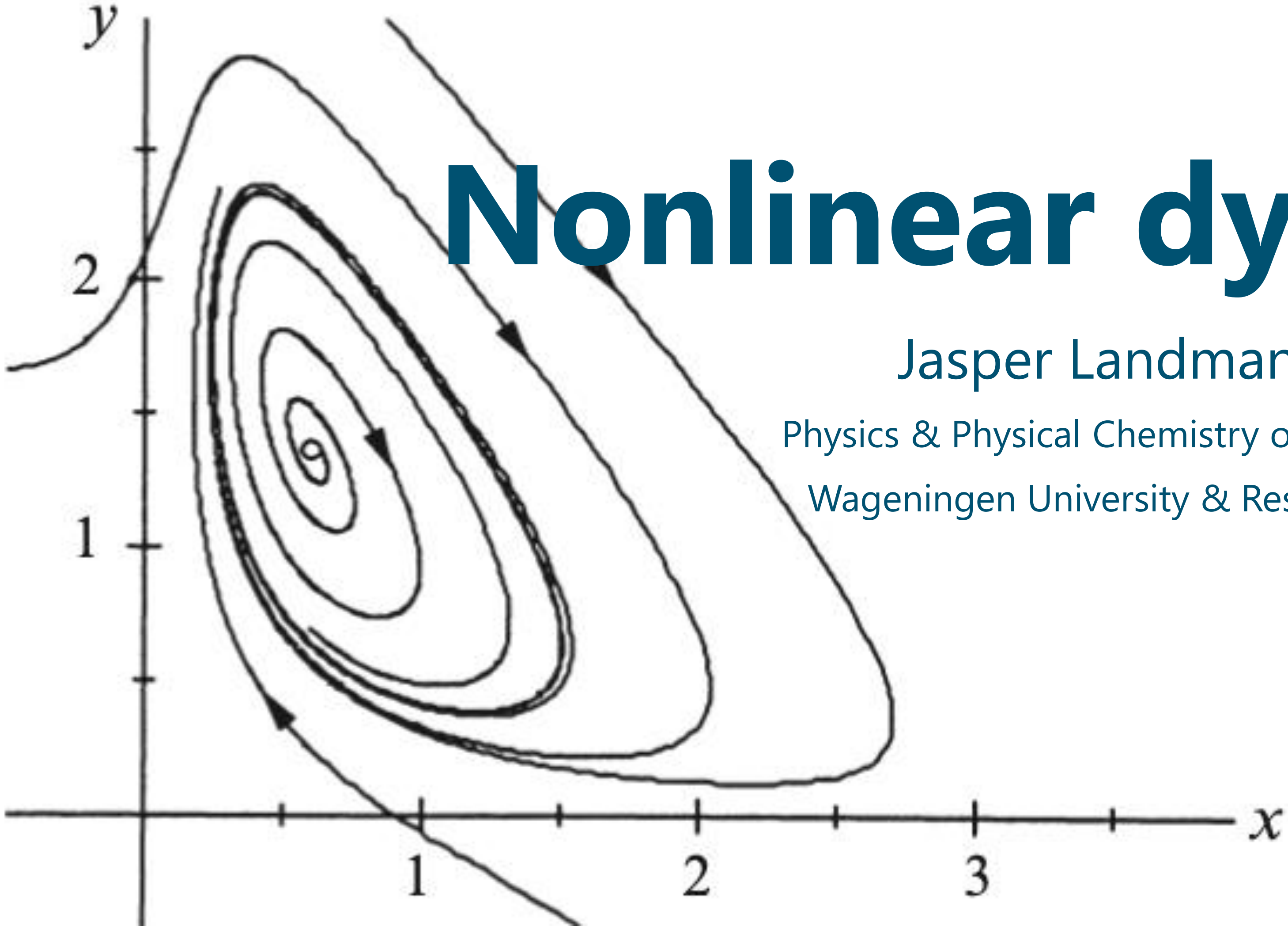
Nonlinear dynamics

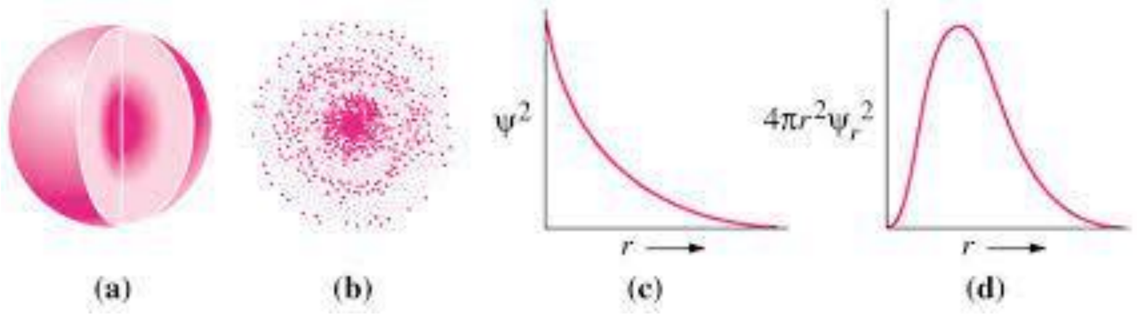


Jasper Landman

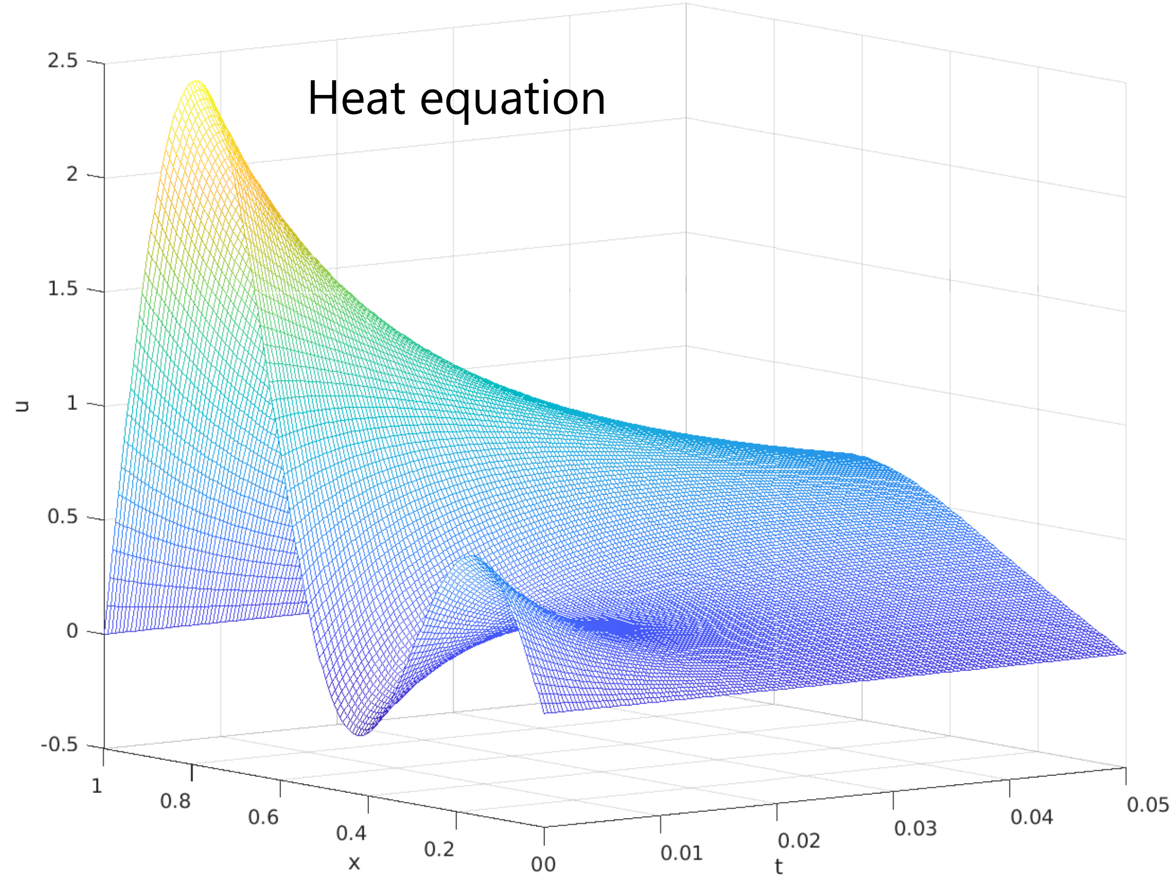
Physics & Physical Chemistry of Foods

Wageningen University & Research

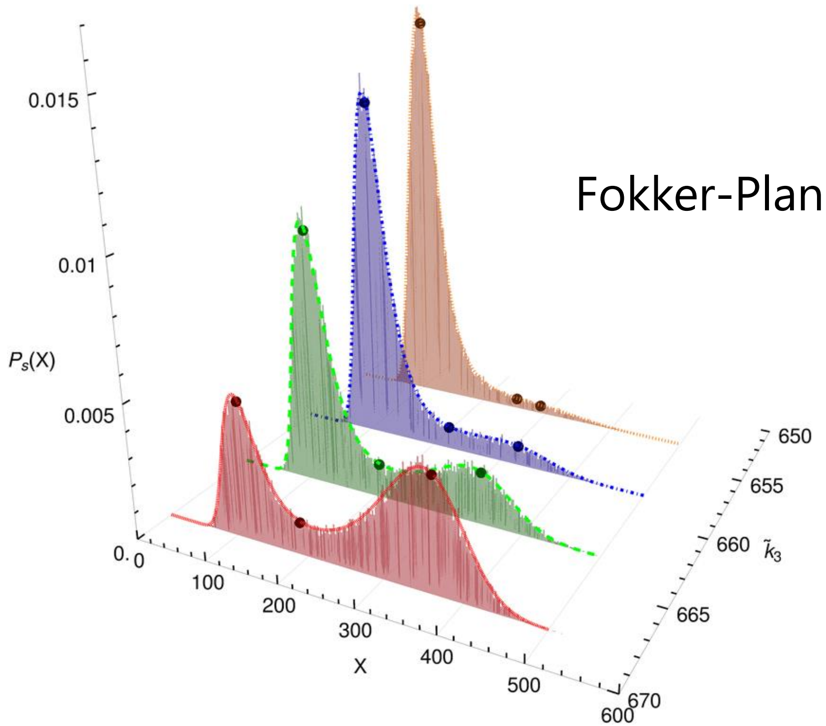
Differential equations



Schrödinger equation



Heat equation



Fokker-Planck equation

Differential equations

Often, the question is not:

“What happens to the system in these very specific conditions?”

but

“At which conditions does the behaviour of the system change qualitatively?”

Nonlinear dynamics – the programme

Today

- Building intuition — A geometric approach to 1D ODEs
- Stationary points
- Linear stability analysis — (for 1D systems)
- Bifurcations
- 2D linear systems

Tomorrow

- 2D nonlinear systems — Linear stability analysis revisited
- Limit cycles and oscillations
- Delay Differential Equations
- Stochastic Differential Equations

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A geometric approach

When $\dot{x} > 0$ then $x(t)$ increases.
And vice versa.

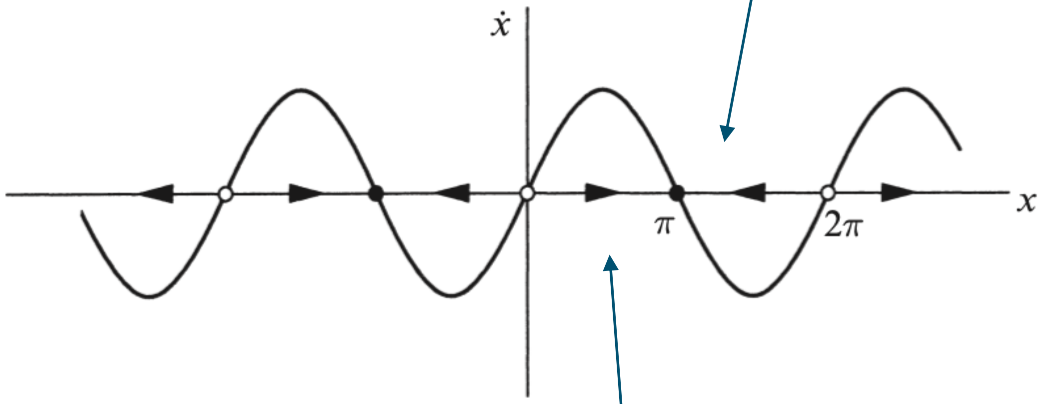
Take the equation $\dot{x} = \sin x$

What do its solutions look like?

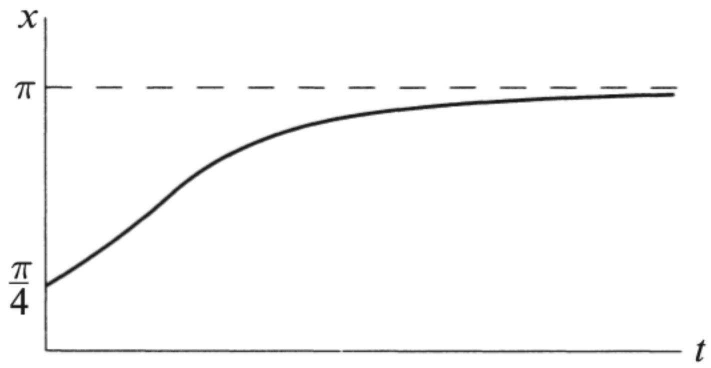
Suppose $x_0 = \pi/4$, what happens to $x(t)$ as $t \to \infty$?

What about an arbitrary initial condition x_0?

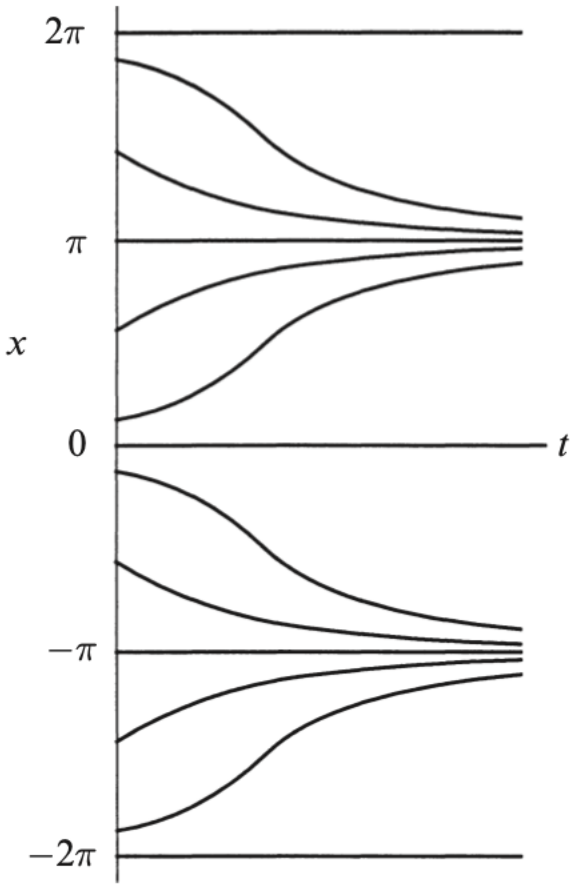
If x_0 is here, solutions move downward towards π



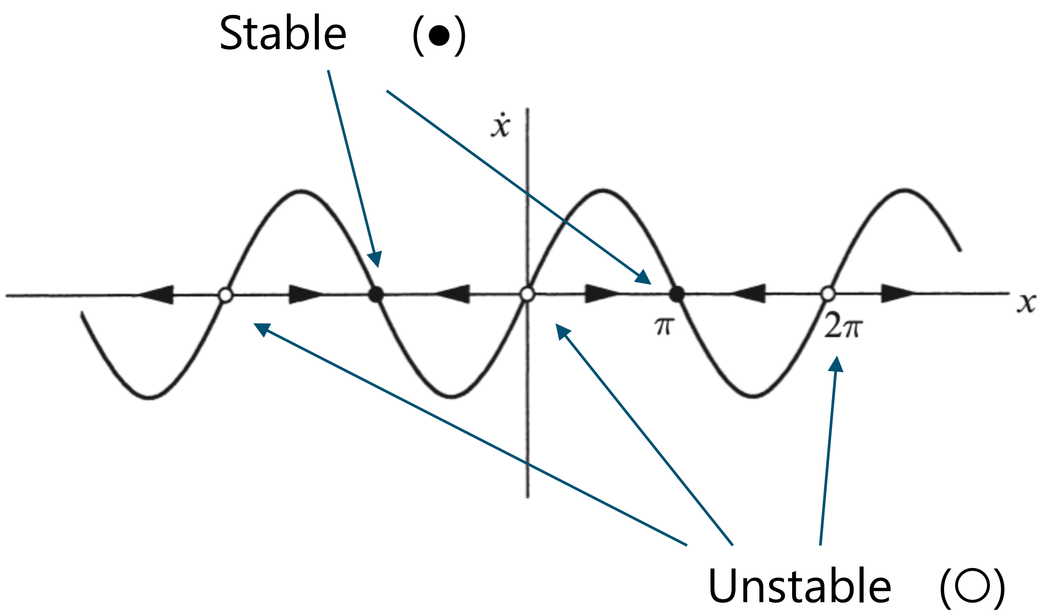
If x_0 is here, solutions move upward towards π



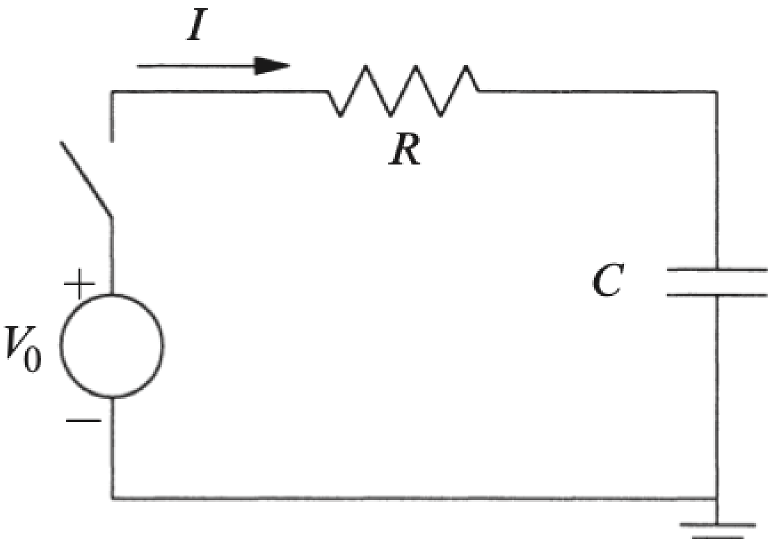
A geometric approach

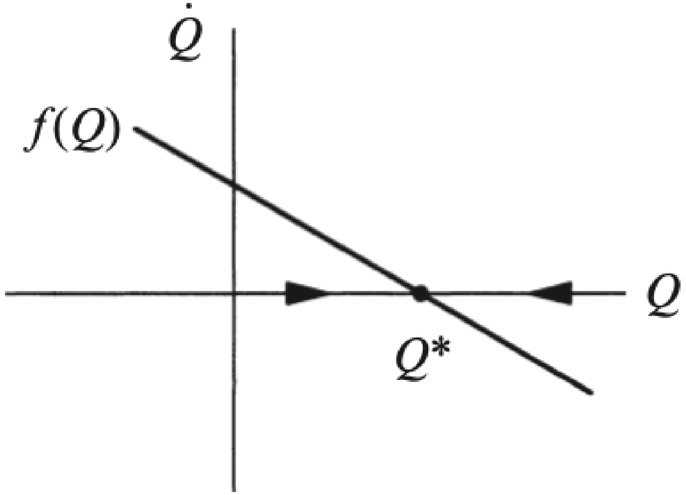


Stationary points



Worked example – RC Circuits





At time $t = 0$ the switch is closed, with no charge on the capacitor initially. Sketch the graph of the charge on the capacitor $Q(t)$.

