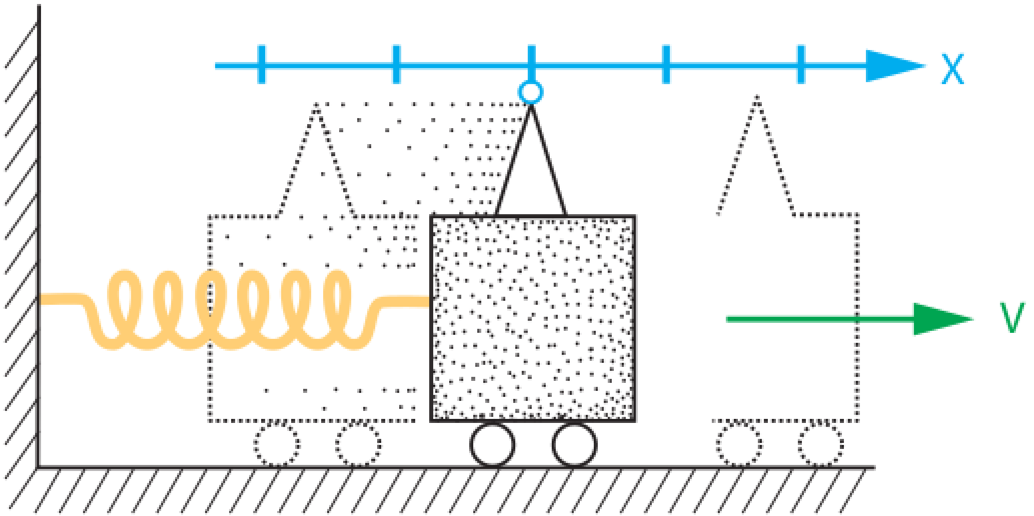
The only way to approach the equilibrium point is to start exactly on the stable axis.
Since the typical trajectory does not lie exactly on the stable axis, a saddle point is considered unstable.

2. Equilibrium points in 2D - different types

spring

X' = V

V' = -X



spring with friction

X' = V

V' = -X - V

spring with negative friction

X' = V

V' = -X + V

2. Equilibrium points in 2D - different types

spring with friction

$X' = V$

$V' = -X - V$

spring with negative friction

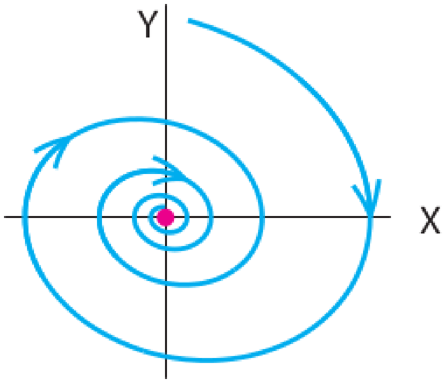
$X' = V$

$V' = -X + V$

spring

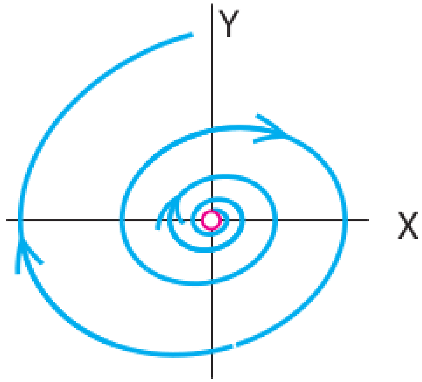
$X' = V$

$V' = -X$



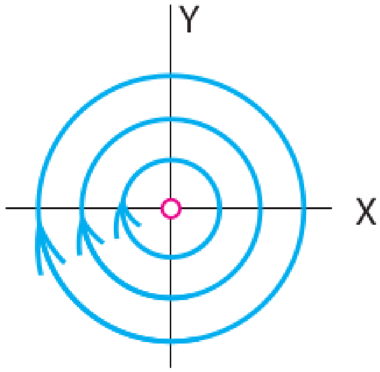
$X' = Y,\ Y' = -X - Y$

stable spiral



$X' = Y,\ Y' = -X + Y$

unstable spiral



$X' = Y,\ Y' = -X$

center

2. Equilibrium points in 2D - determine type linear system

Simplest case:

$$X' = aX$$
$$Y' = dY$$

Matrix differentiation:

$$\begin{pmatrix} X' \\ Y' \end{pmatrix} = \begin{bmatrix} a & 0 \\ 0 & d \end{bmatrix} \begin{pmatrix} X \\ Y \end{pmatrix}$$

Solution:

$$\begin{pmatrix} X(t) \\ Y(t) \end{pmatrix} = \begin{pmatrix} X(0)e^{at} \\ Y(0)e^{dt} \end{pmatrix}$$

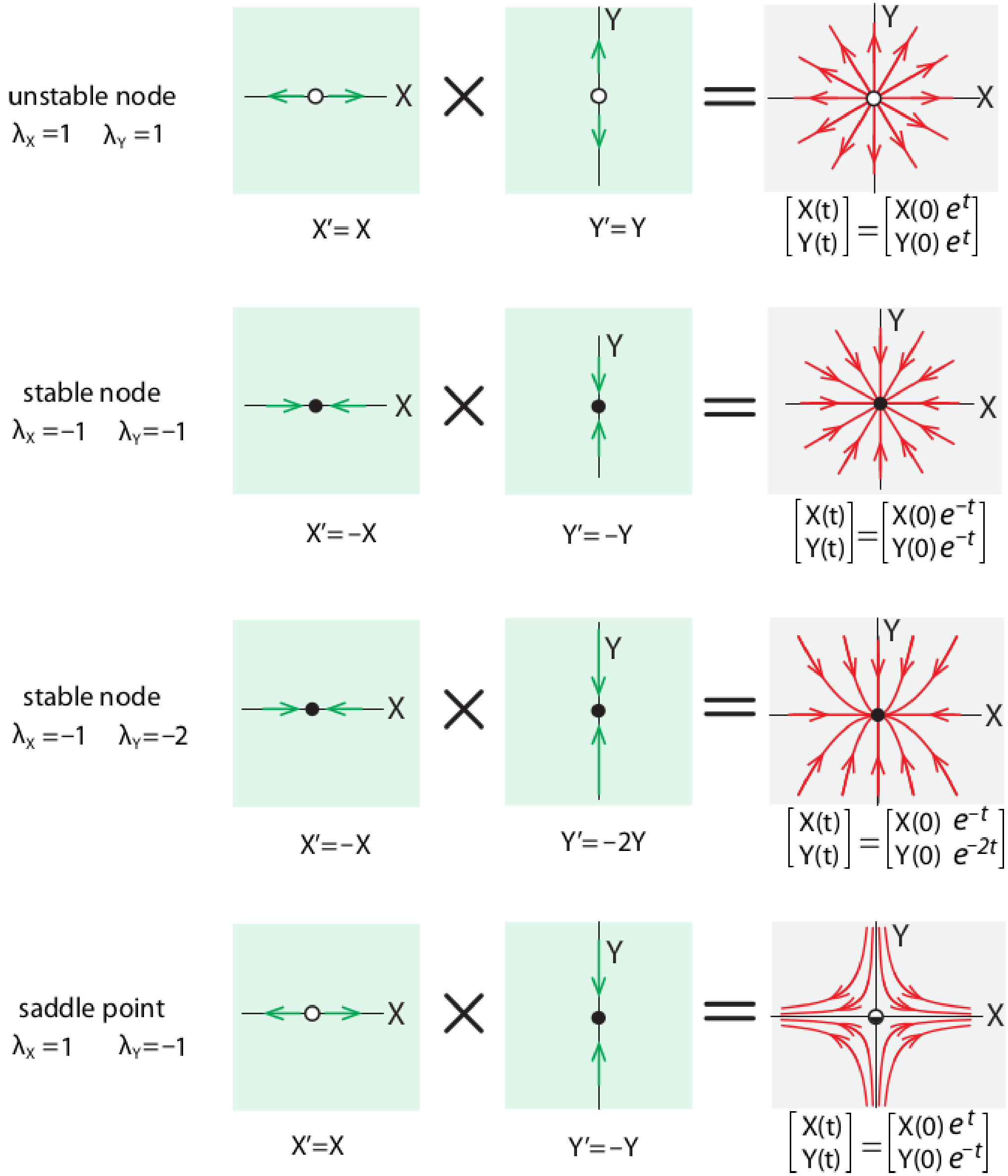
What are the eigenvalues and eigenvectors?

$$\{\mathbf{X}, \mathbf{Y}\} = \left\{ \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right\}$$

$$\lambda_X = a \quad \lambda_Y = d$$

What can you conclude about the solutions?

2. Equilibrium points in 2D - determine type linear system



2. Equilibrium points in 2D - determine type linear system

General case:

$$\left.\begin{aligned} X' &= aX + bY \\ Y' &= cX + dY \end{aligned}\right\} \implies \begin{pmatrix} X' \\ Y' \end{pmatrix} = \underbrace{\begin{bmatrix} a & b \\ c & d \end{bmatrix}}_{\text{M}} \begin{pmatrix} X \\ Y \end{pmatrix}$$

How to solve this case?

Decompose system into its eigenvalues and eigenvectors

$$M\mathbf{U} = \lambda_U \mathbf{U}$$

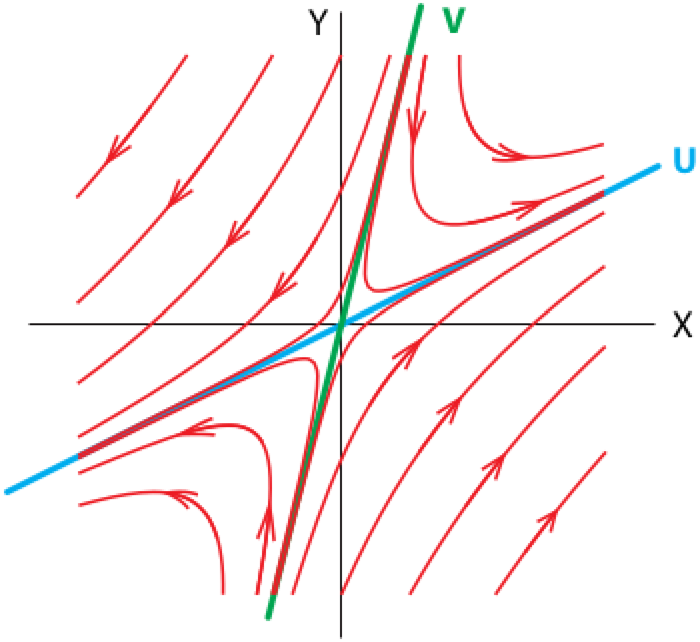
$$M\mathbf{V} = \lambda_V \mathbf{V}$$

If you start at a certain $\mathbf{U}_0$ (length of eigenvector can be chosen)

$$\mathbf{U}' = M\mathbf{U} = \lambda_U \mathbf{U}$$

$$\mathbf{U}(t) = e^{\lambda_U t}\mathbf{U}_0$$

2. Equilibrium points in 2D - determine type linear system



Exercise 3.2.1

2. Equilibrium points in 2D - determine type linear system

General case:

$$\left.\begin{aligned} X' &= \quad X' = aX + bY \\ Y' &= \quad Y' = cX + dY \end{aligned}\right\} \implies \begin{pmatrix} X' \\ Y' \end{pmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{pmatrix} X \\ Y \end{pmatrix}$$

remark: still has (0,0) as equilibrium

What if eigenvalues are complex?

Eigenvalues will be complex conjugates: example

$$\left.\begin{aligned} X' &= V \\ V' &= -X - V \end{aligned}\right\} \implies \begin{pmatrix} X' \\ V' \end{pmatrix} = \begin{bmatrix} 0 & 1 \\ -1 & -1 \end{bmatrix} \begin{pmatrix} X \\ V \end{pmatrix}$$

$$\boldsymbol{M} = \begin{bmatrix} 0 & 1 \\ -1 & -1 \end{bmatrix}$$

$$\Rightarrow \quad \lambda = -\frac{1}{2} \pm \frac{\sqrt{3}}{2}\,\boldsymbol{i} \approx -0.5 \pm 0.866\,\boldsymbol{i}$$

Eigenvectors will also be complex: leading to these solutions

$$\begin{aligned} \mathbf{U}(t) &= e^{(a+bi)t}\mathbf{U_0} \\ &= e^{(a+bi)t}(\mathbf{u_1} + i\mathbf{u_2}) \\ \mathbf{V}(t) &= e^{(a-bi)t}\mathbf{V_0} \\ &= e^{(a-bi)t}(\mathbf{v_1} + i\mathbf{v_2}) \end{aligned}$$

2. Equilibrium points in 2D - determine type linear system

Eigenvectors will also be complex: leading to these solutions

$$\begin{aligned}\mathbf{U}(t) &= e^{(a+bi)t}\mathbf{U_0}\\ &= e^{(a+bi)t}(\mathbf{u_1} + i\mathbf{u_2})\\ \mathbf{V}(t) &= e^{(a-bi)t}\mathbf{V_0}\\ &= e^{(a-bi)t}(\mathbf{v_1} + i\mathbf{v_2})\end{aligned}$$

Theorem. Given a system $\dot{\mathbf{x}} = A\mathbf{x}$, where A is a real matrix. If $\mathbf{x} = \mathbf{x}_1 + i\,\mathbf{x}_2$ is a complex solution, then its real and imaginary parts $\mathbf{x}_1, \mathbf{x}_2$ are also solutions to the system.

Proof. Since $\mathbf{x}_1 + i\,\mathbf{x}_2$ is a solution, we have

$$(\mathbf{x}_1 + i\,\mathbf{x}_2)' = A\,(\mathbf{x}_1 + i\,\mathbf{x}_2) = A\mathbf{x}_1 + i\,A\mathbf{x}_2.$$

Equating real and imaginary parts of this equation,

$$\mathbf{x}_1' = A\mathbf{x}_1\,, \qquad \mathbf{x}_2' = A\mathbf{x}_2\,,$$

which shows exactly that the real vectors $\mathbf{x}_1$ and $\mathbf{x}_2$ are solutions to $\mathbf{x}' = A\mathbf{x}$

We are only interested in the real solutions

2. Equilibrium points in 2D - determine type linear system

Eigenvectors will also be complex: leading to these solutions

$$\begin{aligned}\mathbf{U}(t) &= e^{(a+bi)t}\mathbf{U_0} \\ &= e^{(a+bi)t}(\mathbf{u_1} + i\mathbf{u_2}) \\ \mathbf{V}(t) &= e^{(a-bi)t}\mathbf{V_0} \\ &= e^{(a-bi)t}(\mathbf{v_1} + i\mathbf{v_2})\end{aligned}$$

We are only interested in the real solutions

$$\mathbf{U}(t) = e^{at}(\cos(bt) + i\sin(bt))(\mathbf{u_1} + i\mathbf{u_2})$$

$$\begin{aligned}\mathbf{U}_1(t) &= e^{at}(\mathbf{u}_1\cos(bt) - \mathbf{u}_2\sin(bt)) \\ \mathbf{U}_2(t) &= e^{at}(\mathbf{u}_1\sin(bt) + \mathbf{u}_2\cos(bt))\end{aligned}$$

The general solution is therefore:

$$c_1\mathbf{U}_1(t) + c_2\mathbf{U}_2(t)$$

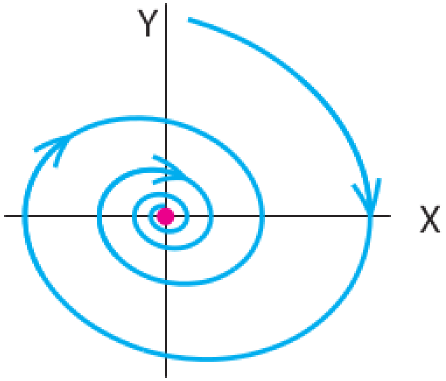
(Same if you start from other eigenvalue)

2. Equilibrium points in 2D - determine type linear system

$$\begin{aligned} \mathbf{U}_1(t) &= e^{at}(\mathbf{u}_1 \cos(bt) - \mathbf{u}_2 \sin(bt)) \\ \mathbf{U}_2(t) &= e^{at}(\mathbf{u}_1 \sin(bt) + \mathbf{u}_2 \cos(bt)) \end{aligned}$$

The general solution is therefore: $c_1\mathbf{U}_1(t) + c_2\mathbf{U}_2(t)$

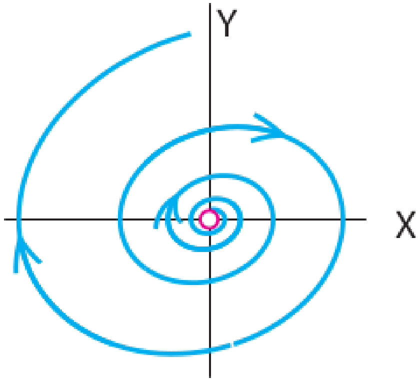
a < 0:



$X' = Y,\ Y' = -X - Y$

stable spiral

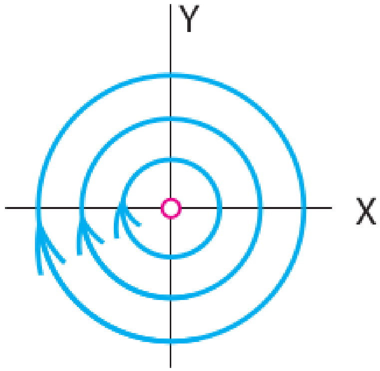
a > 0:



$X' = Y,\ Y' = -X + Y$

unstable spiral

a = 0:



$X' = Y,\ Y' = -X$

center

2. Equilibrium points in 2D - non-linear system

$$X' = f(X,Y)$$
$$Y' = g(X,Y)$$

If $V = (f, g)$, then the matrix

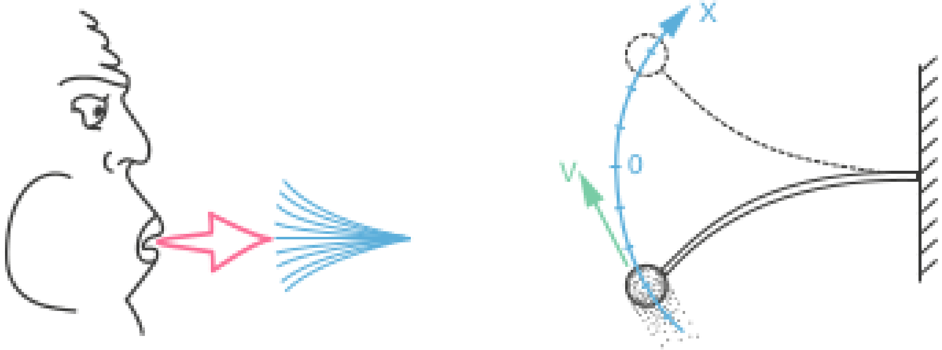
$$\begin{bmatrix} \frac{\partial f}{\partial X} & \frac{\partial f}{\partial Y} \\ \frac{\partial g}{\partial X} & \frac{\partial g}{\partial Y} \end{bmatrix}_{(X_0, Y_0)}$$

represents the linear approximation to V at the point (X_0, Y_0). It is called the Jacobian matrix of V at the point (X_0, Y_0).

The Hartman–Grobman theorem or linearisation theorem is a theorem about the local behaviour of dynamical systems in the neighbourhood of a hyperbolic equilibrium point. It asserts that linearisation -a natural simplification of the system- is effective in predicting qualitative patterns of behaviour.

2. Equilibrium points in 2D - non-linear system

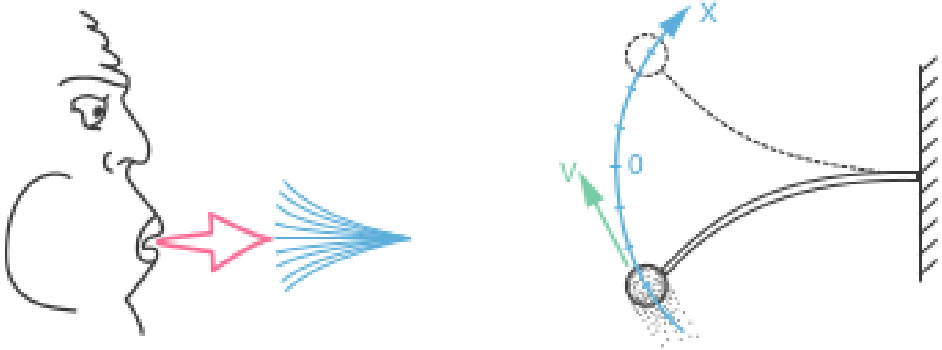
Example: the Rayleigh Oscillator



Rayleigh modeled the reed of the clarinet as a thin, flexible wand attached to a solid object, with a mass on its end. The clarinetist supplies energy to the system by blowing along the long axis of the wand.

2. Equilibrium points in 2D - non-linear system

Example: the Rayleigh Oscillator



If we bend the reed up or down, it will oscillate in a damped manner and eventually return to the equilibrium position.

$$X' = V$$
$$V' = -X - V$$

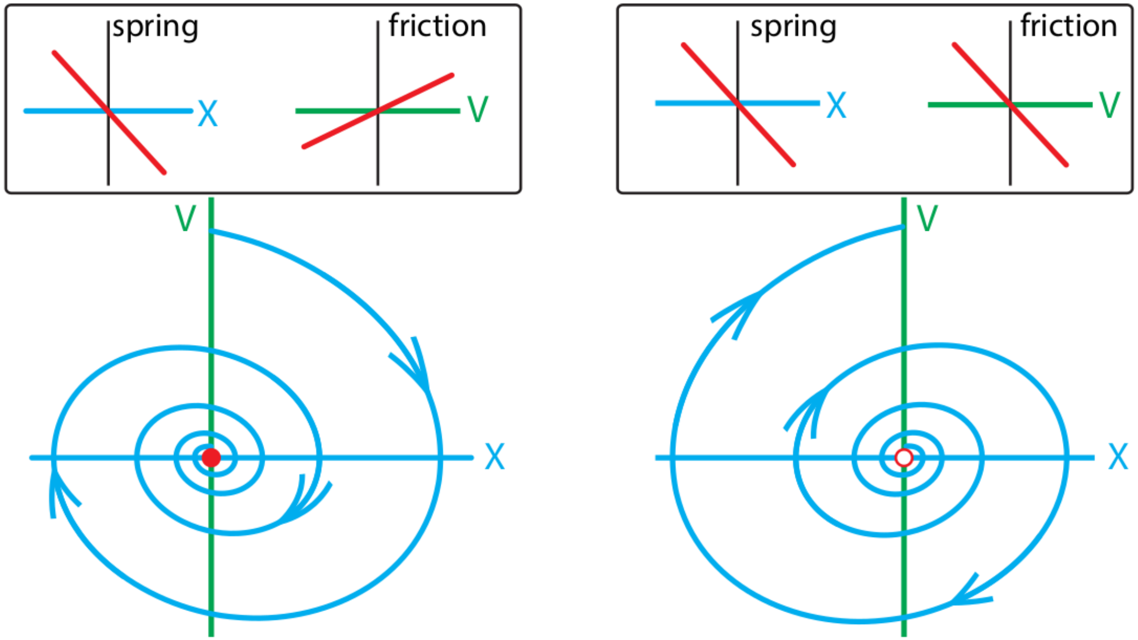
take m = 1

2. Equilibrium points in 2D - non-linear system

Example: the Rayleigh Oscillator

When the clarinetist blows on the reed, the situation is changed!

Blowing supplies energy to the system and therefore acts like the opposite of friction

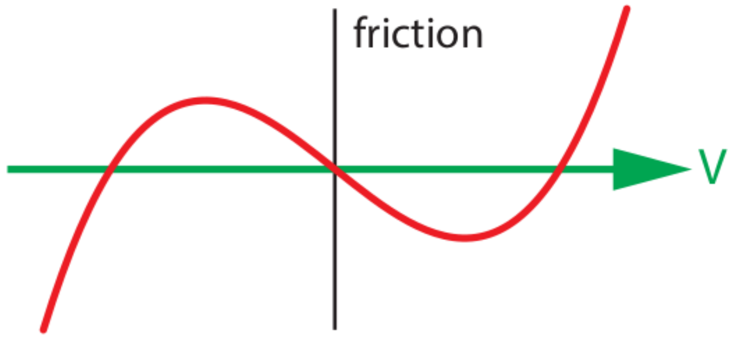


2. Equilibrium points in 2D - non-linear system

Example: the Rayleigh Oscillator

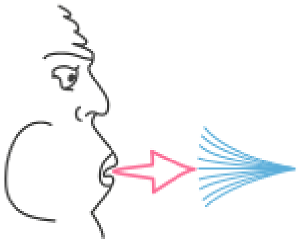
Of course, a trajectory that spirals out forever isn’t realistic.

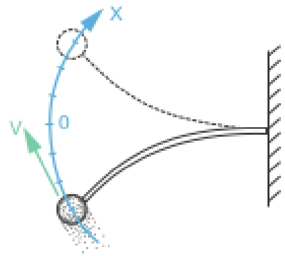
- If the wand is moving slowly (V is small), then blowing on it will actually accelerate it, so the force of the breath is in the same direction as the motion and adds energy to the system.
- But if the velocity of the wand is high, the blowing produces conventional friction (due to air resistance), which retards the motion.