Total voltage drop around the circuit most equal zero:

$$-V_0 + RI + \frac{Q}{C} = 0$$

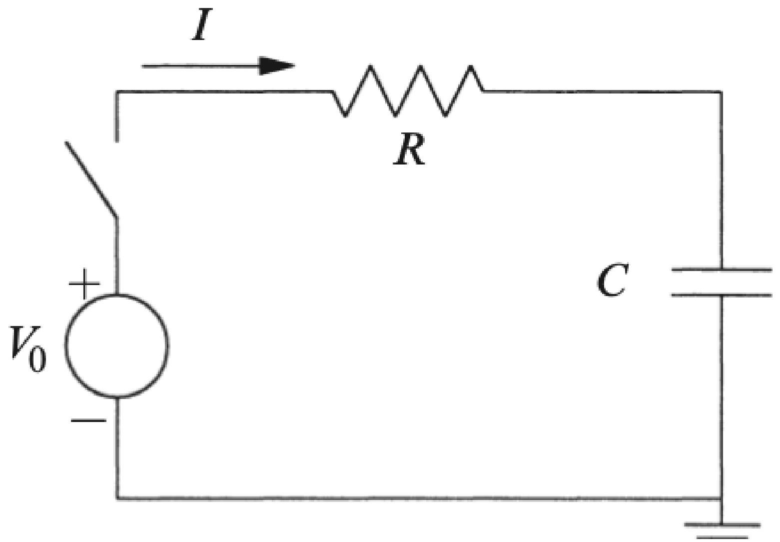
Here, I is the current flowing through the resistor causing the charge to accumulate with a rate $\dot{Q} = I$.

So,

$$\dot{Q} = \frac{V_0}{R} - \frac{Q}{RC}$$

Q^* is a stable point

Worked example – RC Circuits



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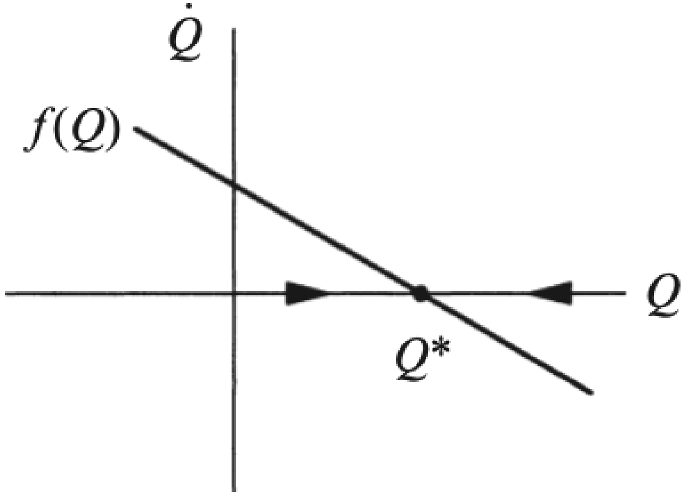
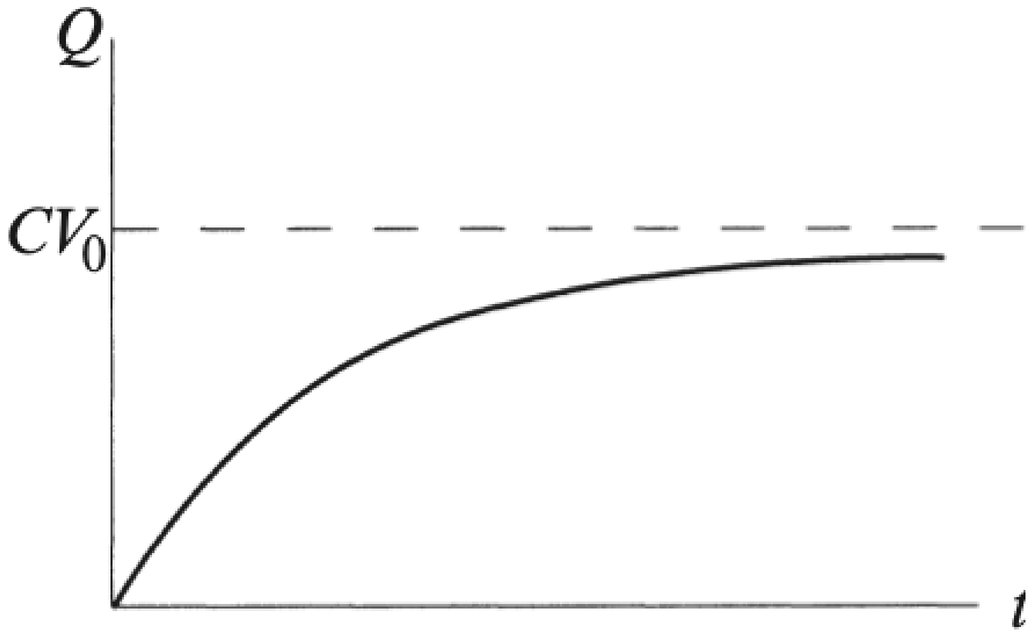
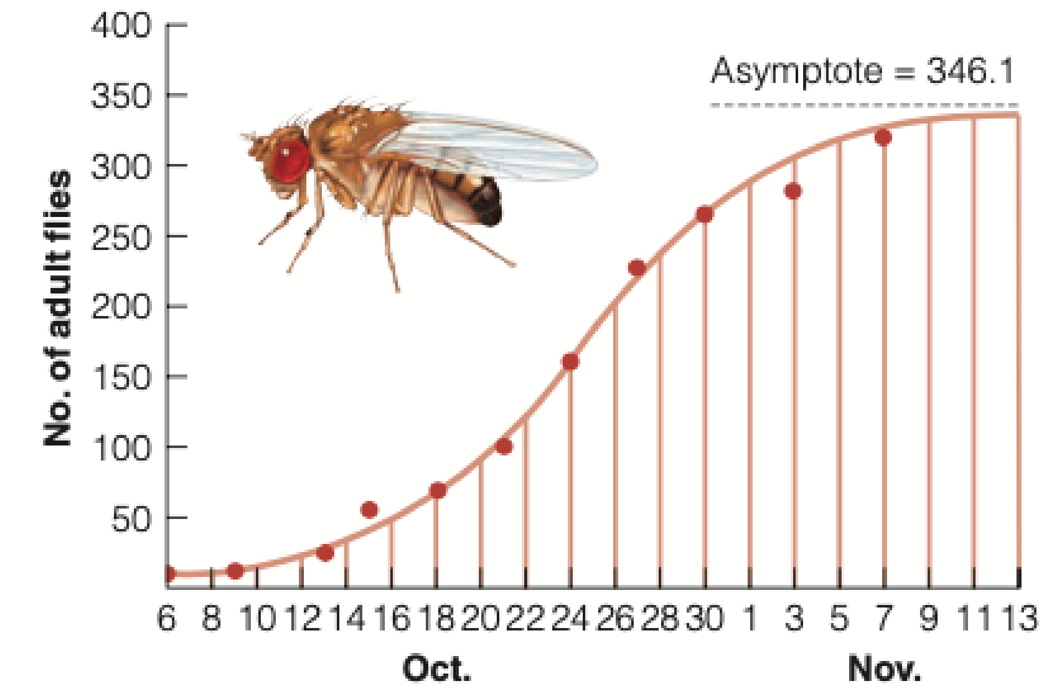
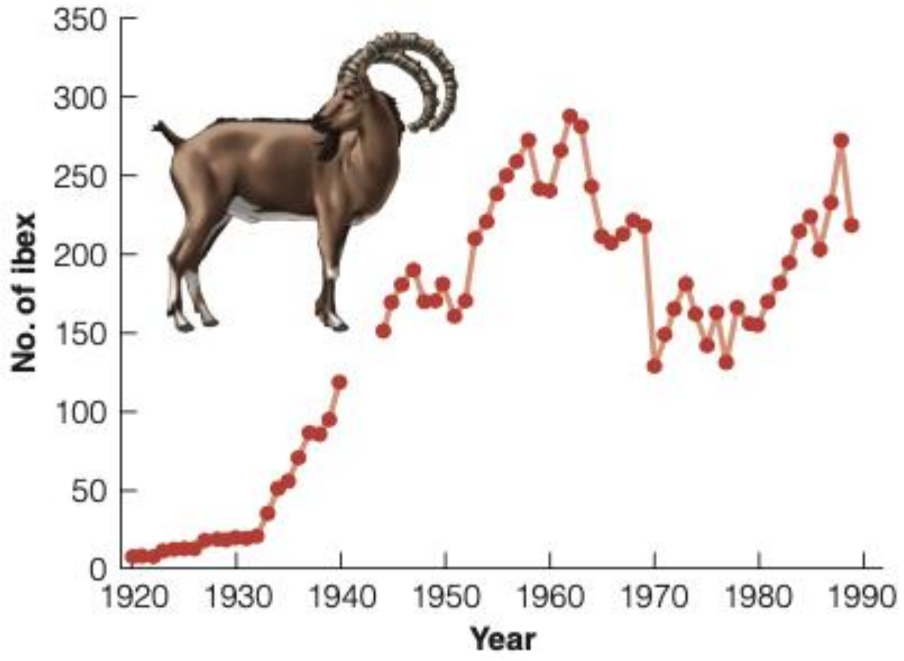




Worked example – Logistic growth





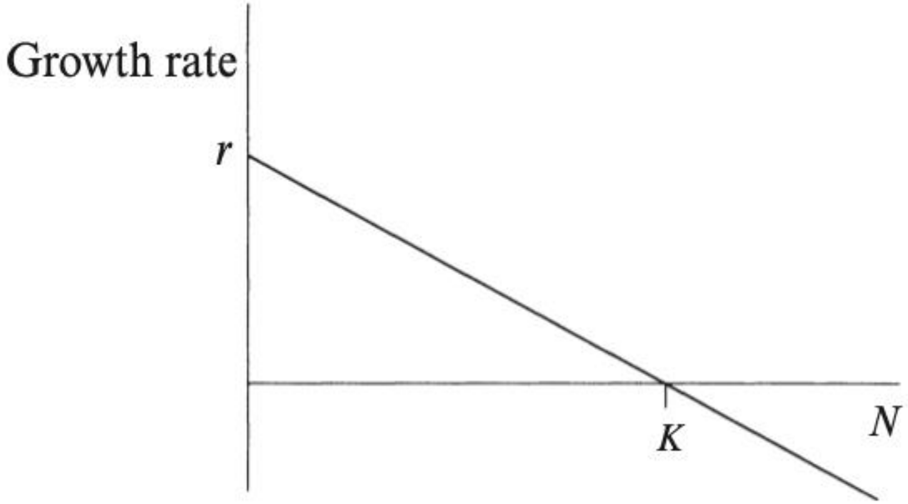
CJ Krebs, Ecology: the experimental analysis of distribution and abundance. 2014

Worked example – Logistic growth

Assumption: at low population, growth rate is linear with population: $\dot{N} = rN$

However, the ecology determines a carrying capacity K above which the growth rate becomes negative.

Simplest case: linear relationship between growth rate and population.



This leads to the **logistic equation**

$$\dot{N} = rN\left(1 - \frac{N}{K}\right)$$

Worked example – Logistic growth

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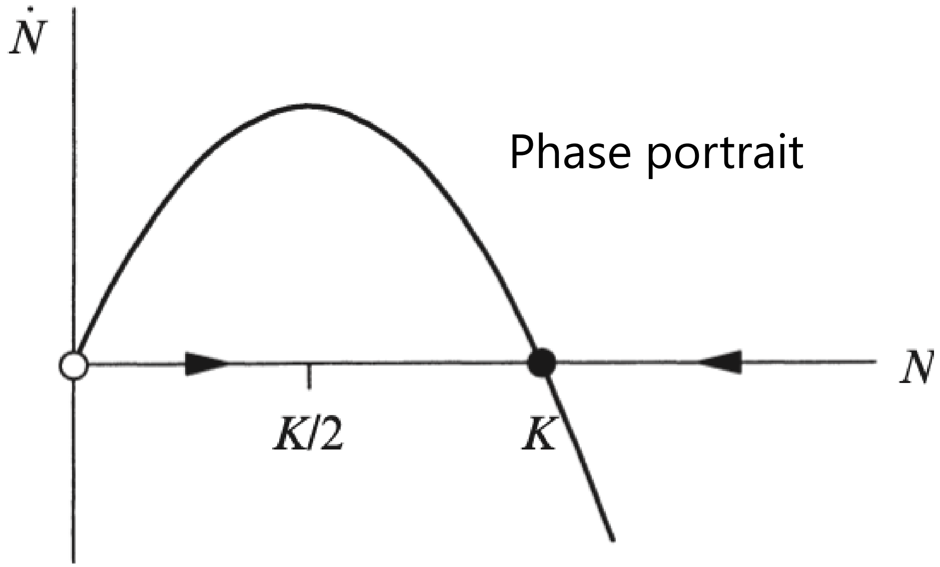
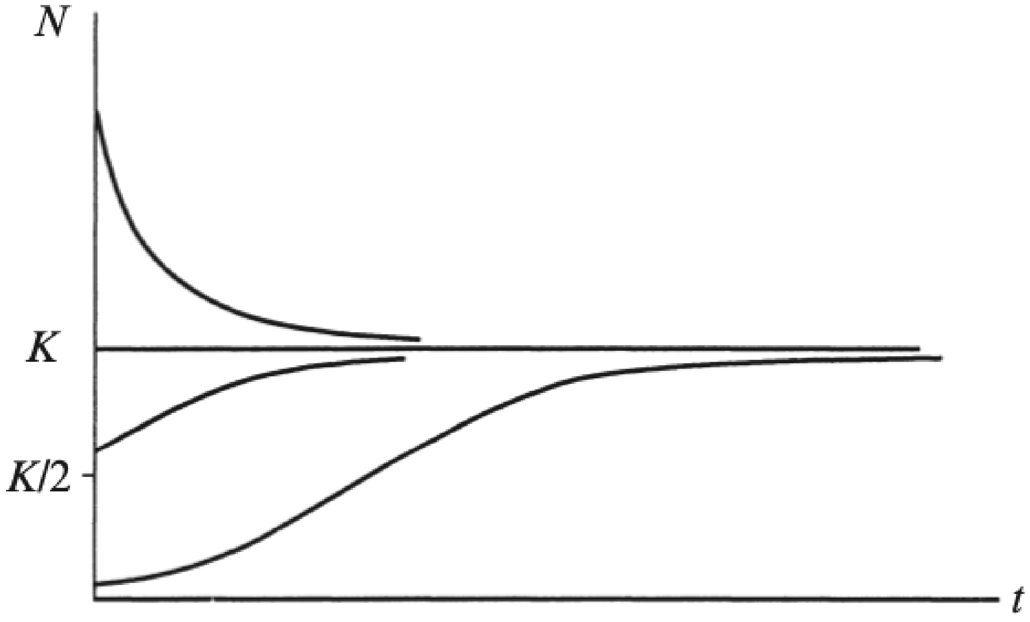
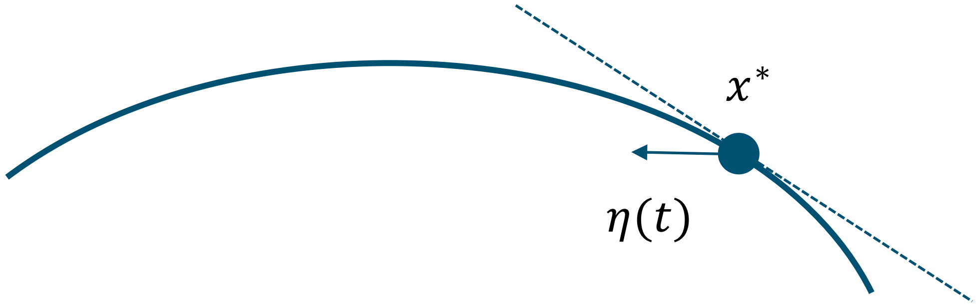




Linear stability analysis



Often we want a quantative method to determine the stability of a stationary point.

Say we have differential equation $\dot{x} = f(x)$, with a stationary point.

Take a small perturbation $\eta(t)$ around stationary point x^*.

Taylor expansion around the stationary point x^* yields

$$f(x^* + \eta) = f(x^*) + \eta f'(x^*) + \mathcal{O}(\eta^2)$$

We know $\quad f(x^*) = 0 \quad$ (why?)

Then, $\quad \dot{x} = \dot{\eta} \approx \eta f'(x^*)$

Differential equations of the form

$$\dot{y} = a\, y$$

have exponential solutions

$$y(t) = \exp a\, t$$

The slope $f'(x^*)$ determines the stability!