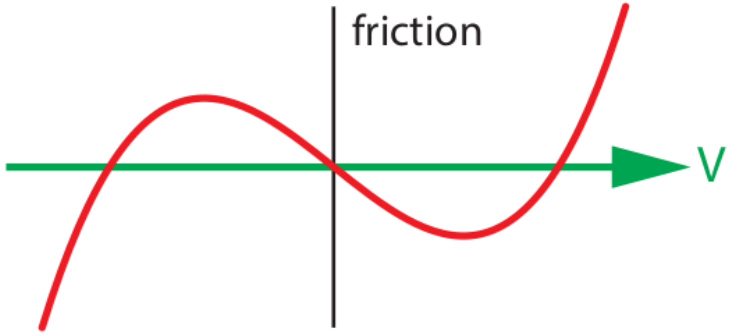


2. Equilibrium points in 2D - non-linear system

Example: the Rayleigh Oscillator







$$X' = V$$

$$V' = -X - (V^3 - V)$$

Exercise 3.2.1

2. Equilibrium points in 2D - non-linear system

When linearization fails

1. None of the eigenvalues of the linearized system can be zero!

$$\begin{aligned} X' &= X - 2Y \\ Y' &= 3X - 6Y \end{aligned} \quad \Rightarrow \quad \boldsymbol{M} = \begin{bmatrix} 1 & -2 \\ 3 & -6 \end{bmatrix} \quad \Rightarrow \quad \lambda^2 + 5\lambda = 0$$

$$\Rightarrow \quad \lambda_1 = 0, \lambda_2 = -5$$

2. Equilibrium points in 2D - non-linear system

When linearization fails

1. None of the eigenvalues of the linearized system can be zero!

$$X' = X - 2Y$$
$$Y' = 3X - 6Y$$

$\rightarrow$ $\lambda_1 = 0, \lambda_2 = -5$ $\boxed{\lambda_1 = 0}$

$$\boldsymbol{M}\mathbf{U} = \lambda_1 \mathbf{U}$$

$$\boldsymbol{M}\mathbf{U} = \begin{bmatrix} 1 & -2 \\ 3 & -6 \end{bmatrix} \begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} X - 2Y \\ 3X - 6Y \end{pmatrix} = \lambda_1 \mathbf{U} = 0 \begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$\begin{cases} X - 2Y = 0 & \Longrightarrow \quad Y = 0.5X \\ 3X - 6Y = 0 & \Longrightarrow \quad Y = 0.5X \end{cases}$$

eigenvector (X, Y) = (2, 1)

2. Equilibrium points in 2D - non-linear system

When linearization fails

1. None of the eigenvalues of the linearized system can be zero!

$$X' = X - 2Y \qquad Y' = 3X - 6Y \quad \Rightarrow \quad \lambda_1 = 0, \lambda_2 = -5 \qquad \boxed{\lambda_2 = -5}$$

$$\boldsymbol{MV} = \lambda_2 \mathbf{V}$$

$$\boldsymbol{MV} = \begin{bmatrix} 1 & -2 \\ 3 & -6 \end{bmatrix} \begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} X - 2Y \\ 3X - 6Y \end{pmatrix} = \lambda_2 \mathbf{V} = -5 \begin{pmatrix} X \\ Y \end{pmatrix} = \begin{pmatrix} -5X \\ -5Y \end{pmatrix}$$

$$\begin{cases} X - 2Y = -5X & \Longrightarrow \quad Y = 3X \\ 3X - 6Y = -5Y & \Longrightarrow \quad Y = 3X \end{cases}$$

eigenvector (X, Y) = (1, 3)

2. Equilibrium points in 2D - non-linear system

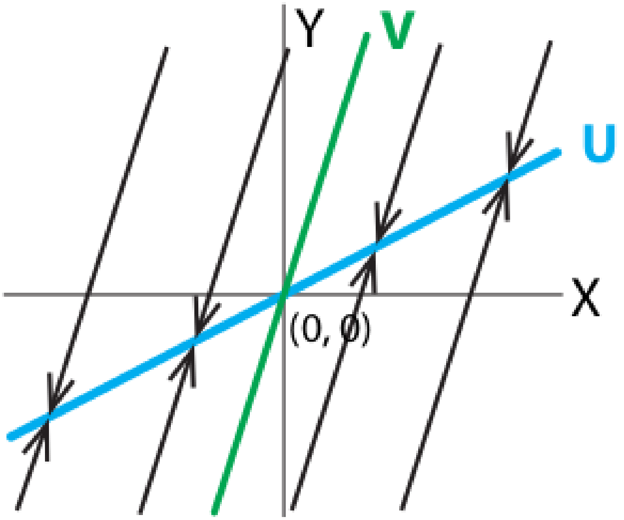
When linearization fails

1. None of the eigenvalues of the linearized system can be zero!

$$X' = X - 2Y$$
$$Y' = 3X - 6Y$$

$\lambda_1 = 0$, eigenvector (X, Y) = (2, 1) = U

$\lambda_2 = -5$ eigenvector (X, Y) = (1, 3) = V



A system like this is not robust!

2. Equilibrium points in 2D - non-linear system

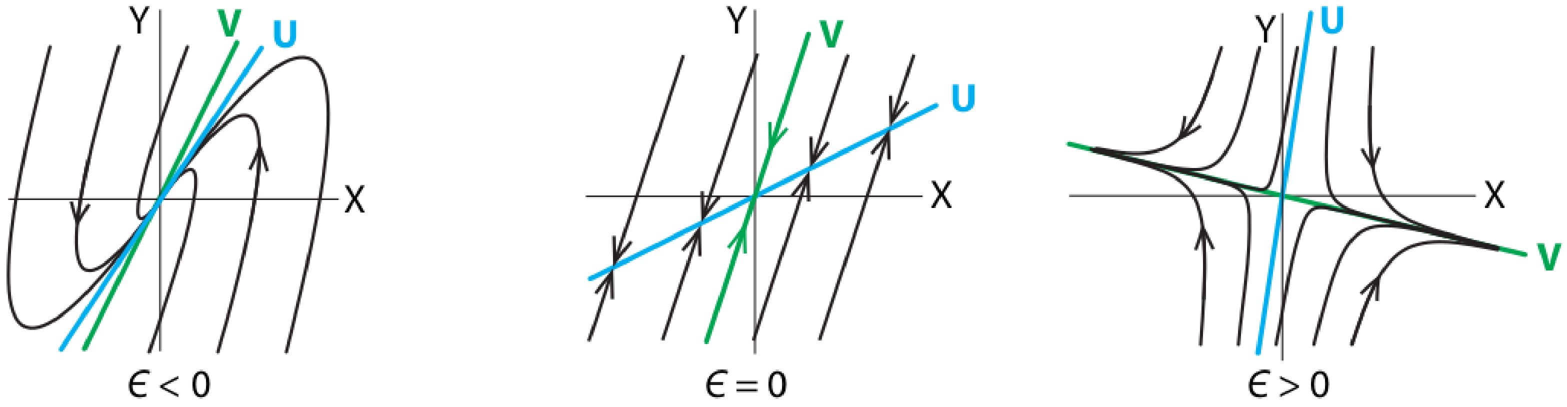
When linearization fails

1. None of the eigenvalues of the linearized system can be zero!

$$X' = X - 2Y$$
$$Y' = 3X - 6Y$$

add tiny factor

$$X' = X - 2Y$$
$$Y' = (3 - \epsilon)X - 6Y$$

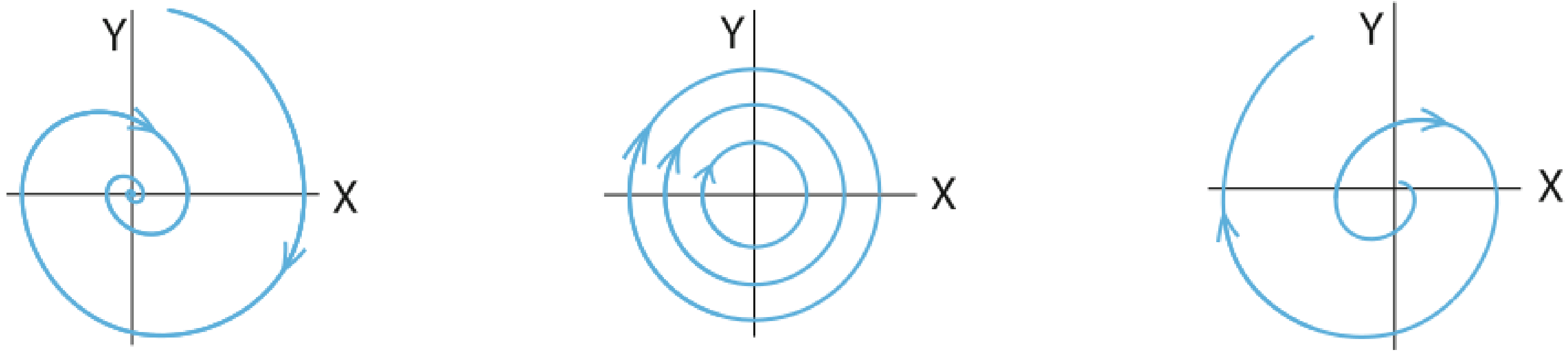


2. Equilibrium points in 2D - non-linear system

When linearization fails

2. Purely imaginary eigenvalues

$$\lambda = \pm k\boldsymbol{i}$$



center

Similar as before: a center will become a stable spiral or unstable spiral

3. Equilibrium points in N dim

3. Equilibrium points in N dimensions

$$\begin{bmatrix} \frac{\partial f_1}{\partial X_1} & \frac{\partial f_1}{\partial X_2} & \cdots & \frac{\partial f_1}{\partial X_n} \\ \frac{\partial f_2}{\partial X_1} & \frac{\partial f_2}{\partial X_2} & \cdots & \frac{\partial f_2}{\partial X_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial X_1} & \frac{\partial f_n}{\partial X_2}, & \ldots, & \frac{\partial f_n}{\partial X_n} \end{bmatrix}_{(X_1, X_2, \ldots, X_n)_0}$$

where $f_1, f_2, \ldots, f_n$ are the n component functions of the vector field V, each of which is a function $\mathbb{R}^n \to \mathbb{R}$.

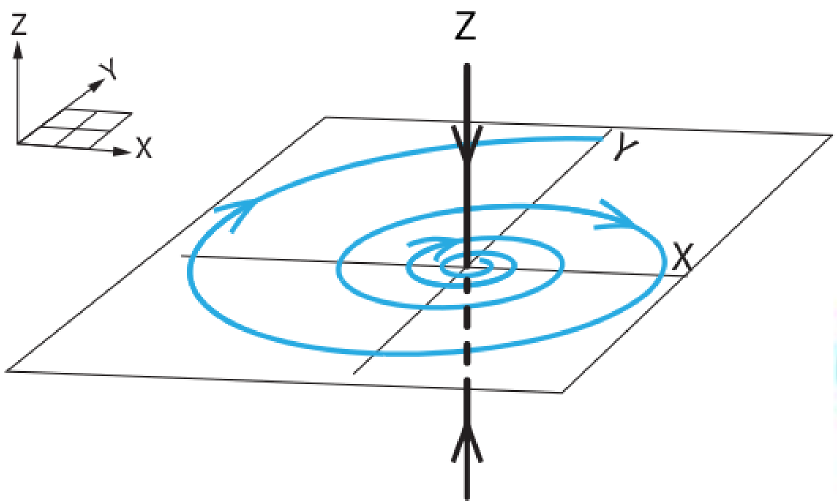
eigenvalues: $\left| \boldsymbol{D} - \lambda \mathbb{I} \right| = 0$

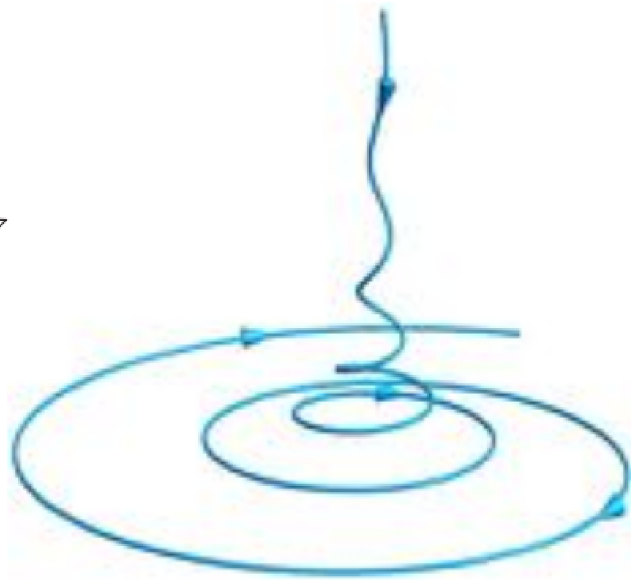
- stable equilibrium point ($\lambda < 0$) (1D subspace) or
- unstable equilibrium point ($\lambda > 0$) (1D subspace) or
- stable spiral ($\lambda = -a \pm b\boldsymbol{i}$) (2D subspace) or
- unstable spiral ($\lambda = +a \pm b\boldsymbol{i}$) (2D subspace).

3. Equilibrium points in N dimensions

Example:

- unstable spiral in X and Y
- a stable node in Z
- => 3D unstable equilibrium point





4. Method with nullclines

4. Method with nullclines

Example: competition between moose and deer

- Deer = D, Moose = M
- No environmental limitations: deer population would grow at a per capita rate 3, moose at 2
- Each animal competes for resources within its own species: -D^2 for deer; -M^2 for moose
- Deer compete with moose: impact for deer is 1
- Moose compete with deer: impact for moose is 0.5

$$D' = 3D - MD - D^2$$
$$M' = 2M - 0.5MD - M^2$$

4. Method with nullclines

Example: competition between moose and deer

$$D' = 3D - MD - D^2$$
$$M' = 2M - 0.5MD - M^2$$

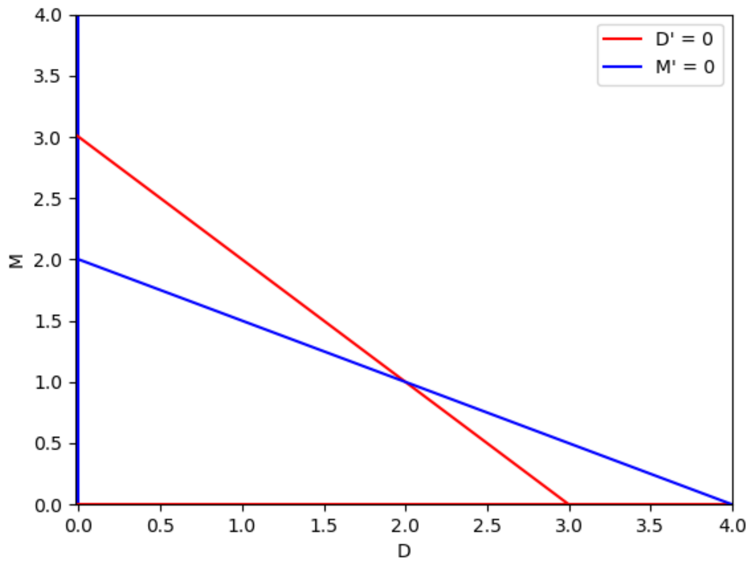
What are the equilibrium points?

Set D' = 0; M' = 0: (D*, M*) = (0, 0); (0, 2); (3, 0); (2, 1)