$f'(x^*) > 0,$ exponential growth

$f'(x^*) < 0,$ exponential decay

Magnitude relates to the timescale over which $x(t)$ varies:

$$\tau = \frac{1}{f'(x^*)}$$

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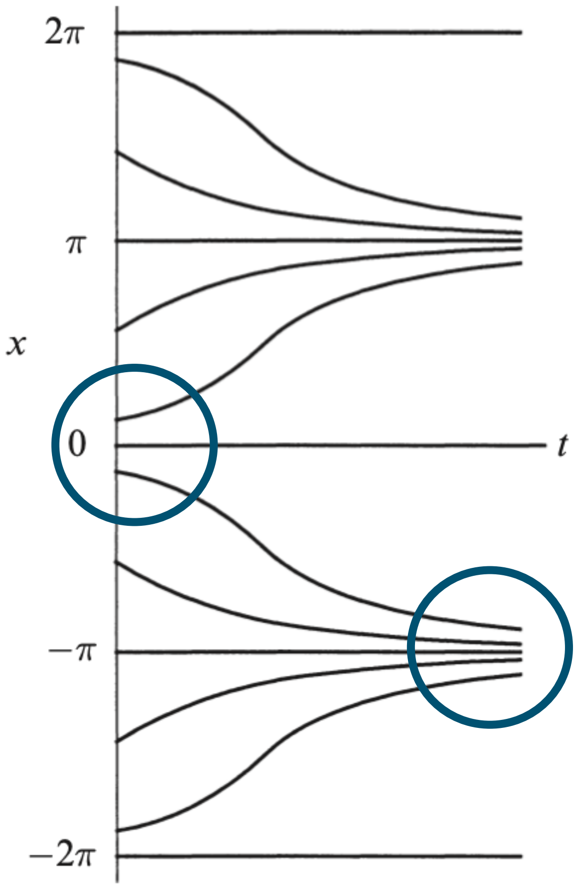
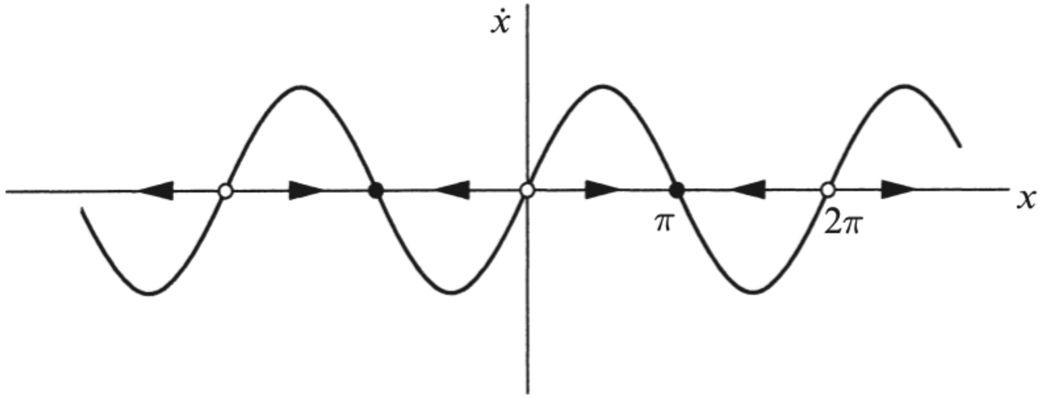
Linear stability analysis



Slope positive around stationary point
→ exponential growth away from it



Slope negative around stationary point
→ exponential decay towards it

Nonlinear dynamics – the programme

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- Building intuition A geometric approach to 1D ODEs
- Stationary points
- Linear stability analysis (for 1D systems)
- **Bifurcations**
- 2D linear systems

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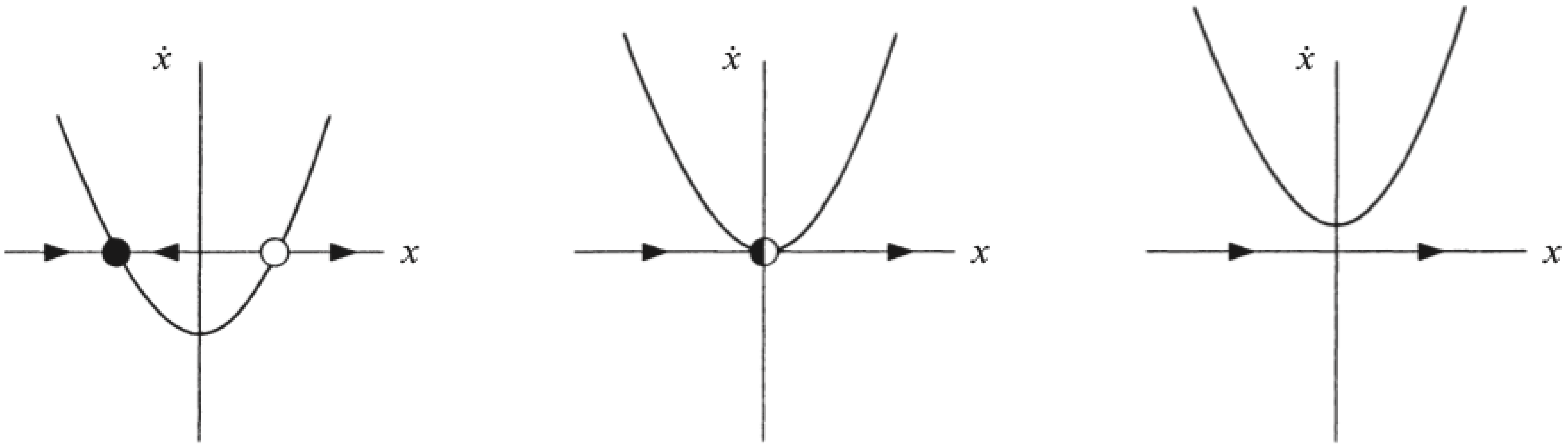
Bifurcations

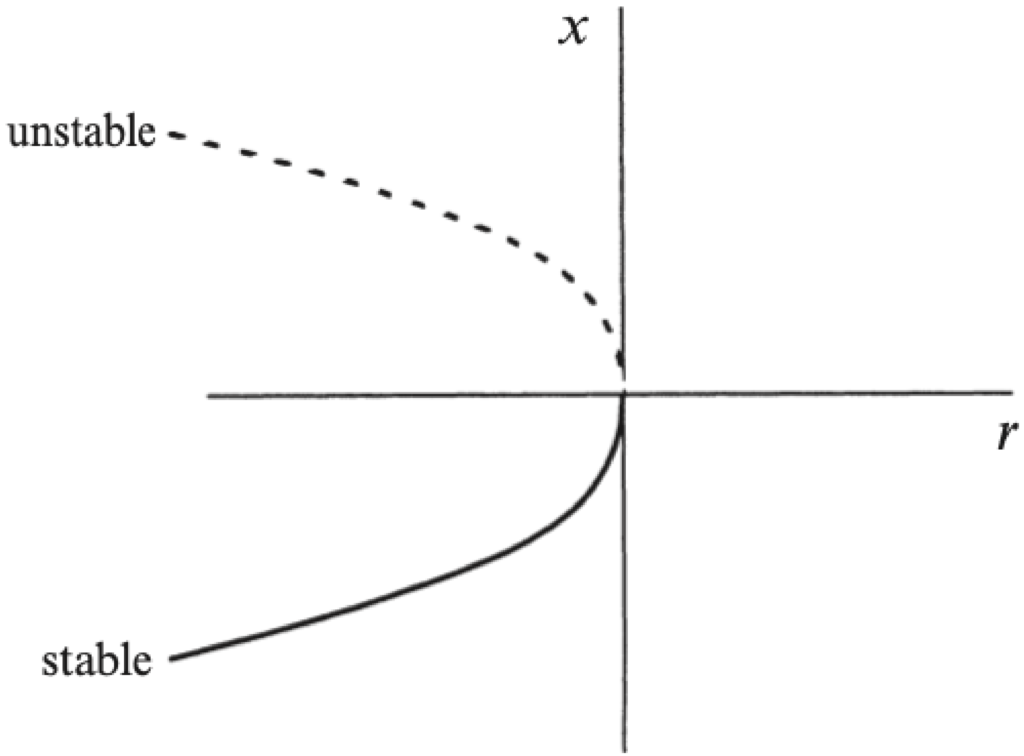
Example: $\dot{x} = r + x^2$

'saddle-node' bifurcation



(a) $r<0$ (b) $r=0$ (c) $r>0$

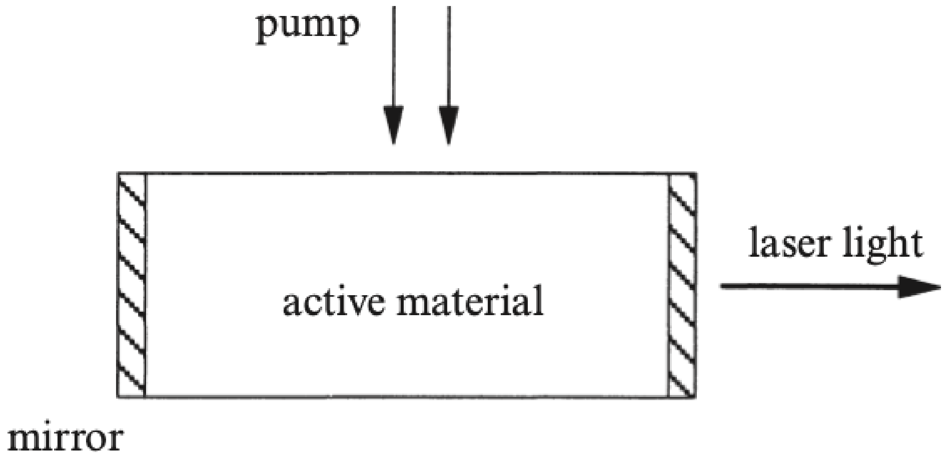
Bifurcations



Bifurcation diagram

Solid line for stable points
Broken line for unstable points

Worked example – laser threshold



Dynamical variable is the number of photons $n(t)$ in the laser field

$$\begin{aligned}\dot{n} &= \text{gain} - \text{loss} \\ &= GnN \;\; - kn\end{aligned}$$

Gain comes from stimulated emission of N excited atoms by $n(t)$ photons, with $G > 0$ an efficiency constant.

Loss comes from escape of photons with rate constant k.

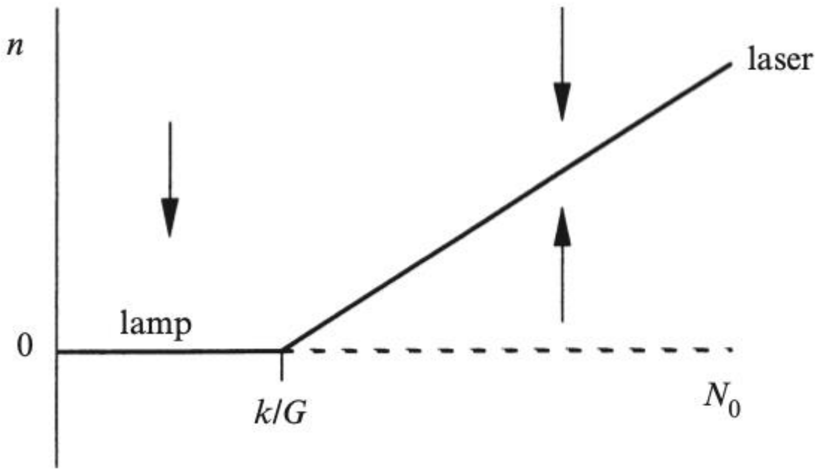
Emitting a photon drops an excited atom to ground state.

$$N(t) = N_0 - \alpha n$$

steady state w/o laser action (pump rate)

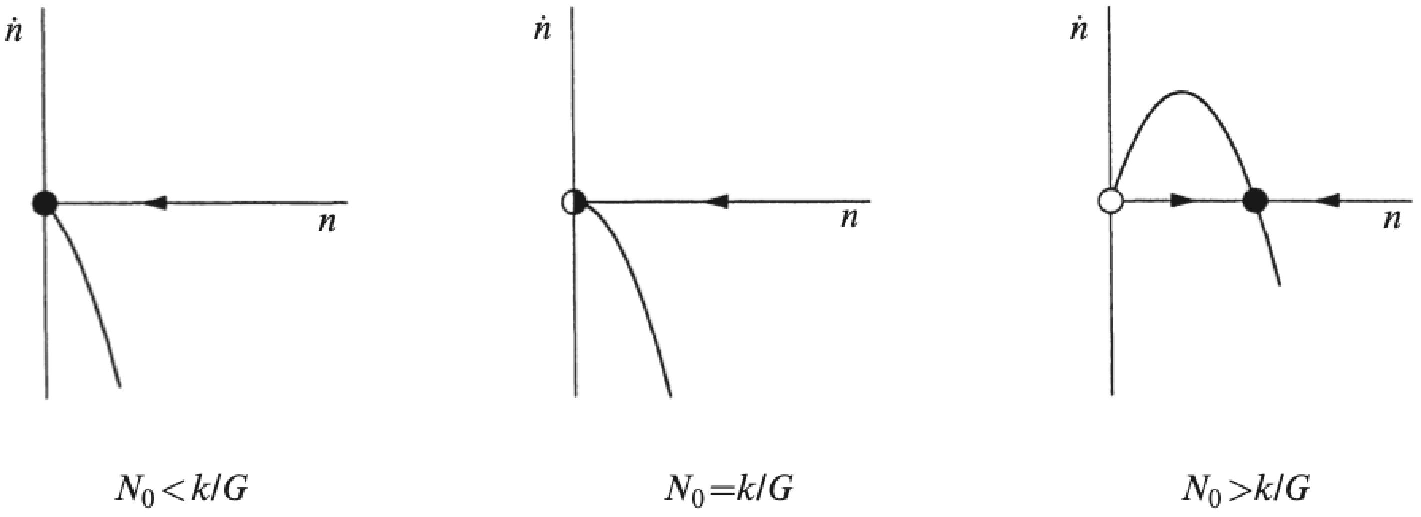
rate of relaxation

Worked example – laser threshold



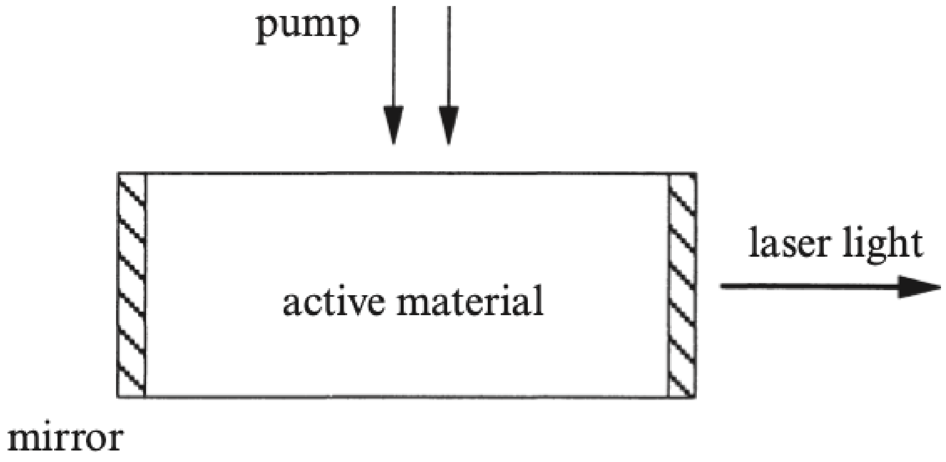
$$\dot{n} = Gn(N_0 - \alpha n) - kn$$
$$= (GN_0 - k)n - \alpha G n^2$$

The pump rate N_0 is now a bifurcation parameter



The stationary point at the origin switches from stable to unstable!

Worked example – laser threshold



See exercises for more physical models for laser threshold

Another worked example in exercises: Biochemical switches

Two-dimensional systems (and more…)

Let's start with the easy case …

two-dimensional **linear** systems

$$\dot{x} = ax + by$$
$$\dot{y} = cx + dy$$

Or in matrix form

$$\dot{\boldsymbol{x}} = A\boldsymbol{x}$$

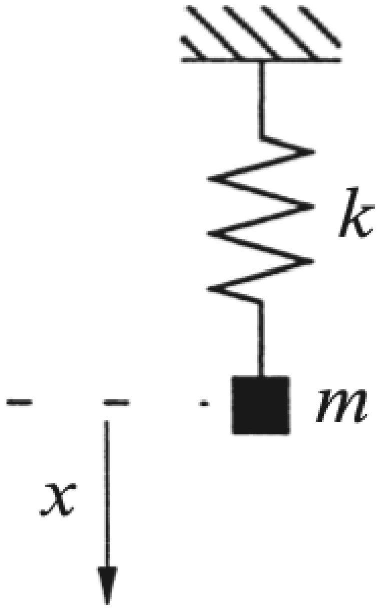
with

$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ and $\boldsymbol{x} = \begin{pmatrix} x \\ y \end{pmatrix}$

Solutions are also linear:
If $\boldsymbol{x}_1$ and $\boldsymbol{x}_2$ are solutions, then linear combinations are solutions too

Harmonic oscillator

Calculate the vibrations of a mass m hanging from a spring with spring constant k



From classical mechanics

$$m\ddot{x} + kx = 0$$

The state of the system is characterised by both current position x and velocity v.

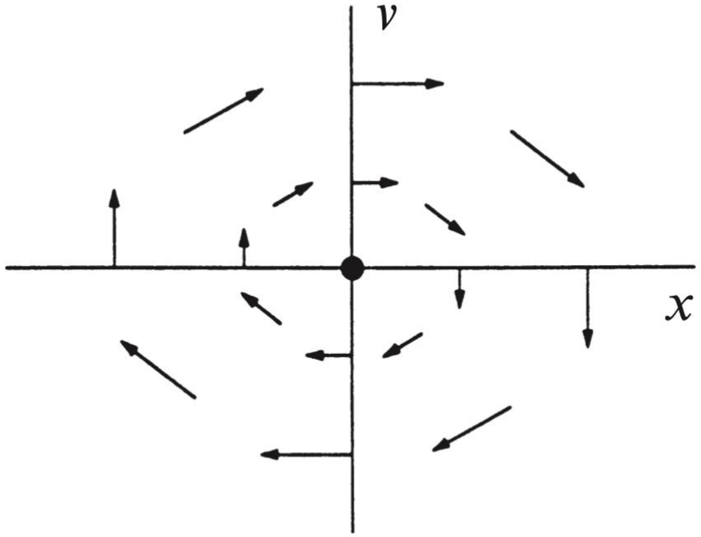
We can rewrite the 2nd order differential equation as a linear system of 1st order

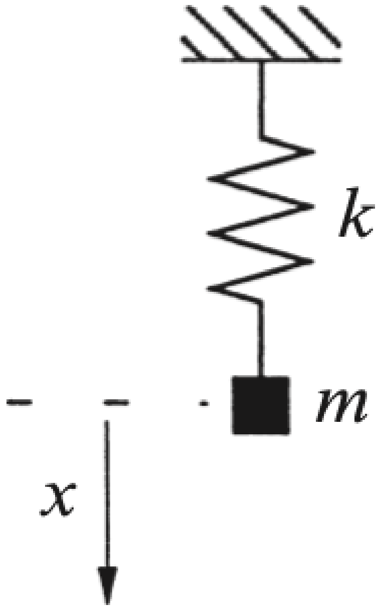
$$\dot{x} = v$$
$$\dot{v} = -\frac{k}{m}x = -\omega^2 x$$

Harmonic oscillator

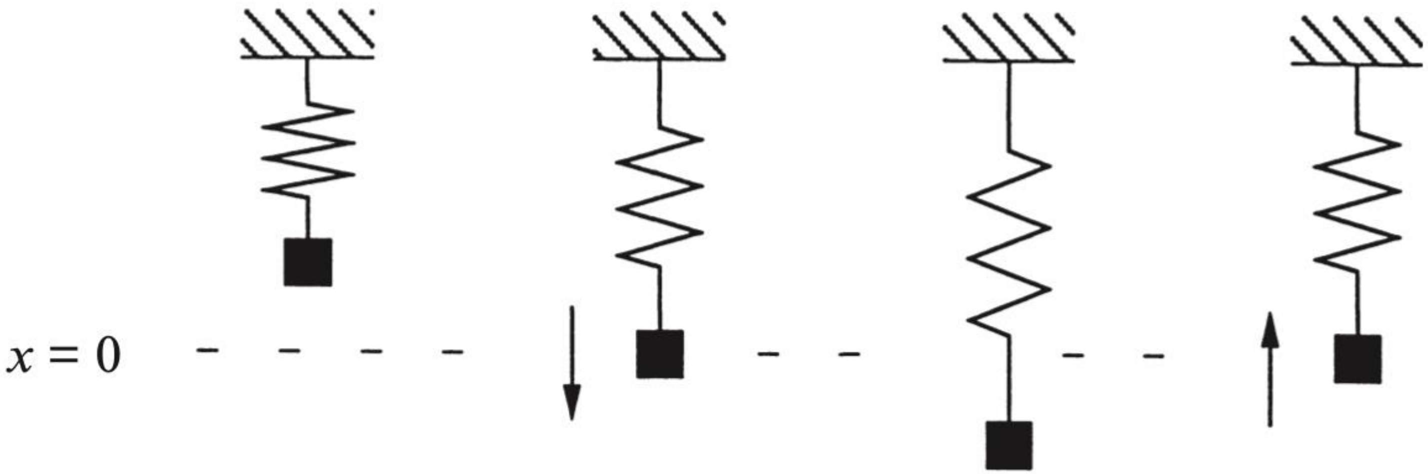
At each point in the (x, v) phase plane, the equations define a vector $(\dot{x}, \dot{v}) = (v, -\omega^2 x)$

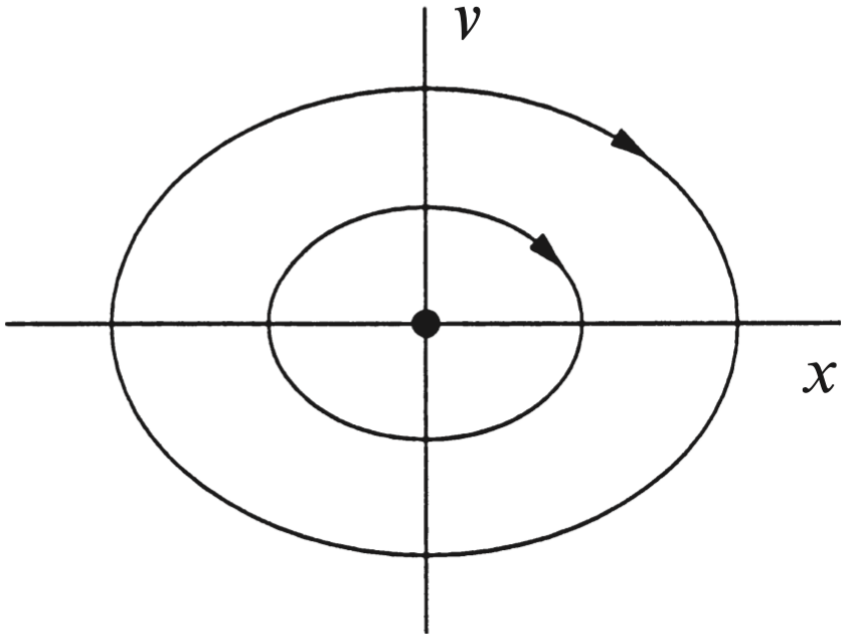
$$\dot{x} = v$$
$$\dot{v} = -\frac{k}{m}x = -\omega^2 x$$





Harmonic oscillator





This system leads to closed orbits around the origin

What happens at the origin?

Stability of linear systems

Can we say something more general about the stability of a linear system?

Example:

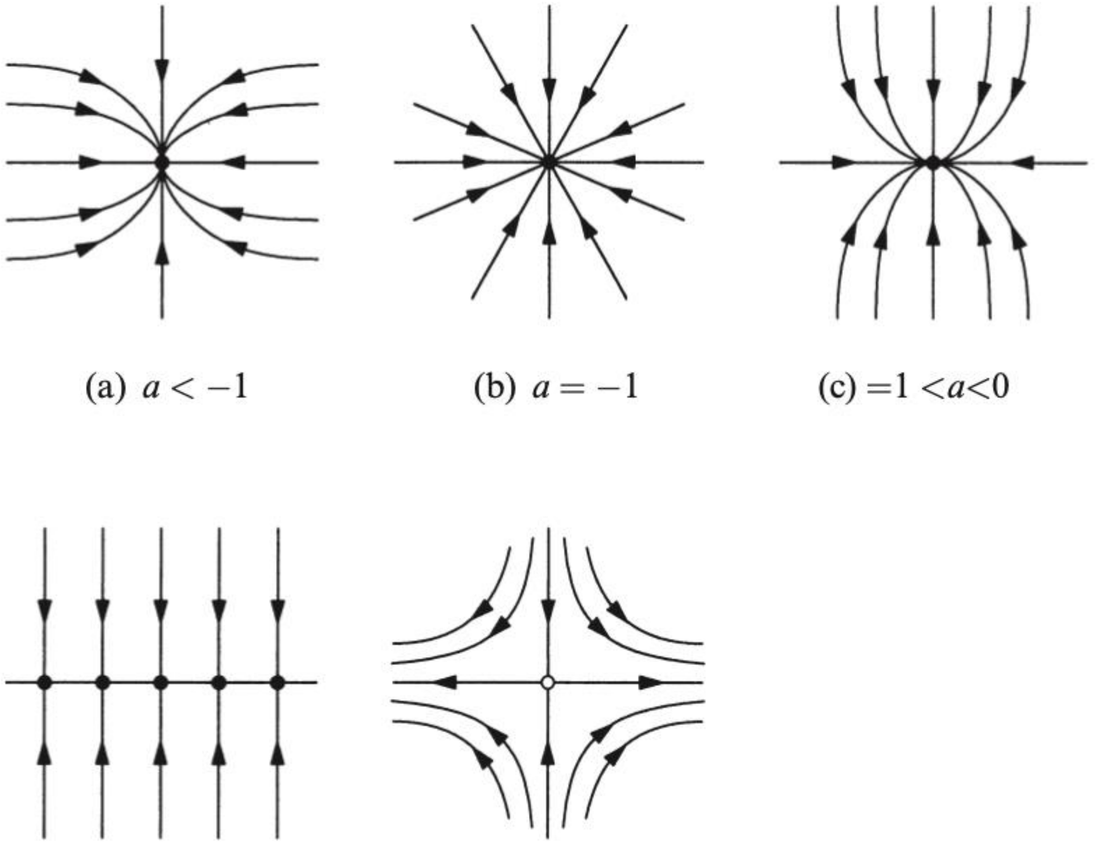
$\dot{\boldsymbol{x}} = A\boldsymbol{x}$, where $A = \begin{pmatrix} a & 0 \\ 0 & -1 \end{pmatrix}$

The system can also be written as

$$\dot{x} = ax$$
$$\dot{y} = -y$$

Each equation can be solved independently, with solutions

$$x(t) = x_0 e^{at}$$
$$y(t) = y_0 e^{-t}$$



(a) $a < -1$ (b) $a = -1$ (c) $=1 < a < 0$

(d) $a = 0$ (e) $a > 0$

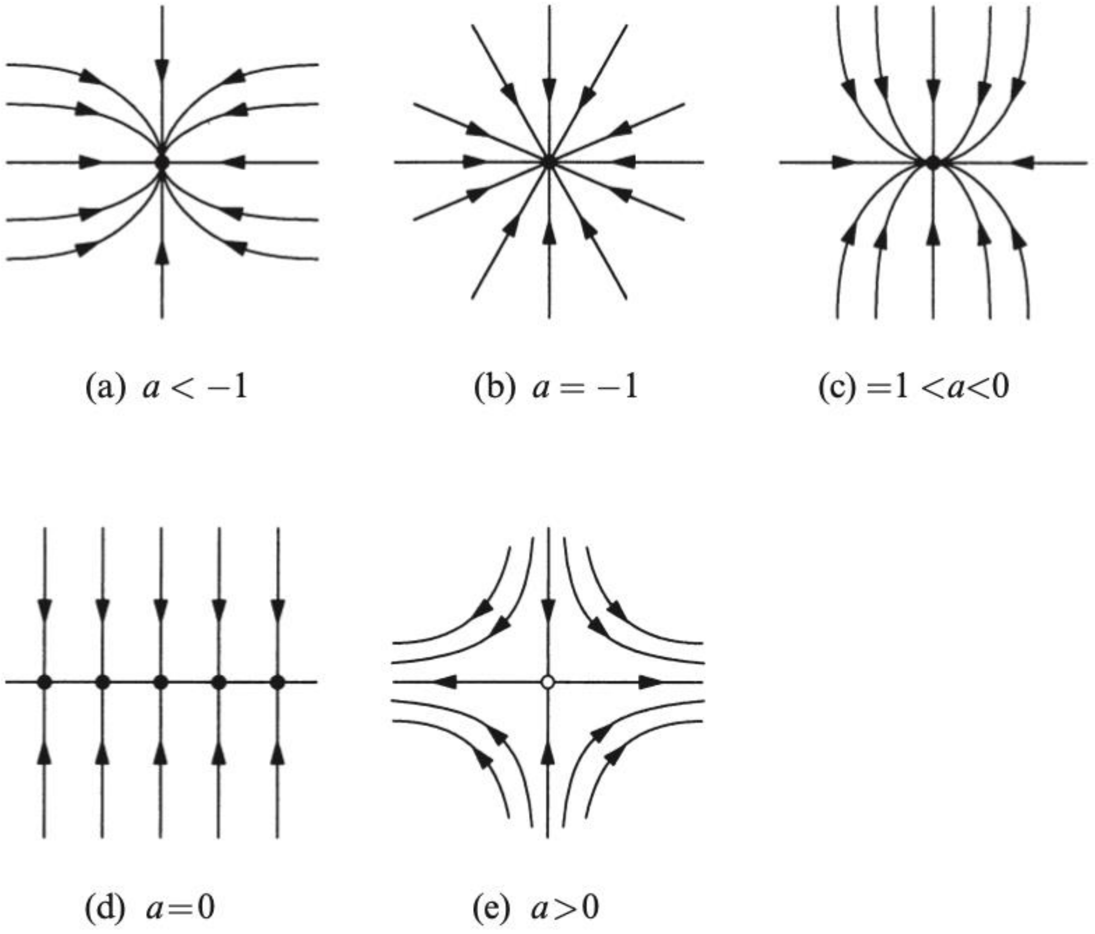
Stability of linear systems

Trajectories on one of the axes stay on the axes and grow or decay exponentially

Why?

Both axes are independent in this system.

Are there similar ‘straight line’ trajectories when the system is not diagonal?



‘Straight-line’ trajectories

We seek trajectories of the form

$$\boldsymbol{x}(t) = e^{\lambda t}\boldsymbol{v}$$

with $\boldsymbol{v}$ a vector (to be determined)
and λ a growth rate (also to be determined)

Substitute into $\dot{\boldsymbol{x}} = A\boldsymbol{x}$, to get

$$\lambda e^{\lambda t}\boldsymbol{v} = e^{\lambda t}A\boldsymbol{v}$$

The factors $e^{\lambda t}$ cancel out and we get

$$\lambda\boldsymbol{v} = A\boldsymbol{v} \qquad \text{(Eigenvalue-equation)}$$

Solutions exist if $\boldsymbol{v}$ is an eigenvector!

Anyone remember how to find eigensolutions?

The Eigenvalue problem

When $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, then the eigenvalues of this matrix are given by the characteristic equation

$$\det \begin{pmatrix} a-\lambda & b \\ c & d-\lambda \end{pmatrix} = 0$$

We expand the determinant

$$\lambda^2 - \tau\lambda + \Delta = 0$$

with

$$\tau = \mathrm{trace}(A) = a + d$$
$$\Delta = \det(A) = ad - bc$$

Quadratic equation with solutions

$$\lambda_{1,2} = \frac{\tau \pm \sqrt{\tau^2 - 4\Delta}}{2}$$

Eigenvalues λ_1, λ_2 are typically not the same:
Two eigensolutions with eigenvectors $\boldsymbol{v}_1, \boldsymbol{v}_2$.

(How to find the eigenvectors?)

The 'straight-line' trajectories are then

$$\boldsymbol{x}_1(t) = e^{\lambda_1 t}\boldsymbol{v}_1$$
$$\boldsymbol{x}_2(t) = e^{\lambda_2 t}\boldsymbol{v}_2$$

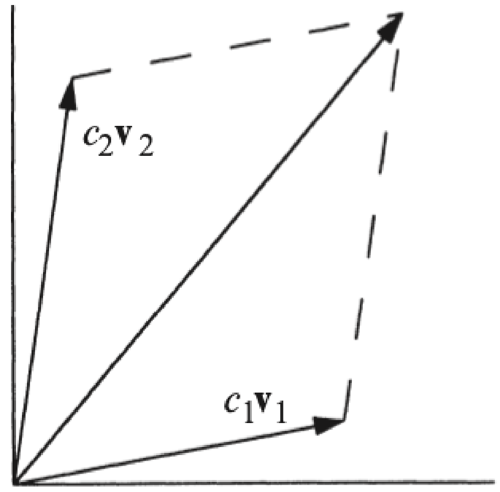
General solution of a 2D linear system

Eigenvalues λ_1, λ_2 are typically not the same:
Two eigensolutions with eigenvectors $\boldsymbol{v}_1, \boldsymbol{v}_2$.

(How to find the eigenvectors?)

Any initial value can be written as a linear combination of the eigenvectors

$$\boldsymbol{x}_0 = c_1\boldsymbol{v}_1 + c_2\boldsymbol{v}_2$$



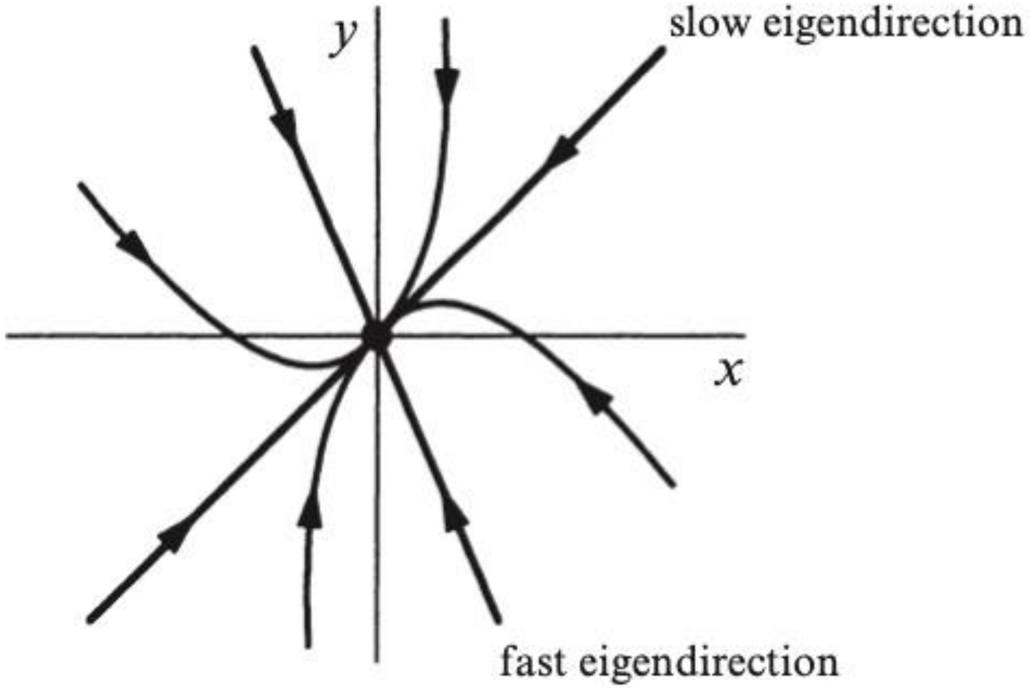
The 'straight-line' trajectories are then

$$\boldsymbol{x}_1(t) = e^{\lambda_1 t}\boldsymbol{v}_1$$
$$\boldsymbol{x}_2(t) = e^{\lambda_2 t}\boldsymbol{v}_2$$

And with general solution

$$\boldsymbol{x}(t) = \boldsymbol{c}_1 e^{\lambda_1 t}\boldsymbol{v}_1 + \boldsymbol{c}_2 e^{\lambda_2 t}\boldsymbol{v}_2$$

Different decay timescales



If $\lambda_2 < \lambda_1 < 0$

One eigenvector is associated with slower decay than the other.

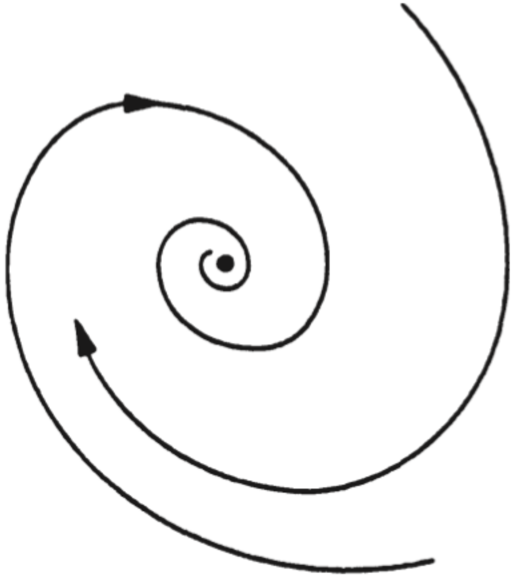
General solutions collapse quickly onto a trajectory close and tangent to the slow eigendirectory…

… and then slowly decay towards the stable point.

‘Straight-line’ trajectories

Eigenvalues are completely determined by τ and Δ

$$\lambda_{1,2} = \frac{\tau \pm \sqrt{\tau^2 - 4\Delta}}{2}$$



So what happens when $\tau^2 - 4\Delta < 0$?