Easy way to find them: nullclines

D' = 0: D = 0 and M = 3 - D

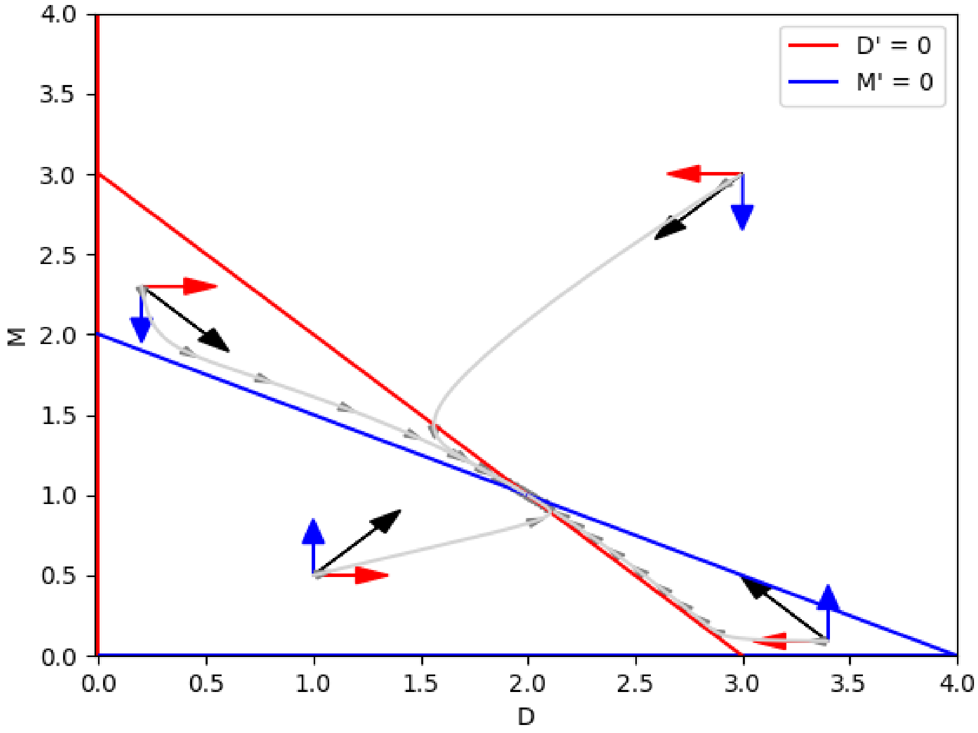
M' = 0: M = 0 and M = 2 - D/2



4. Method with nullclines

Example: competition between moose and deer

4 sections

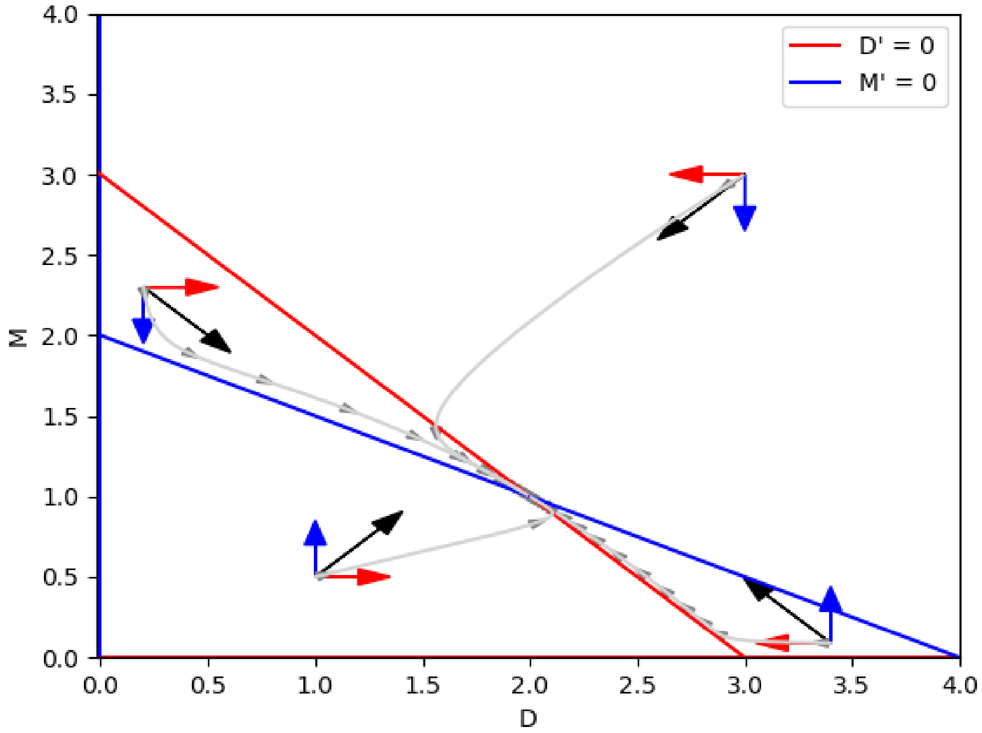


Equilibrium is stable!

4. Method with nullclines

Example: competition between moose and deer

4 sections

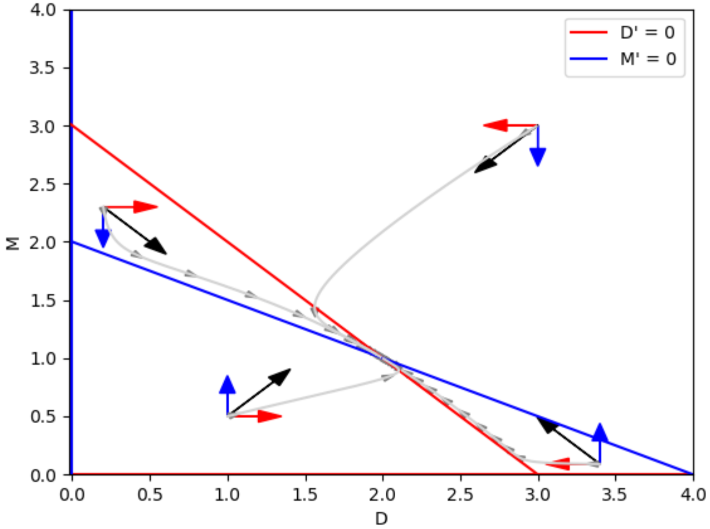


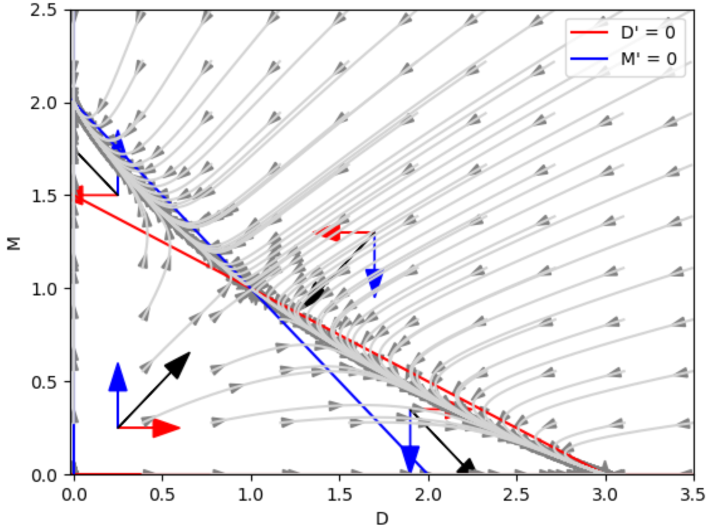
Equilibrium is stable!

4. Method with nullclines

$$D' = 3D - MD - D^2$$
$$M' = 2M - 0.5MD - M^2$$

$$D' = 3D - 2MD - D^2$$
$$M' = 2M - DM - M^2$$





4. Method with nullclines

Why bother with nullclines?

In case we do not know the exact parameters, we cannot simulate

$$D' = D(r_D - k_D M - c_D D)$$
$$M' = M(r_M - k_M D - c_M M)$$

$$D' = D(r_D - k_D M - c_D D) = 0$$

$$D = 0 \quad \text{or} \quad M = -\frac{c_D}{k_D} D + \frac{r_D}{k_D}$$

This is a vertical line and a line from (0, rD/kD) to (rD/cD, 0)

In this way, plotting nullclines can allow us to sketch an approximate vector field and get a sense of the system's dynamics without having numerical parameter values

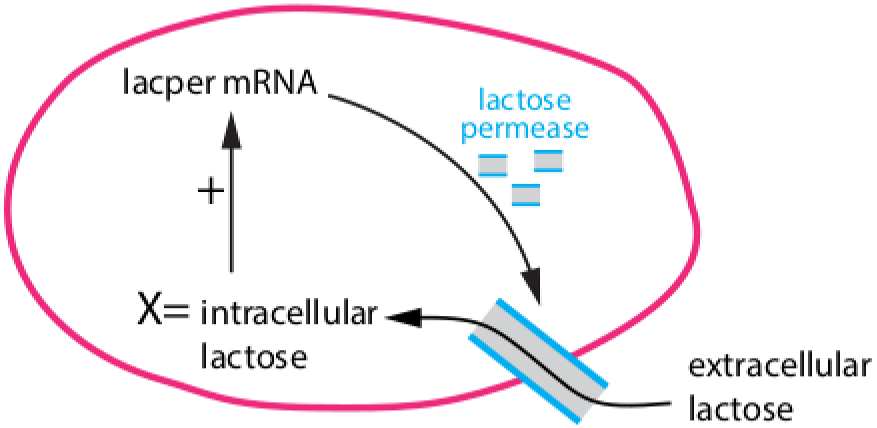
4. Method with nullclines - switch

E. Coli

- E. coli can use **extracellular lactose** for energy,
- In order to import extracellular lactose into the cell, cell needs a transport protein → **lactose permease**, to transport the extracellular lactose across the cell boundary.
- Making lactose permease costs a lot of resources. Only advantageous for cell to make this protein in large amounts only when lactose concentrations are high.
- In that case, it wants to “switch on” lactose permease production