Eigenvalues can be complex: $\lambda = \alpha + i\omega$

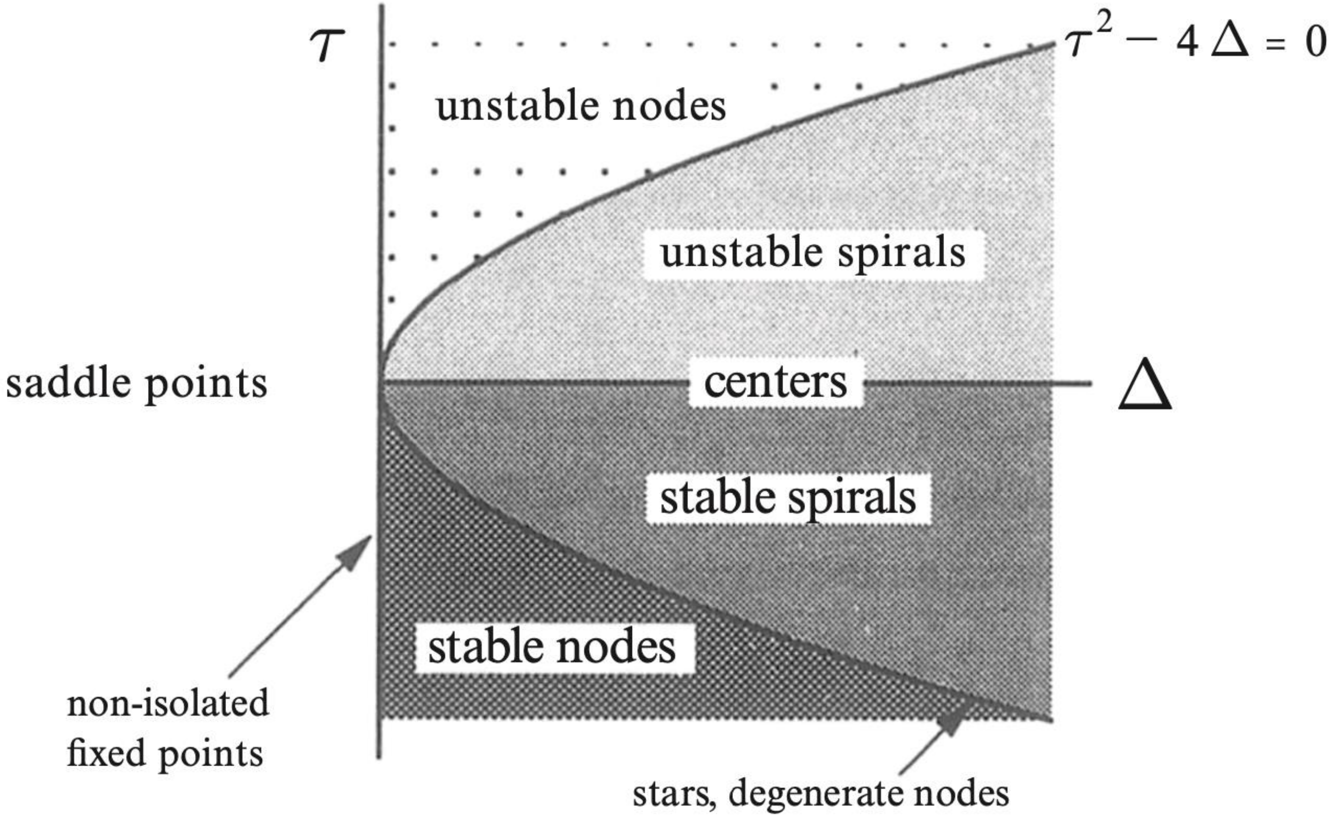
... and the resulting solutions are spirals.

$$\begin{aligned} \boldsymbol{x}_{1,2}(t) &= \boldsymbol{v}_{1,2} e^{\alpha t + i\omega t} \\ &= \boldsymbol{v}_{1,2}\, e^{\alpha t} \times e^{i\omega t} \end{aligned}$$

This is a rotation (with frequency ω)

This is exponential growth or decay

General classification of stationary points



Love for linear systems

Romeo is in love with Juliet, but the more Romeo loves her, the more Juliet wants to run away and hide.

$R(t)$ = Romeo's love/hate for Juliet at time t.
$J(t)$ = Juliet's love/hate for Romeo at time t.

(positive values signify love, negative signify hate)

A model for their star-crossed romance is

$$\dot{R} = aJ$$
$$\dot{J} = -bR$$

(with parameters a, b positive)

What is the long-term outcome of this love affair?

Love for linear systems

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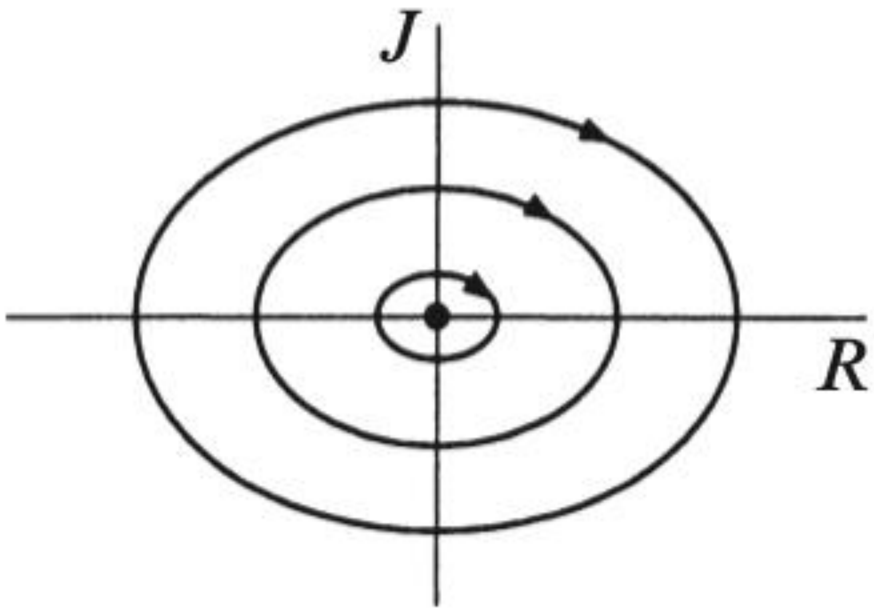


Love for linear systems

Let's generalise the model

Happy pride month!

$$\dot{R} = aR + bJ$$
$$\dot{J} = cR + dJ$$

What would happen if both are 'cautious lovers'?

$$\dot{R} = aR + bJ$$
$$\dot{J} = bR + aJ$$

with $a < 0, b > 0$

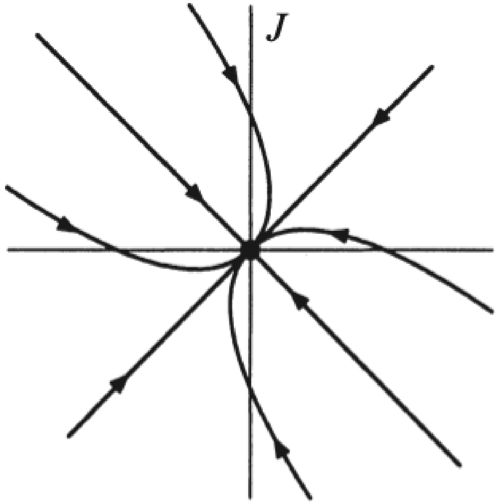
What is the long-term outcome of this love affair?

Love for linear systems

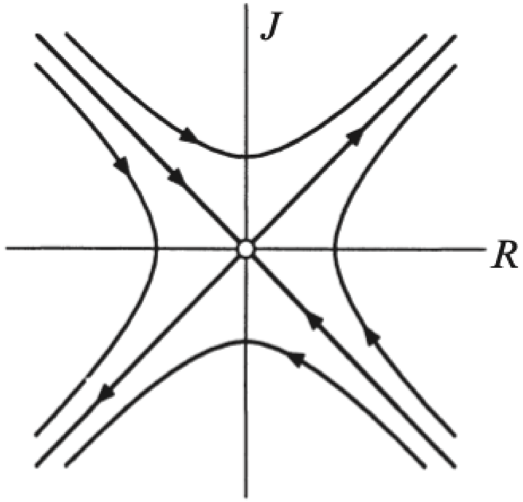
$$\dot{R} = aR + bJ$$
$$\dot{J} = bR + aJ$$

with $a < 0, b > 0$

$$\tau = 2a < 0, \qquad \Delta = a^2 - b^2, \qquad \tau^2 \quad -4\Delta = 4b^2 > 0$$



$a^2 > b^2$



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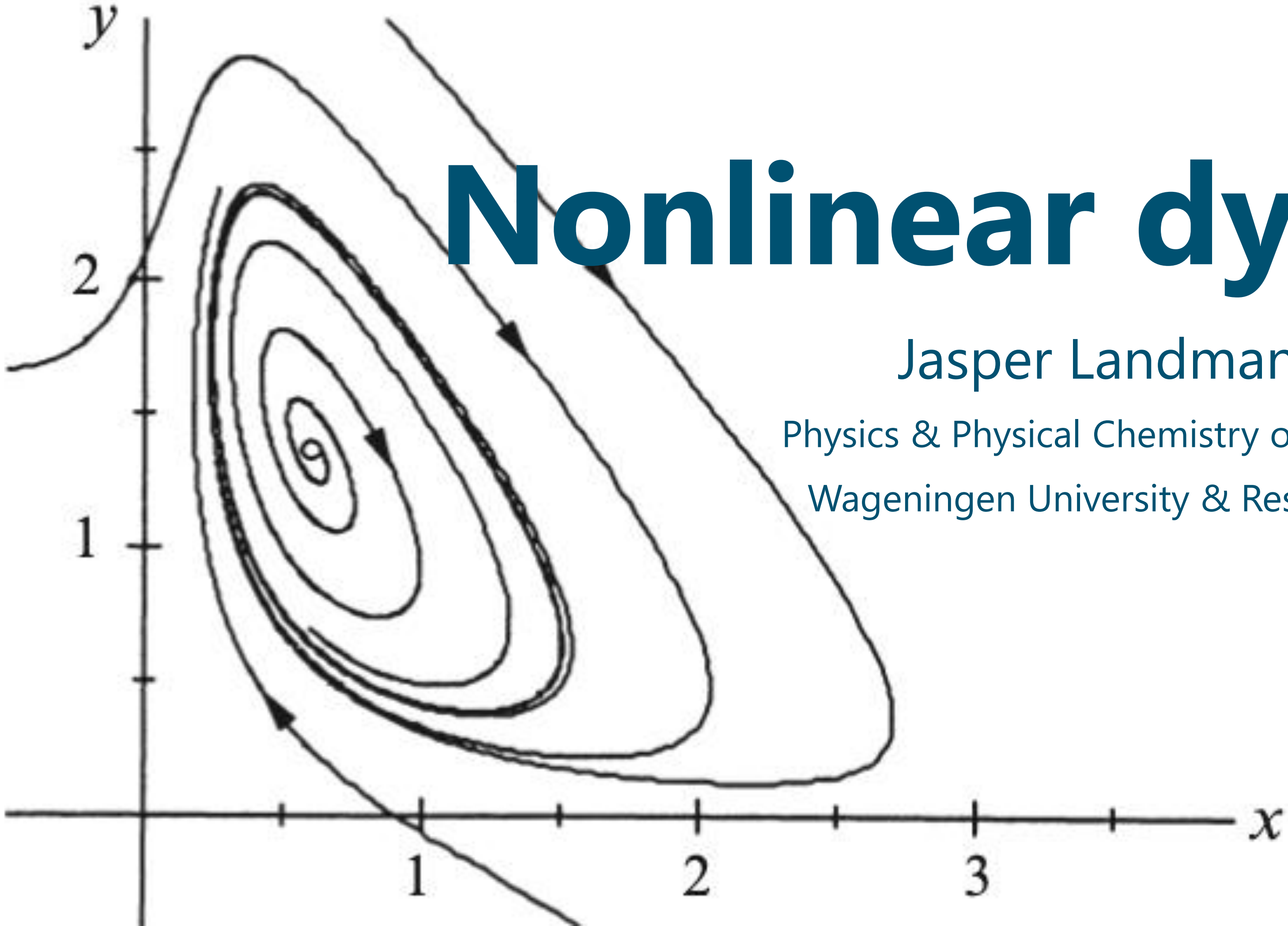

Nonlinear dynamics

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Nonlinear dynamics – the programme

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- Stationary points
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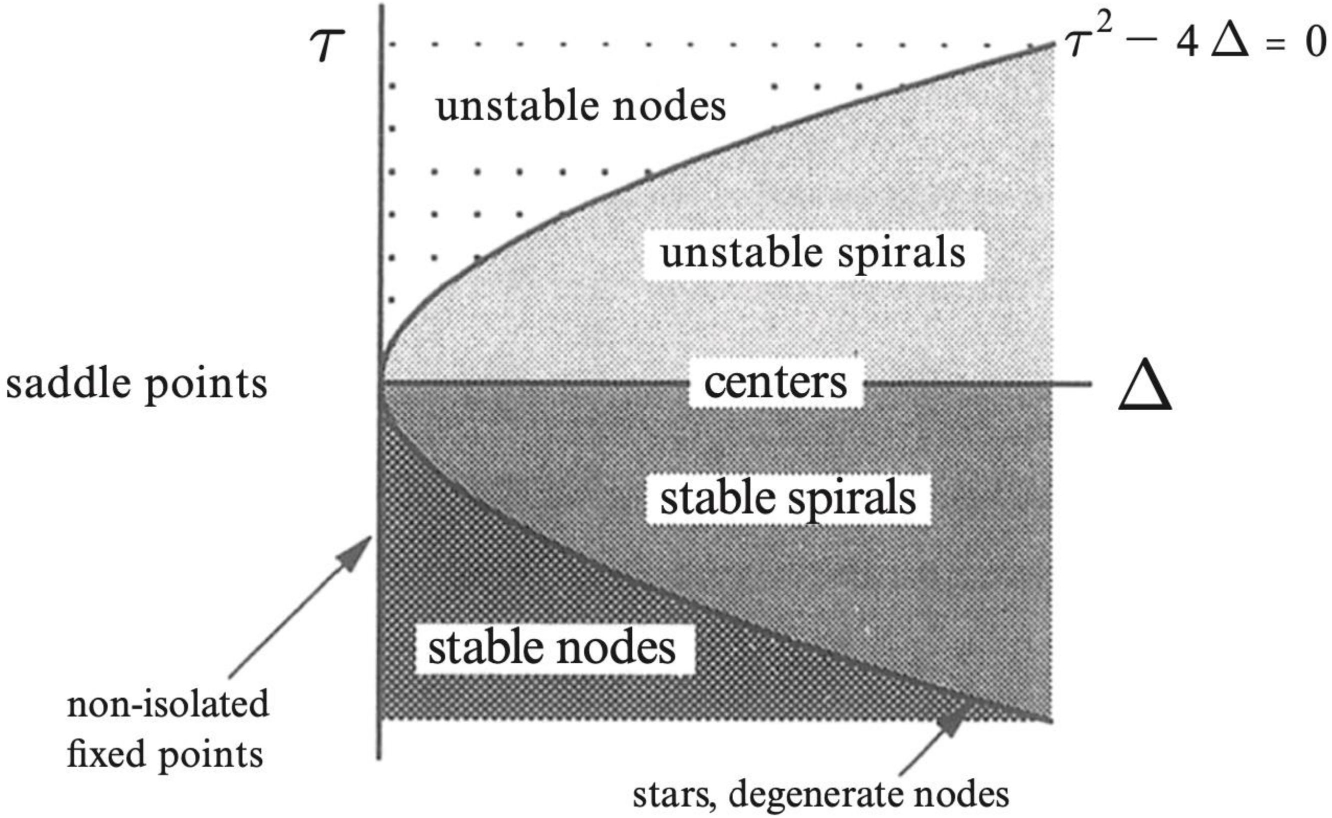


Nonlinear twodimensional systems

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$$

with $\boldsymbol{x} = (x_1, x_2, \dots)$ and $\boldsymbol{f}(\boldsymbol{x}) = (f_1(\boldsymbol{x}), f_2(\boldsymbol{x}), \dots)$

In general these systems can't be evaluated analytically

A good place to start is by plotting the **nullclines** of the system – where one of the differentials equals 0.

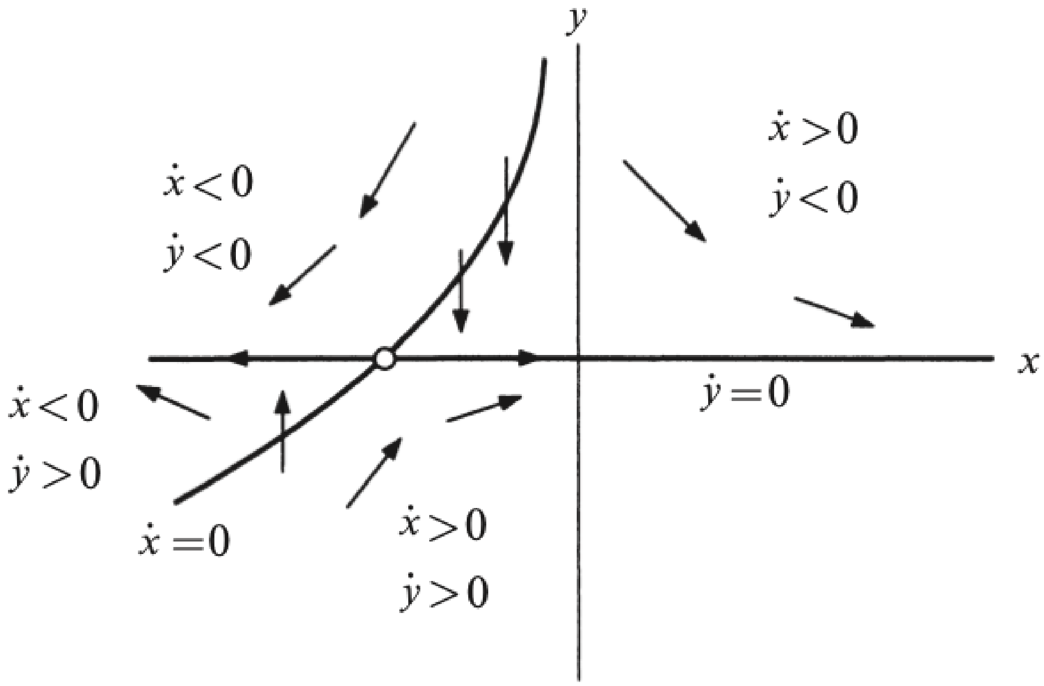
Example

$$\dot{x} = x + e^{-y}$$
$$\dot{y} = -y$$

Nullclines are given by

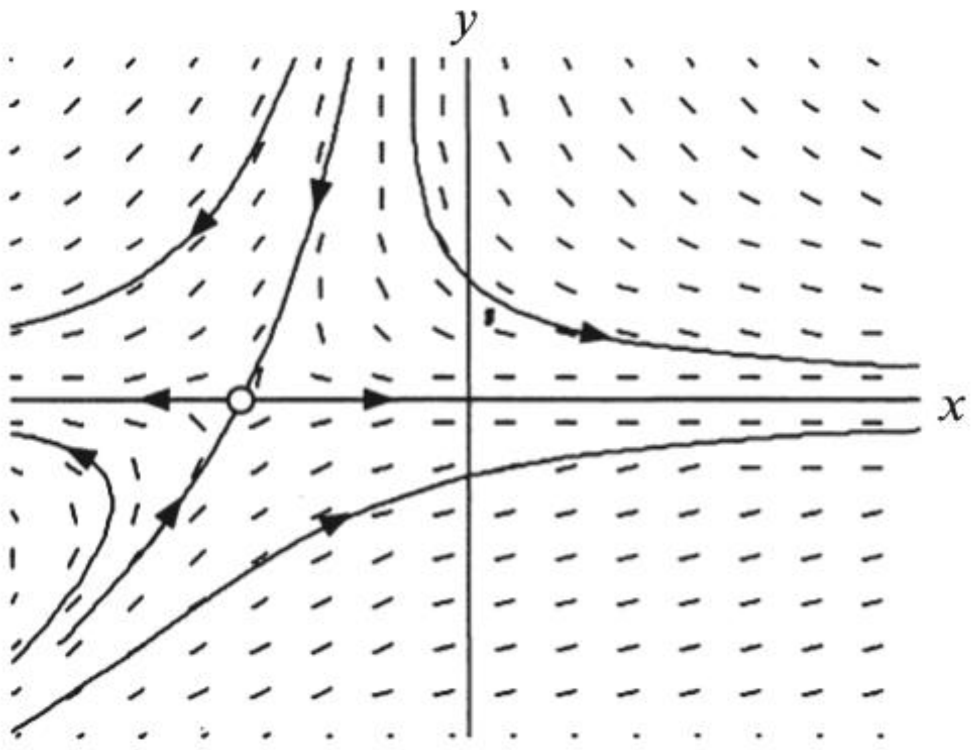
$$\dot{x} = x + e^{-y} = 0$$
$$\dot{y} = -y = 0$$

Intersections of the nullclines are stationary points



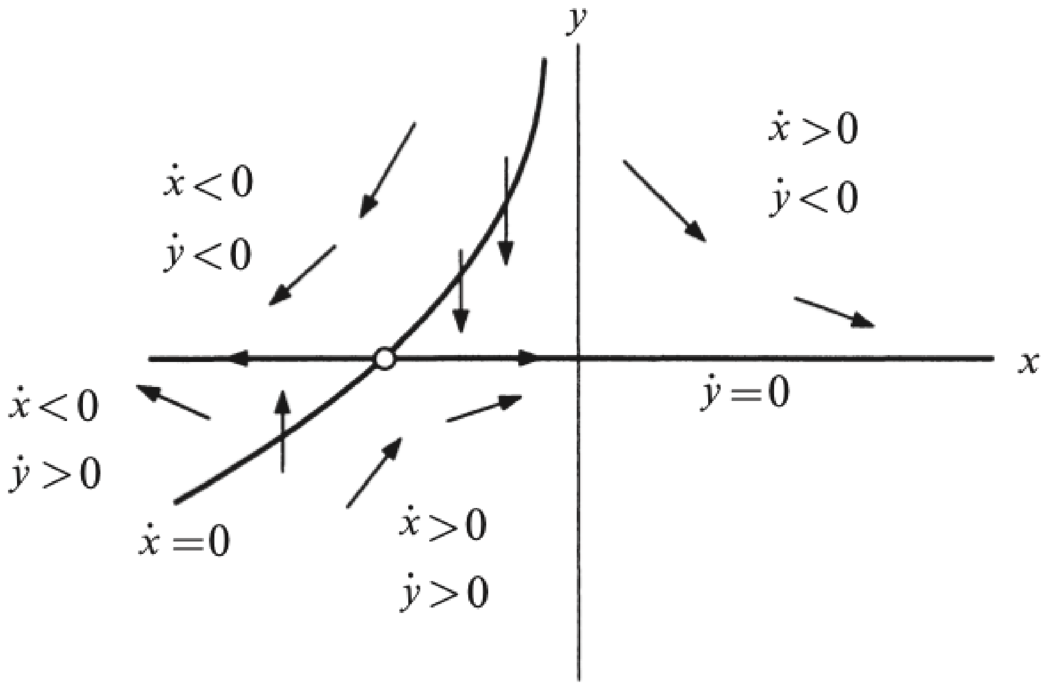
The nullclines separate regions where $\dot{x}, \dot{y}$ have various signs

Nonlinear twodimensional systems



Numerical calculation

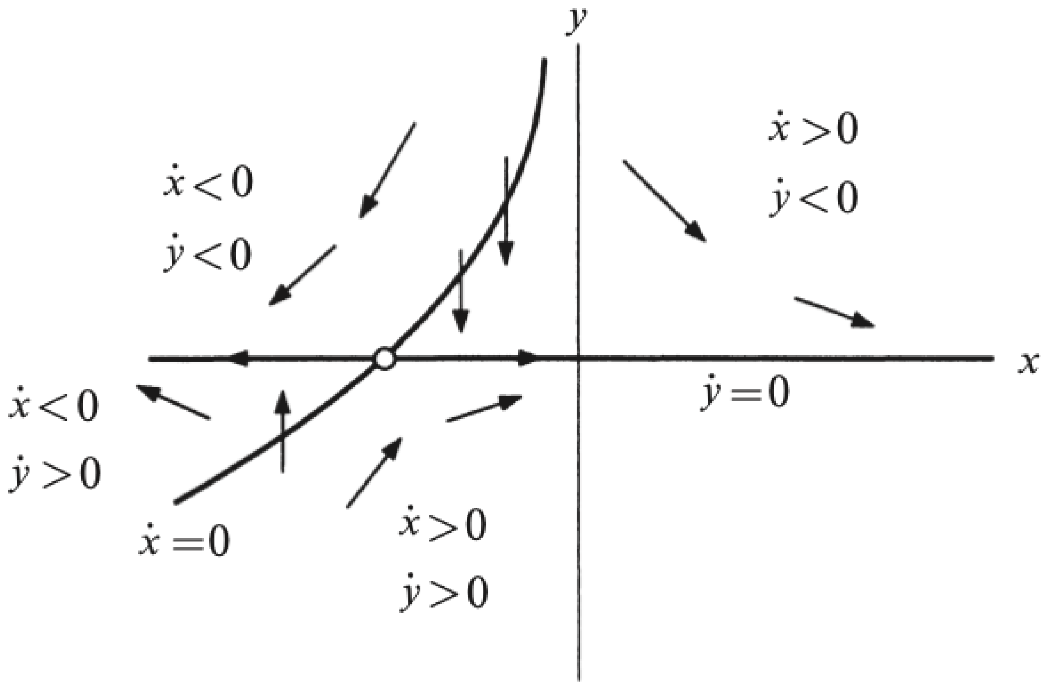
Intersections of the nullclines are stationary points



The nullclines separate regions where $\dot{x}, \dot{y}$ have various signs

What about the stability of 2D nonlinear stationary points?

How would you go about evaluating the stability of the stationary point here?



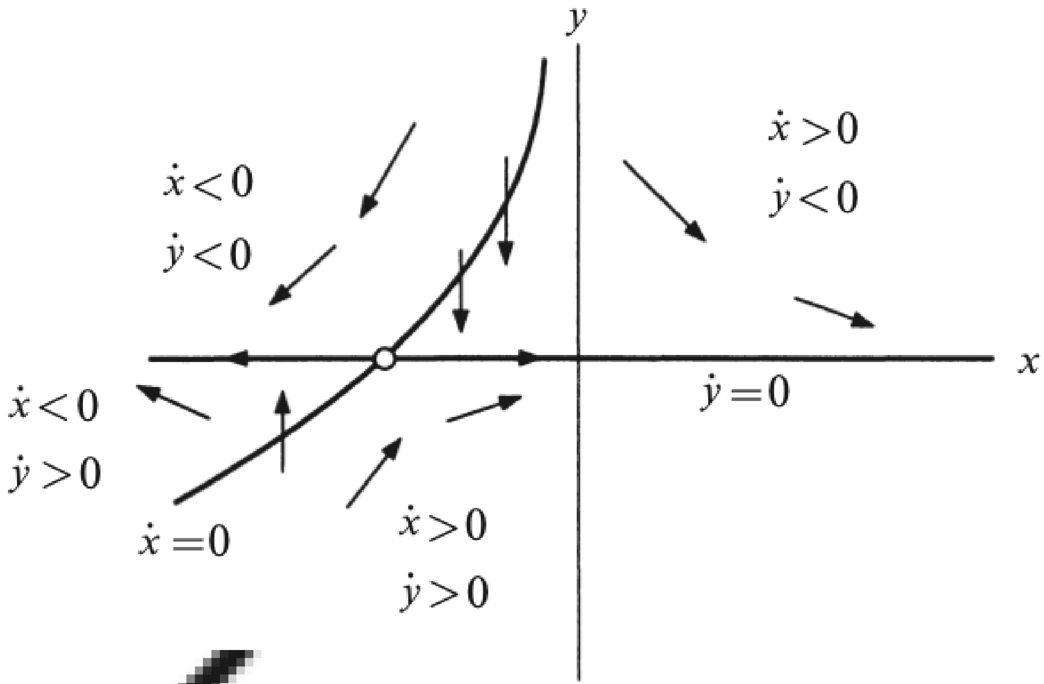
What about the stability of 2D nonlinear stationary points?

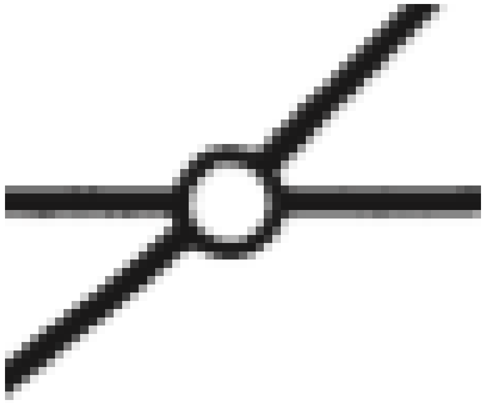
How would you go about evaluating the stability of the stationary point here?

Close to the stationary point, the system looks almost linear!

As before with 1D systems, we can linearise the system.

How?





Taylor expansion of 2D nonlinear systems

$$\dot{x}_1 = f_1(x_1, x_2)$$
$$\dot{x}_2 = f_2(x_1, x_2)$$

$$f_1(x_1^*, x_2^*) = f_2(x_1^*, x_2^*) = 0$$

Taylor expansion of f at (x_1^*, x_2^*)

$$f_i(x_1, x_2) = f_i(x_1^*, x_2^*) + \frac{\partial f_i}{\partial x_1}(x_1^*, x_2^*)(x_1 - x_1^*) + \frac{\partial f_i}{\partial x_2}(x_1^*, x_2^*)(x_2 - x_2^*) + \mathcal{O}(x_i^2)$$

Make the replacement $u_i = x_i - x_i^*$

$$\dot{\boldsymbol{u}} = \begin{pmatrix} \dfrac{\partial f_1(x_1^*, x_2^*)}{\partial x_1} & \dfrac{\partial f_1(x_1^*, x_2^*)}{\partial x_2} \\ \dfrac{\partial f_2(x_1^*, x_2^*)}{\partial x_1} & \dfrac{\partial f_2(x_1^*, x_2^*)}{\partial x_2} \end{pmatrix} \boldsymbol{u}$$

That's a linear system
(which we've already treated before)

Jacobian of $\boldsymbol{f}$ at (x_1^*, x_2^*)

Lotka-Volterra model – Rabbits vs Sheep

Let’s model competition between two animal species competing for the same resource.

- Logistic growth in absence of the other species up to carrying capacity
- When sheep and rabbit meet, there is trouble

$$\dot{x} = x(3 - x) - 2xy$$
$$\dot{y} = y(2 - y) - xy$$

What are the fixed points?

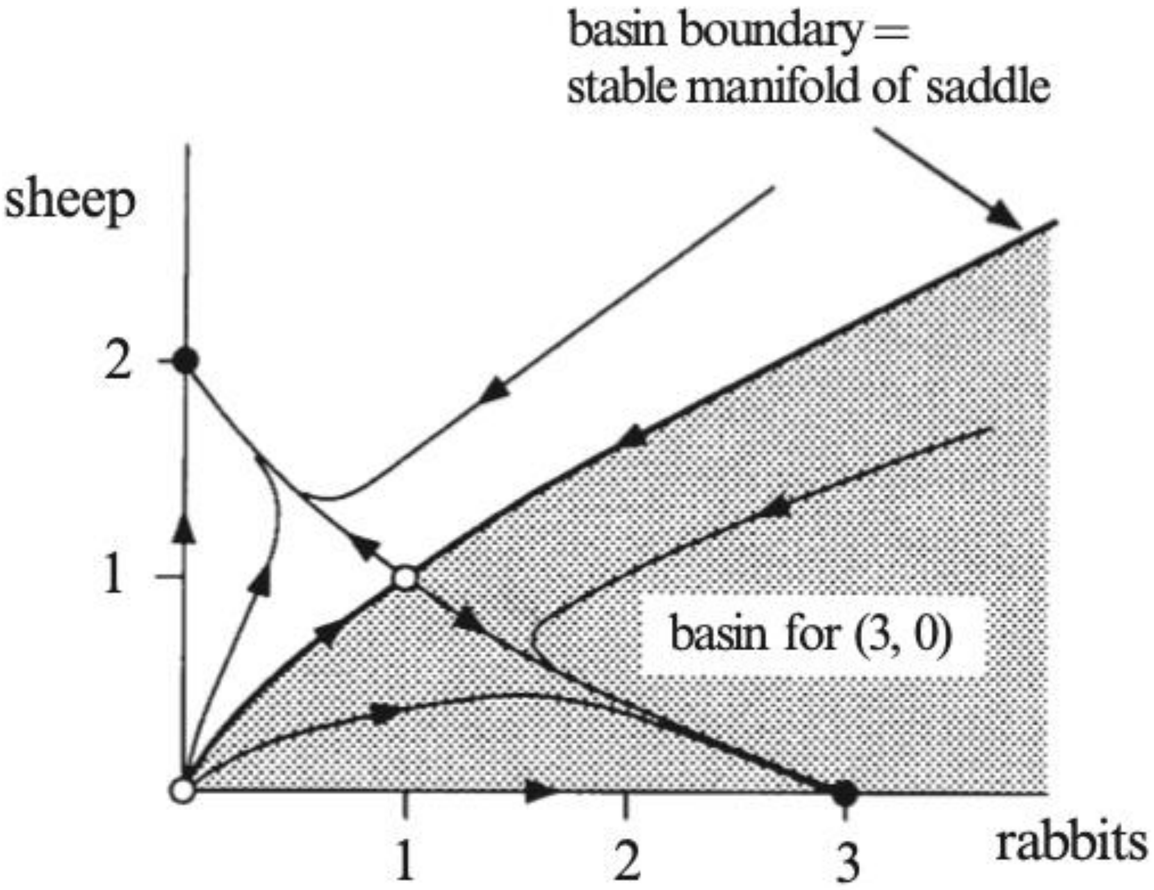
What is the Jacobian at each fixed point?

What is the stability of each point?

Draw the phase portrait

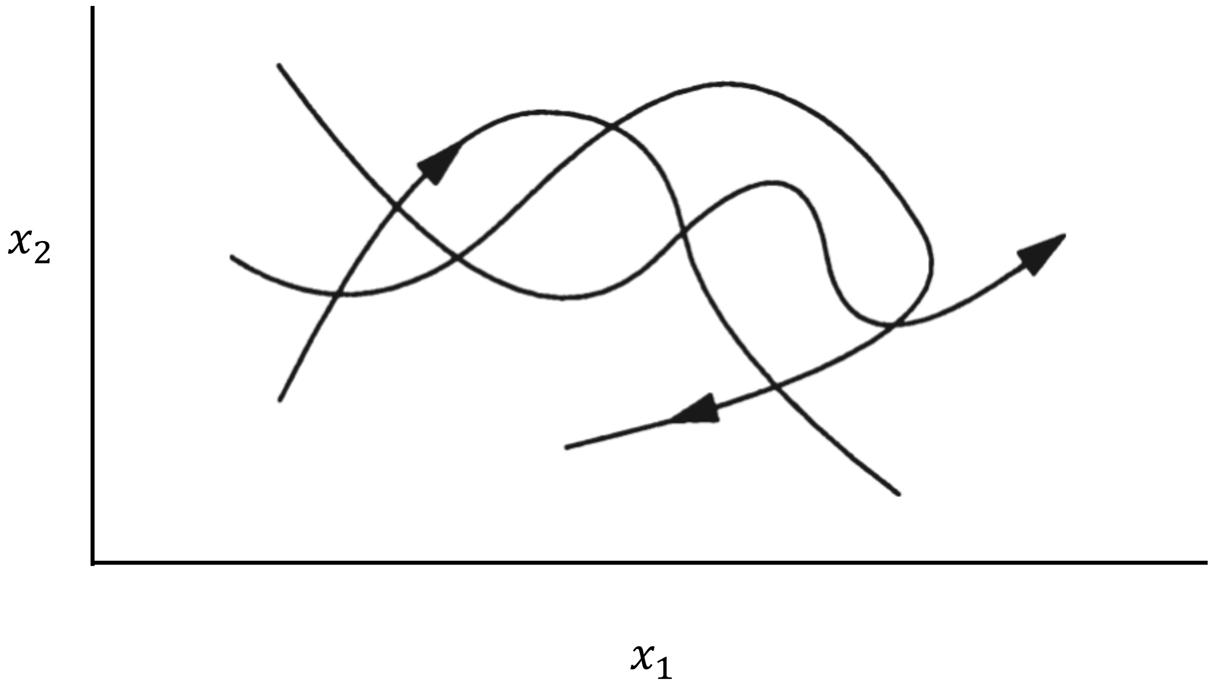
Lotka-Volterra model – Rabbits vs Sheep

Lotka-Volterra model – Rabbits vs Sheep



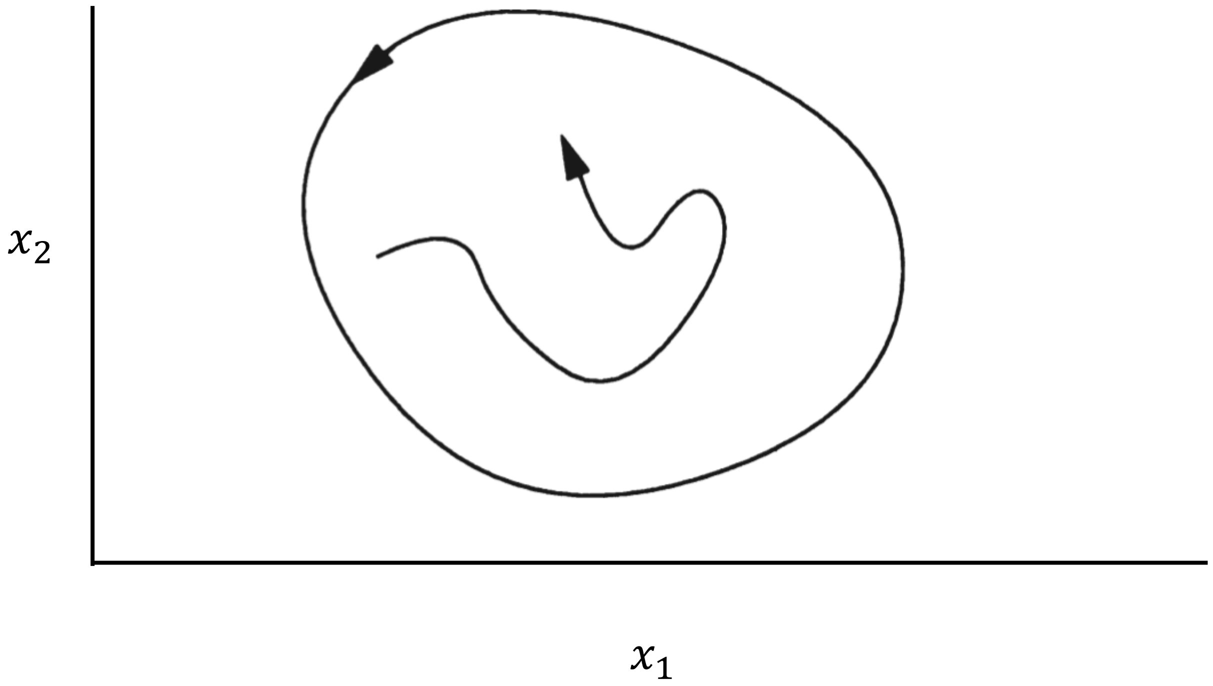
Trajectories in phase space

Can two trajectories cross in phase space?