4. Method with nullclines - switch

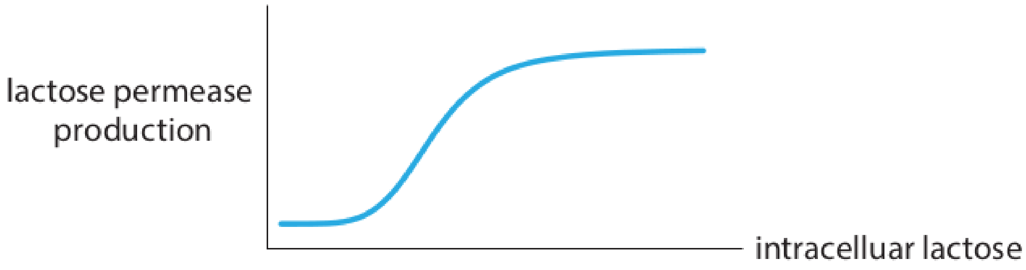
X = concentration internal lactose



X' = lactose import − lactose metabolism

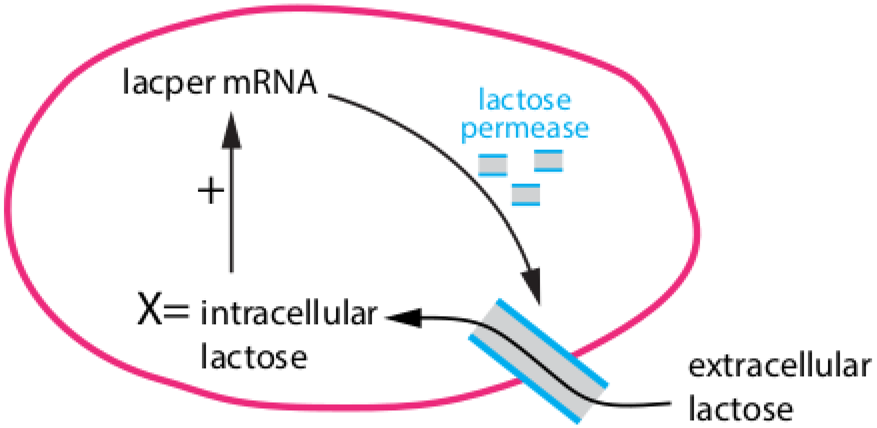
kX

$$\text{lactose import rate} = \text{amount of lactose permease} = f(X) = \frac{a + X^2}{1 + X^2}$$



4. Method with nullclines - switch

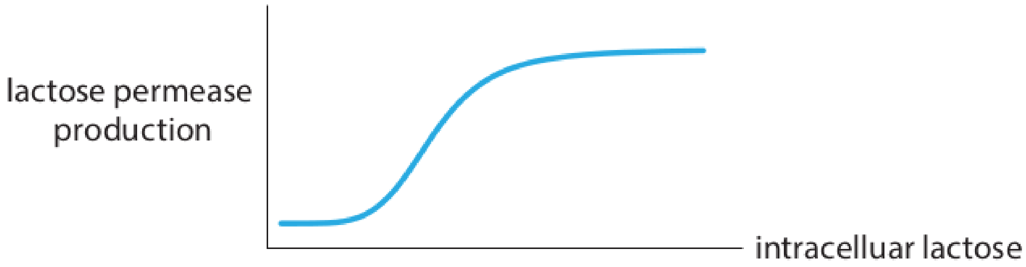
X = concentration internal lactose



X' = lactose import − lactose metabolism

kX

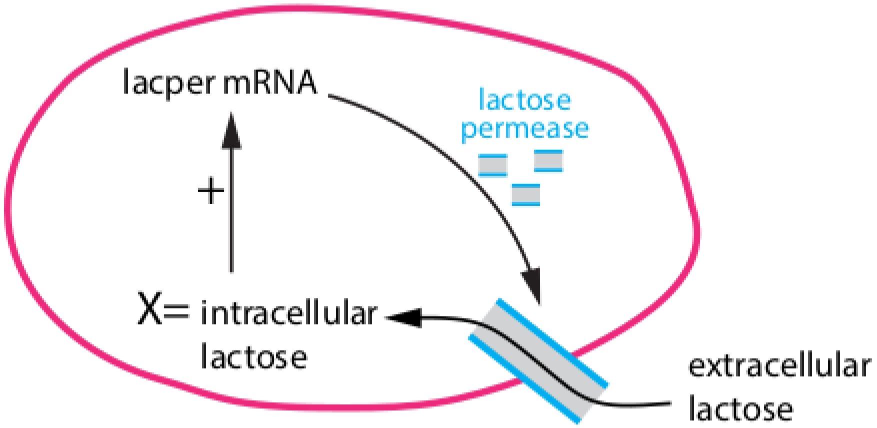
$$\text{lactose import rate} = \text{amount of lactose permease} = f(X) = \frac{a + X^2}{1 + X^2}$$



sigmoid

4. Method with nullclines - switch

X = concentration internal lactose

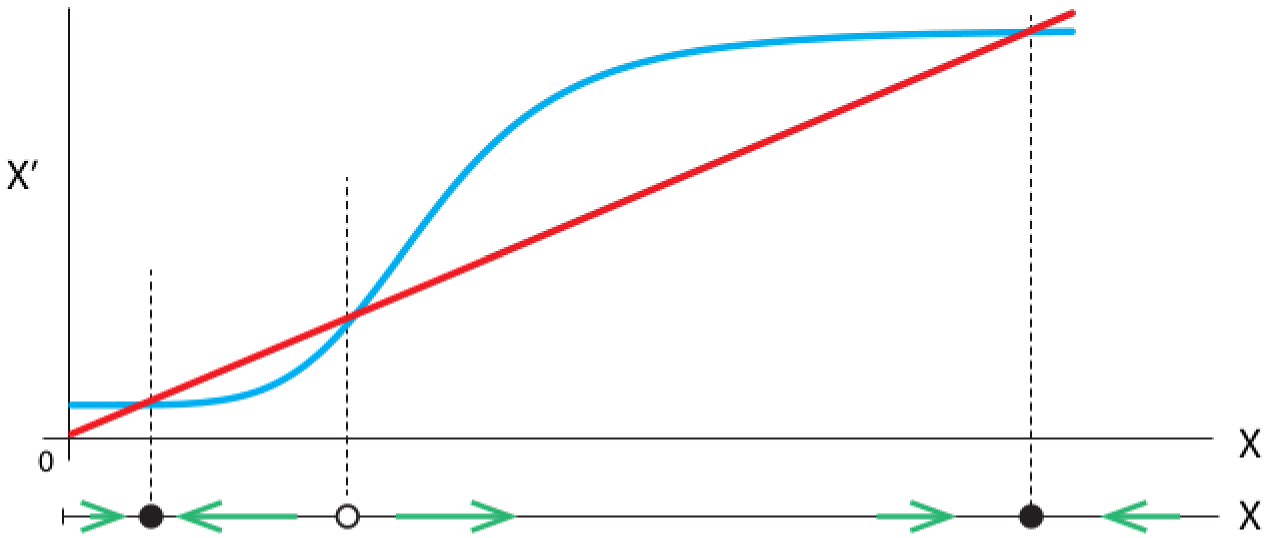


X' = lactose import − lactose metabolism

$$\underbrace{X'}_{\text{change in lactose}} = \underbrace{\frac{a + X^2}{1 + X^2}}_{\text{lactose import}} - \underbrace{0.4X}_{\text{lactose metabolic degradation}}$$

4. Method with nullclines - switch

$$\underbrace{X'}_{\text{change in lactose}} = \underbrace{\frac{a + X^2}{1 + X^2}}_{\text{lactose import}} - \underbrace{0.4X}_{\text{lactose metabolic degradation}}$$



depending on starting concentrations: switch

4. Method with nullclines - switch

The Collins Genetic Toggle Switch

- Phage lambda = virus → infects the bacterium E. coli
- It faces an uncertain environment:
  1. In a healthy cell: virus → into the genome of E. Coli → passed the progeny (nakomelingen) = **lysogenic growth** = default mode.
  2. Sick or damaged cell: virus → **lytic growth** = virus uses host to produce hundreds of copies of the virus → cell bursts
- How does the viral cell sense unhealthy host → **lytic growth**?
- Two genes in virus:
  repressor: produces protein **R**
  control of repressor: produces protein **C**
- R and C form feedback loops that inhibit their own production as well as that of the other.

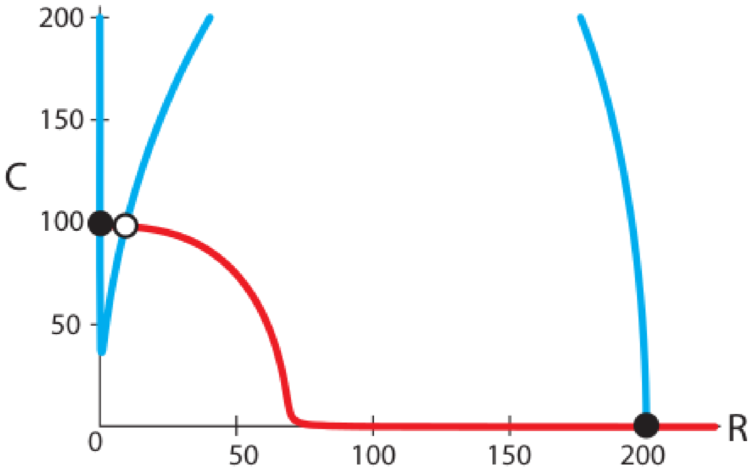
4. Method with nullclines - switch

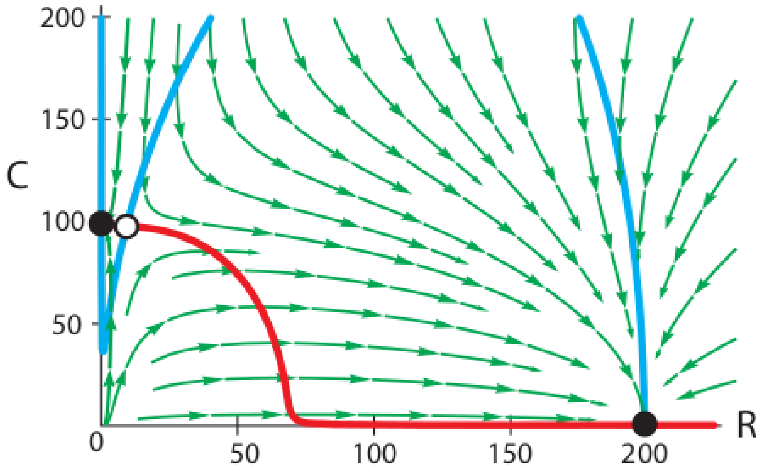
The Collins Genetic Toggle Switch

$$R' = F_R - d_R \cdot R$$
$$C' = F_C - d_C \cdot C$$

$$F_R = \frac{a + 10 \cdot a \cdot k_1 \cdot (\frac{R}{2})^2}{1 + k_1 \cdot (\frac{R}{2})^2 + k_1 \cdot k_2 \cdot (\frac{R}{2})^3 + k_3 \cdot \frac{C}{2} + k_4 \cdot k_3 \cdot (\frac{C}{2})^2}$$

$$F_C = \frac{b + b \cdot k_3 \cdot \frac{C}{2}}{1 + k_1 \cdot (\frac{R}{2})^2 + k_2 \cdot k_1 \cdot (\frac{R}{2})^3 + k_3 \cdot \frac{C}{2} + k_4 \cdot k_3 \cdot (\frac{C}{2})^2}$$





4. Method with nullclines - switch

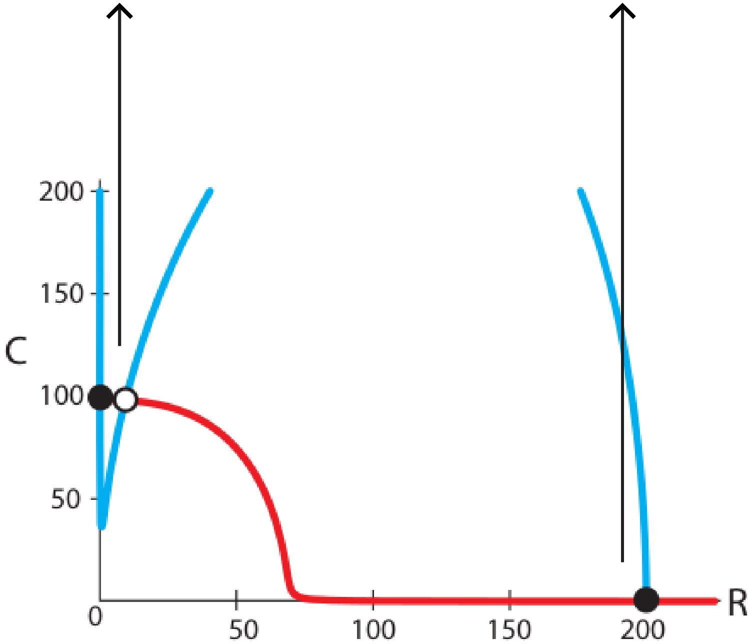
The Collins Genetic Toggle Switch

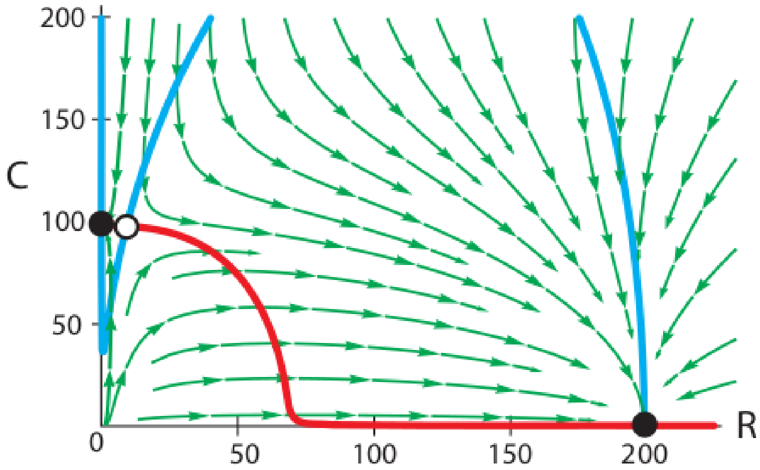
$$R' = F_R - d_R \cdot R$$
$$C' = F_C - d_C \cdot C$$

d_r = 0.02

lytic state

lysogenic state (default)



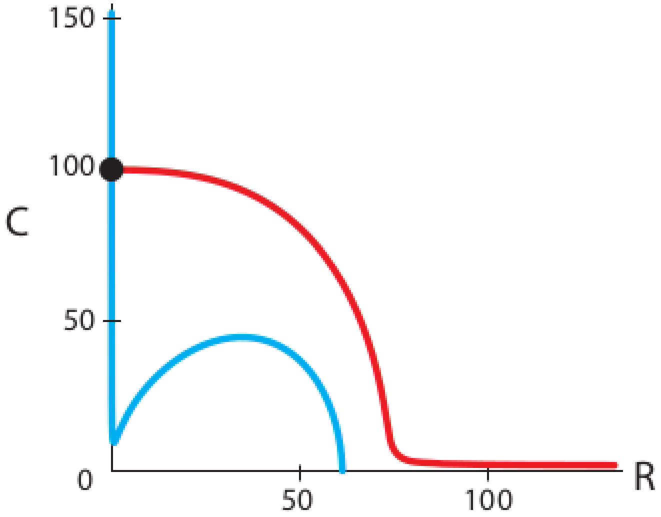


4. Method with nullclines - switch

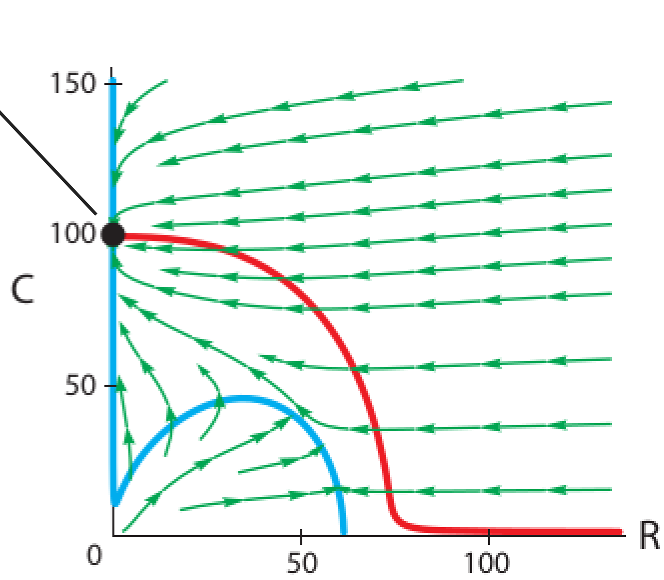
The Collins Genetic Toggle Switch

$$R' = F_R - d_R \cdot R$$
$$C' = F_C - d_C \cdot C$$

d_r = 0.2 when the cell is damaged



lytic state



4. Method with nullclines - switch

The Collins Genetic Toggle Switch

In 2000, a group at Boston University led by James Collins using genetic engineering techniques in the bacterium E. coli to construct two genes that neatly repressed each other:

$$R' = \frac{k}{1 + C^4} - R$$

$$C' = \frac{k}{1 + R^4} - C \qquad \text{where } k = 5$$

Exercise: investigate this model! Bi-stable behavior!

Exercise 3.2.2

4. Method with nullclines - switch

The concept of a switch plays in important role in many biologically processes:

- Hormone or enzyme production is “switched on” by regulatory mechanisms when certain signals pass “threshold” values
- Cells in development pass the switch point, after which they are irreversibly committed to developing into a particular type of cell (say, a neuron or a muscle cell). This is of critical importance in both embryonic development and in the day-to-day replacement of cells
- In neurons and cardiac cells, the voltage V is stable unless a stimulus causes V to pass a “threshold,” which switches on the action potential