Trajectories in phase space

If a trajectory makes a closed loop, what happens to any trajectories within the loop?



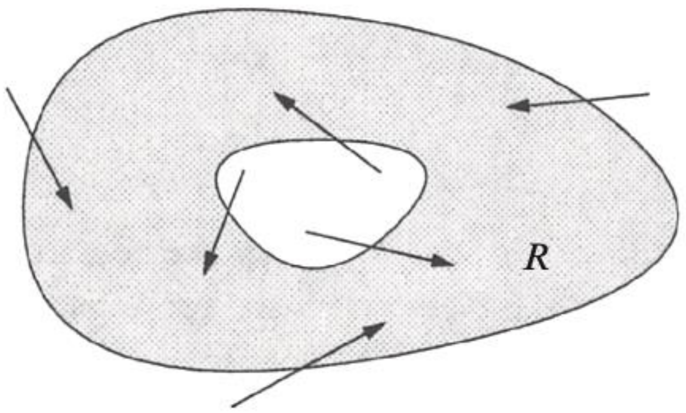
Is there a stable stationary point inside the loop?

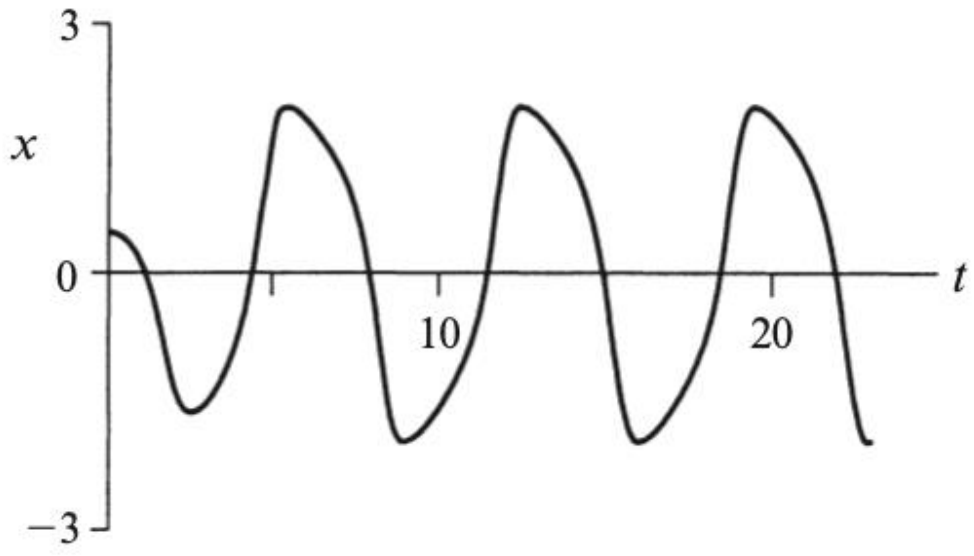
Limit cycles – oscillations

A special type of behaviour is the emergence of limit cycles – oscillatory behaviour!

Existence of a limit cycle follows the Poincaré-Bendixon theorem

1. Area of phase space R that's closed and bounded
2. R needs to be a trapping region
3. R does not contain any fixed points





This sounds very obscure and theoretical but let's apply it

Oscillatory glycolysis

Yeast cells break down sugar in an oscillatory fashion. A model for this process is given by

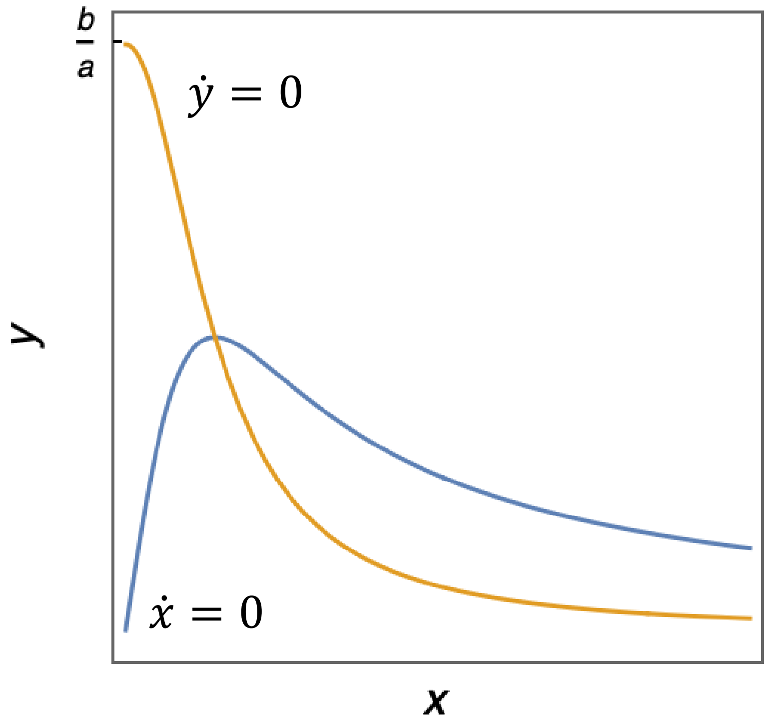
$$\dot{x} = -x + ay + x^2 y$$
$$\dot{y} = b - ay - x^2 y$$

Here x is the concentration fo ADP and y is the concentration of fructose-6-phosphate (F6P).

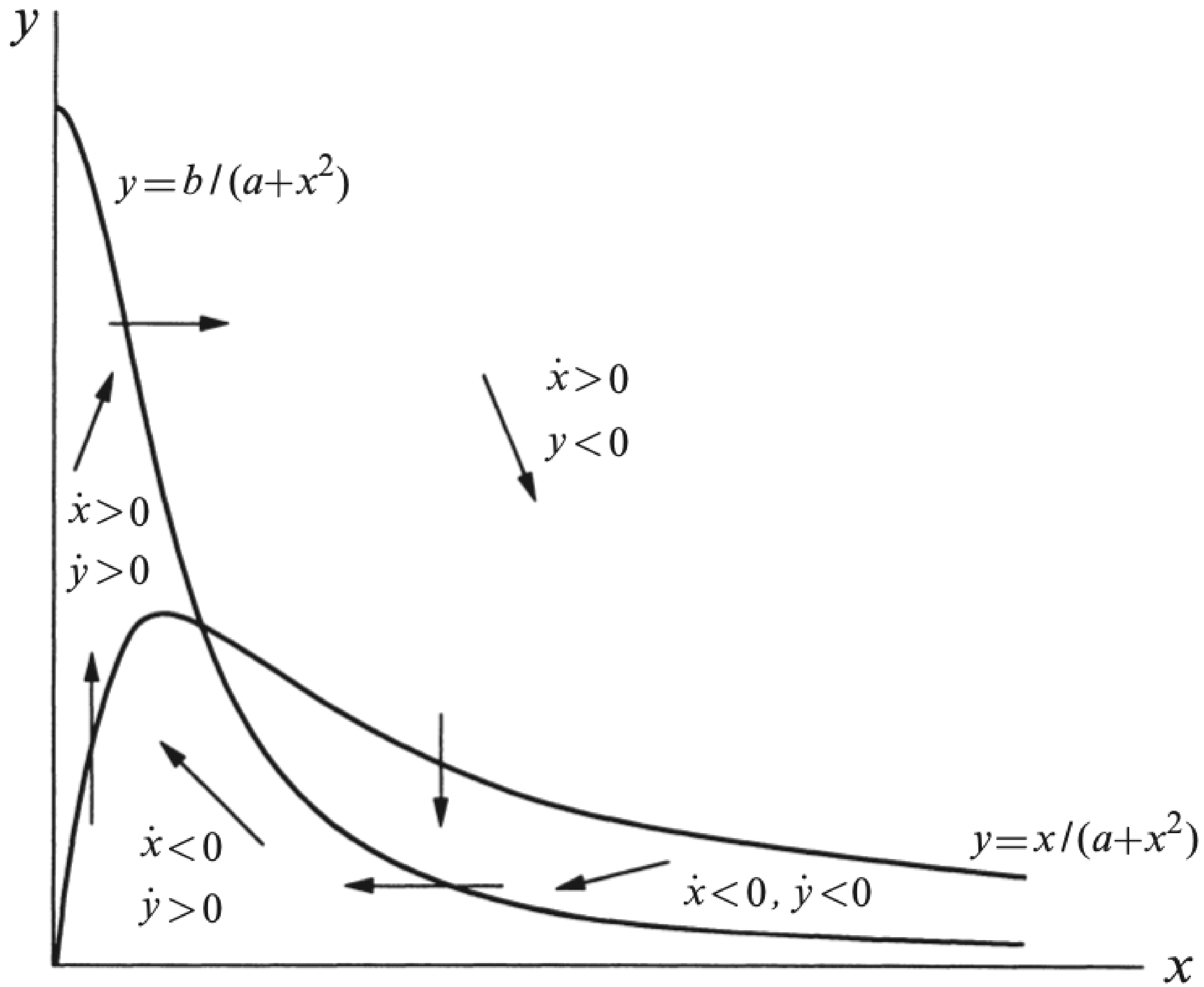
Group exercise: construct a trapping zone for this model.

Hints:

- start with plotting the nullclines and draw the directions of the vector field
- Since $\dot{x} + \dot{y} = b - x$, the slope $-\dot{y} > \dot{x}$ whenever $x > b$. The vector field is therefore always steeper than -1 in that area.



Drawing a trapping area



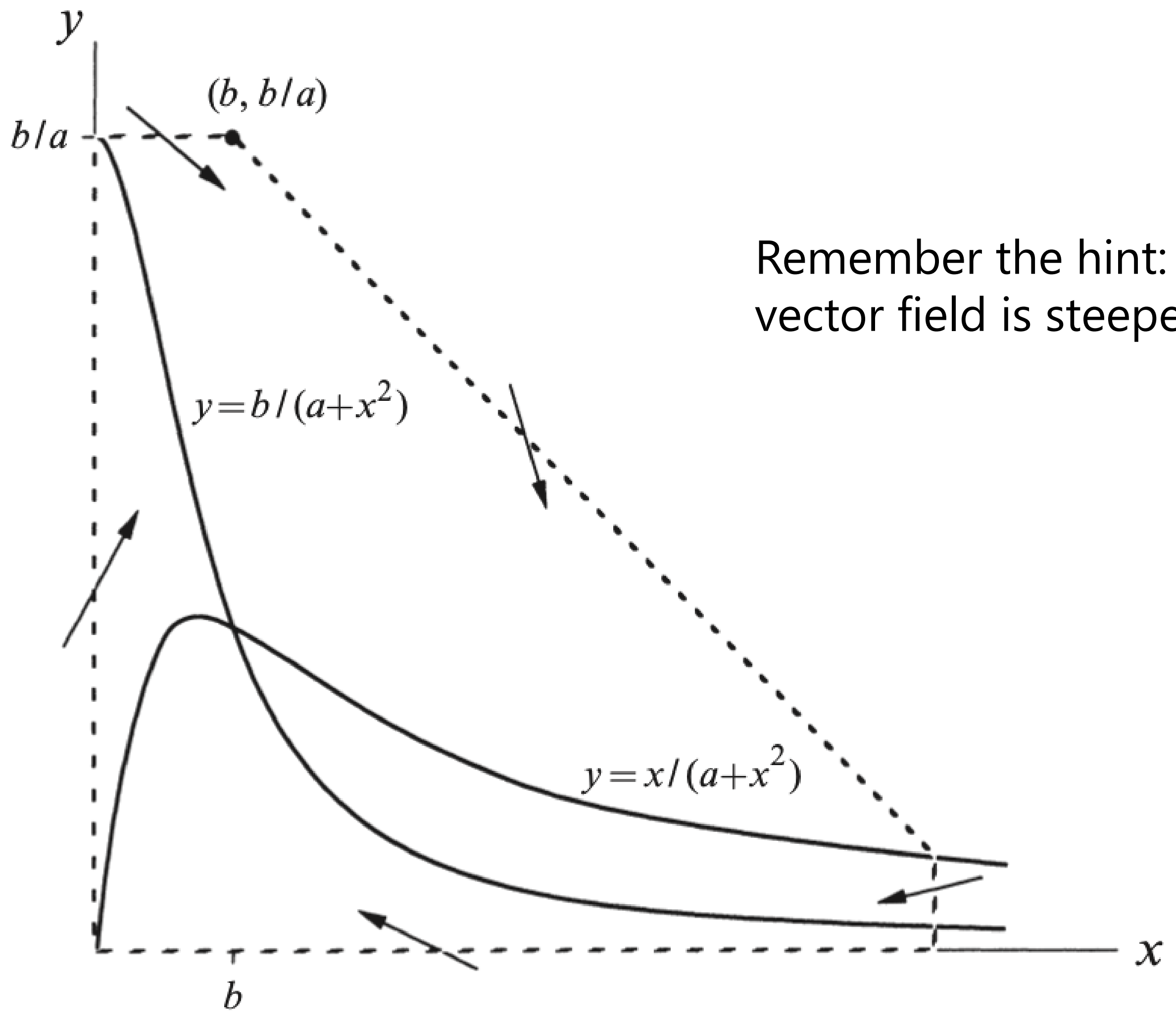
The nullclines follow

$$\dot{x} = 0, \qquad y = \frac{x}{a + x^2}$$

$$\dot{y} = 0, \qquad y = \frac{b}{a + x^2}$$

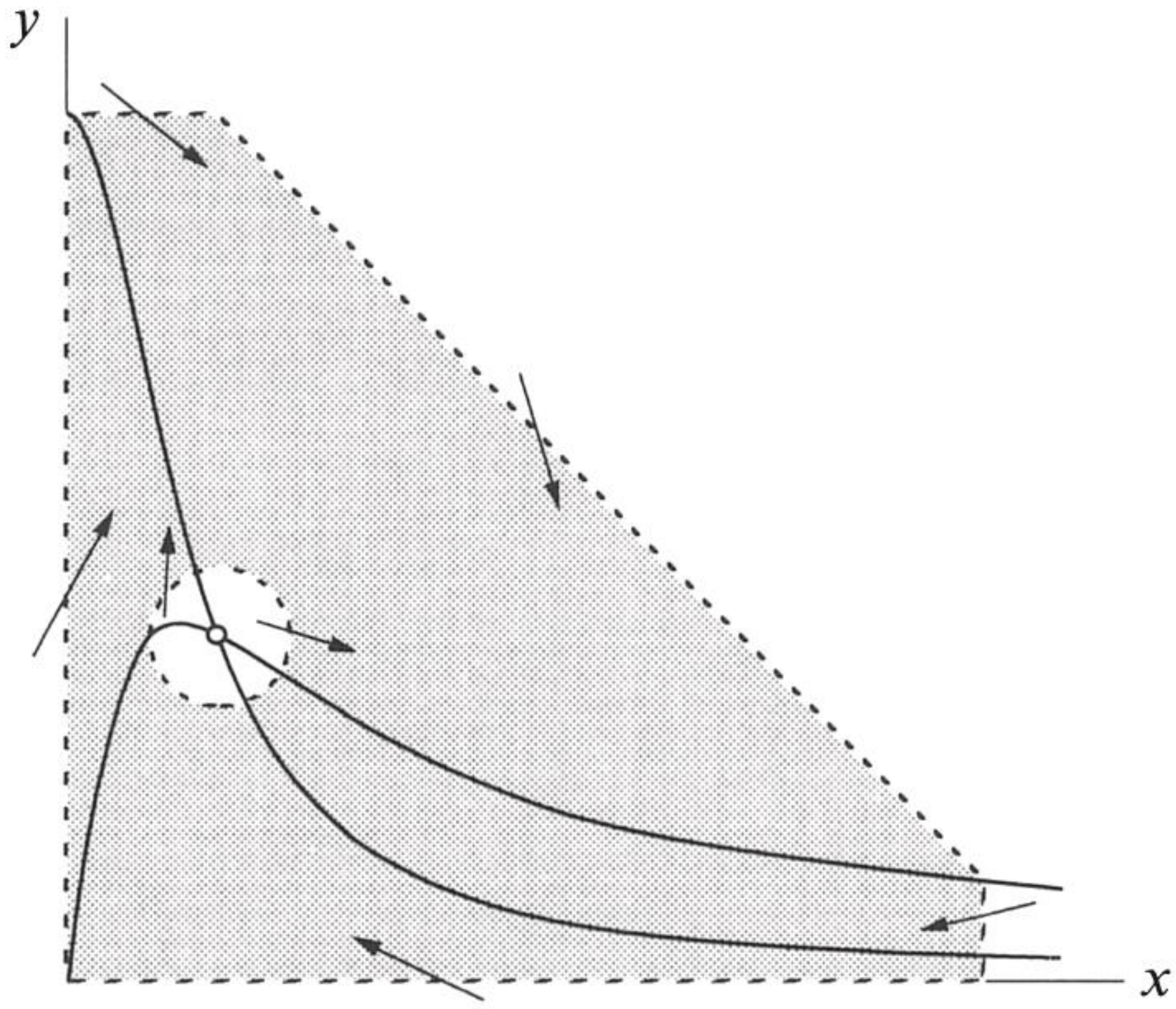
Decreases monotonally from $\frac{b}{a}$

Drawing a trapping area



Remember the hint: when $x > b$ the slope of the vector field is steeper than -1

Drawing a trapping area



An infinitessimal area around the stationary point can be excluded from R …

… but R is only a trapping area when that stationary point is repulsive.

Why?

Oscillatory glycolysis

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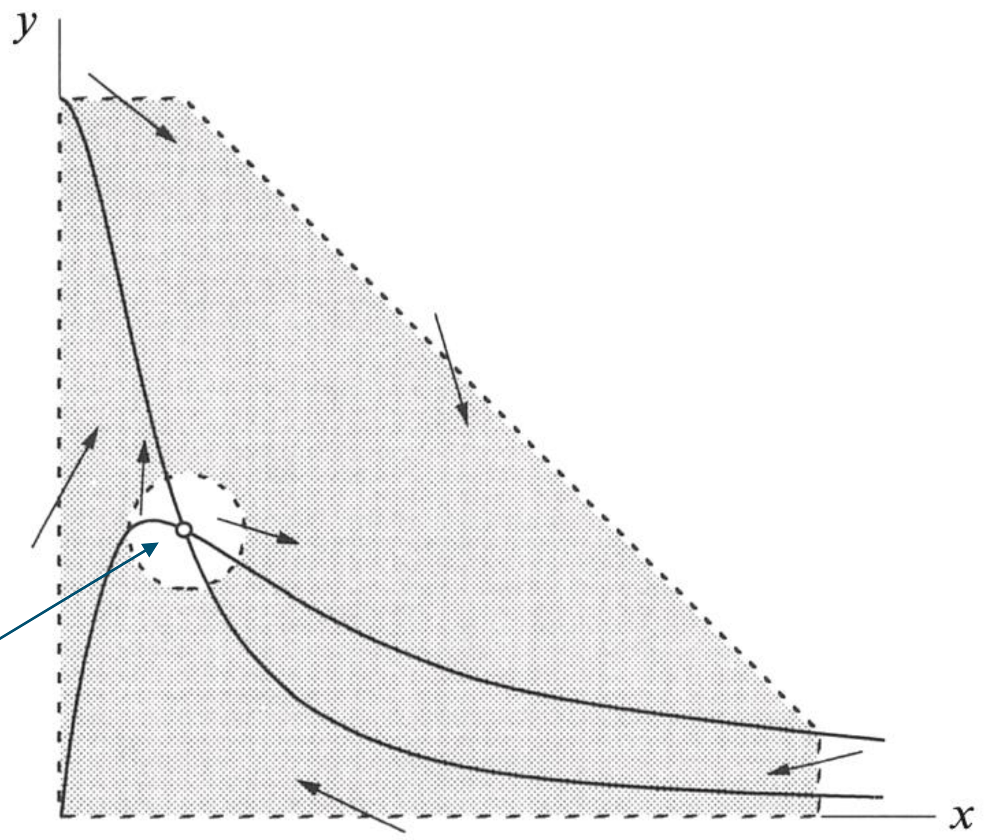
Here x is the concentration fo ADP and y is the concentration of fructose-6-phosphate (F6P).

Group exercise: prove that a closed oscillatory orbit exists for some combination of a, b

We just need to prove that for some combination of a, b the fixed point is repelling.

Hint: start by constructing the Jacobian



Oscillatory glycolysis

Yeast cells break down sugar in an oscillatory fashion. A model for this process is given by

$$\dot{x} = -x + ay + x^2 y$$
$$\dot{y} = b - ay - x^2 y$$

The Jacobian is

$$J = \begin{pmatrix} -1 + 2xy & a + x^2 \\ -2xy & -(a + x^2) \end{pmatrix}$$

The fixed point can be found at

$$x^* = b, \qquad y^* = \frac{b}{a + b^2}$$

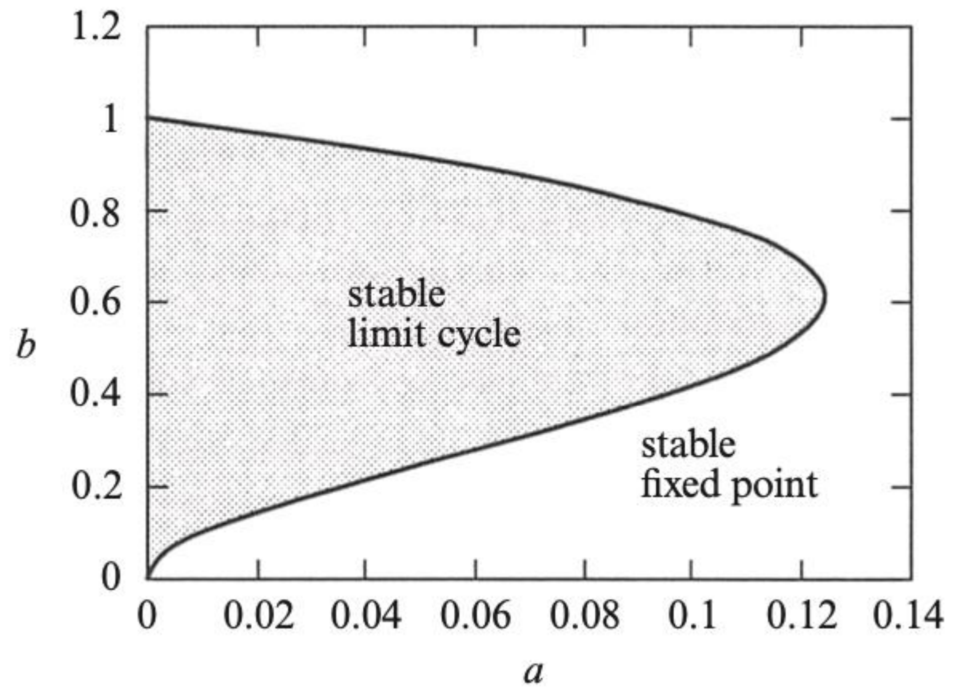
Fill in and find the determinant and trace

$$\Delta = a + b^2 > 0, \qquad \tau = -\frac{b^4 + (2a-1)b^2 + (a + a^2)}{a + b^2}$$

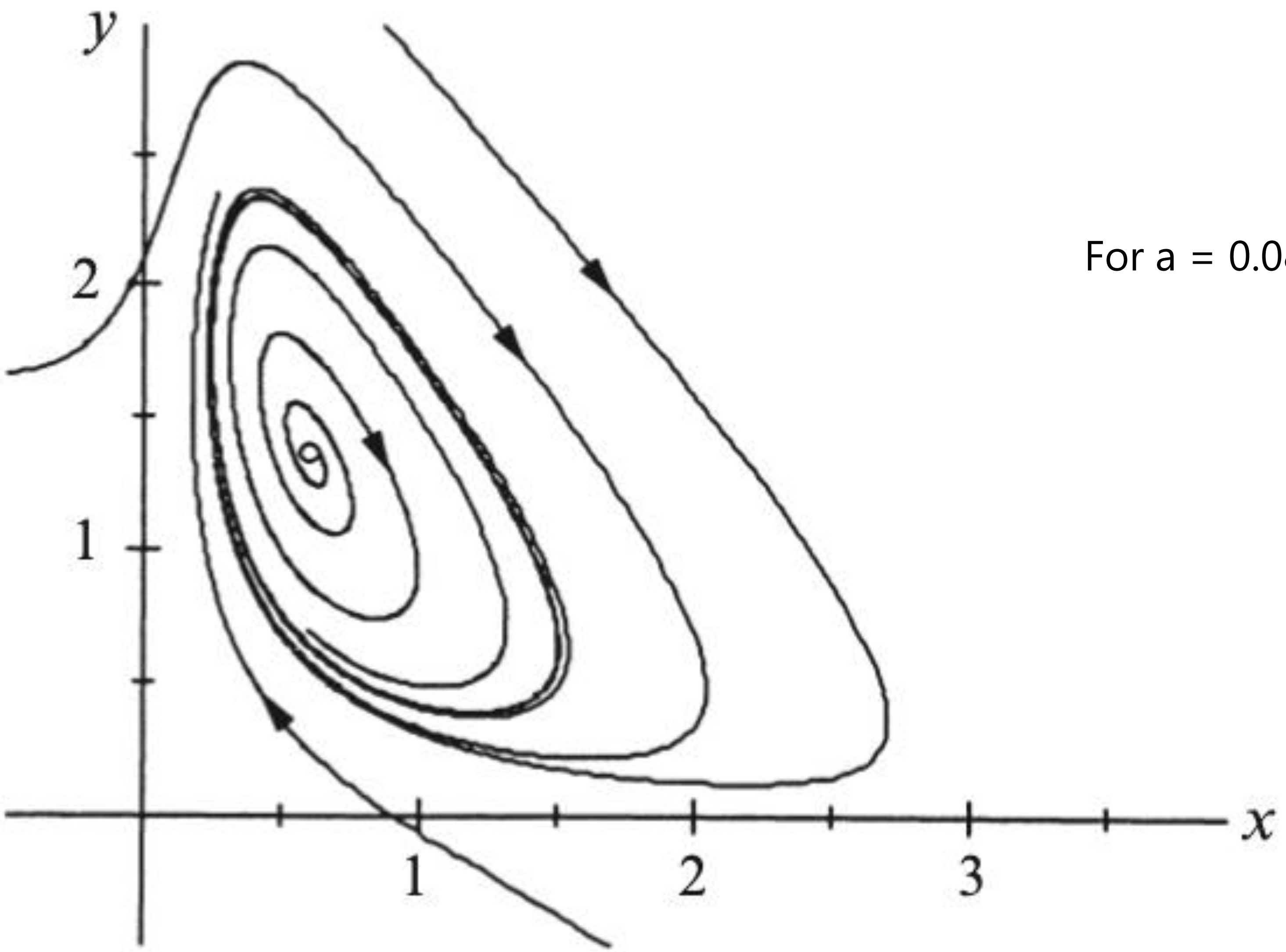
The fixed point is unstable when $\tau > 0$

The dividing line is at

$$b^2 = \frac{1}{2}\left(1 - 2a \pm \sqrt{1 - 8a}\right)$$

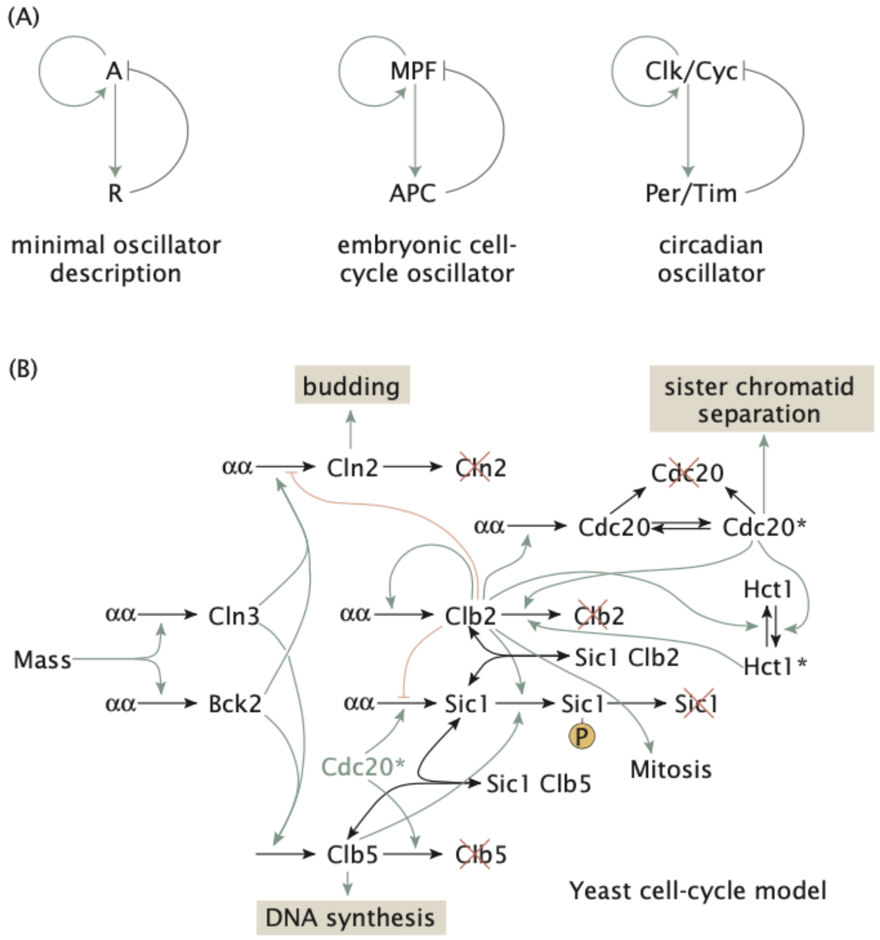


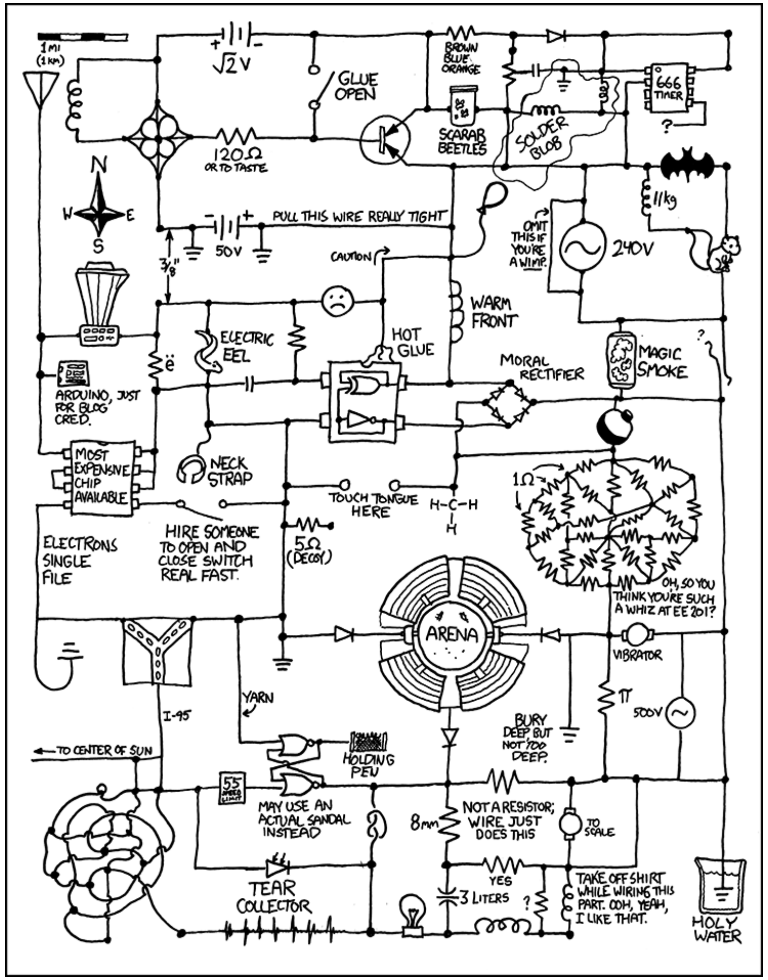
Oscillatory glycolysis



For a = 0.08, b=0.6

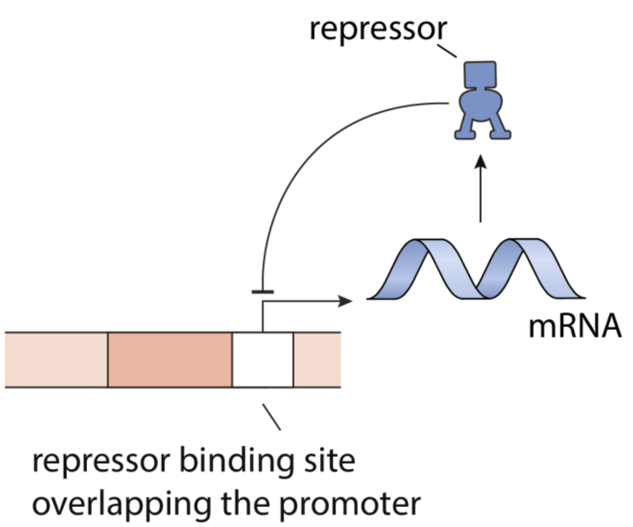
Gene regulation circuits can be very complex



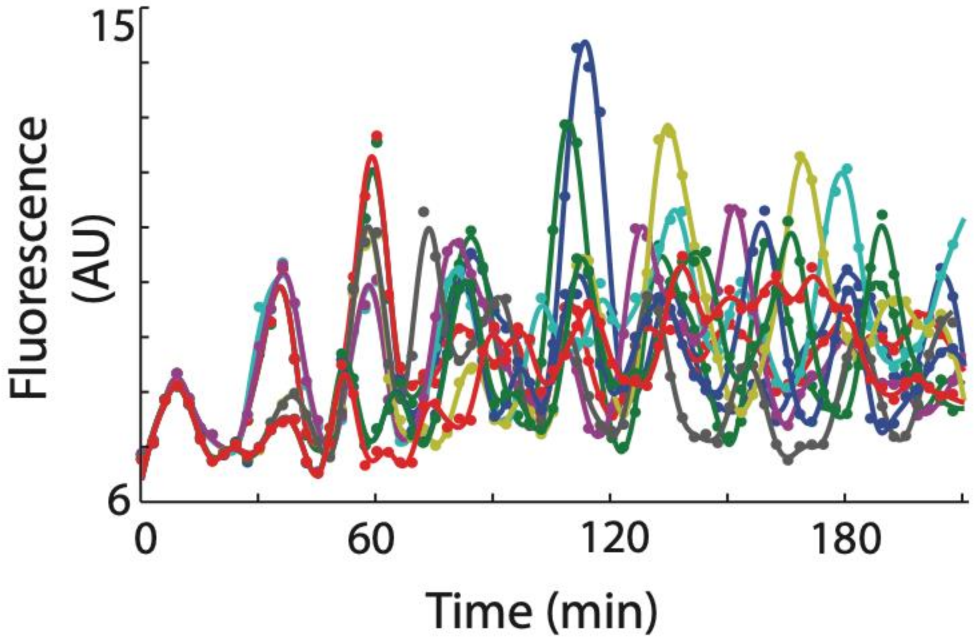


Is there a way we can quantitatively predict their outcome?

Oscillations in gene circuits



Single direct feedback loop in E. coli
LacI repressor with O1 operator site overlapping promoter
+ inducer IPTG



Stricker *et al. Nature* 2008

Normalised response function

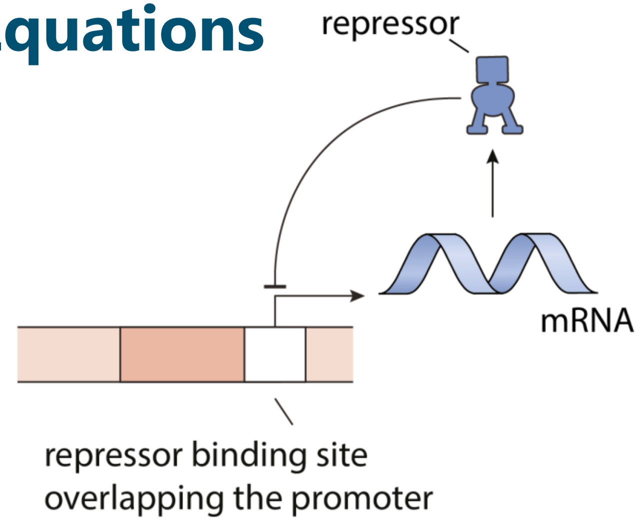
Modelling the circuit

$$\dot{m} = -\gamma_m m + \gamma_m \Phi(p)$$
$$\dot{p} = -\gamma_p p + \gamma_p m$$

Here, m, p are normalised concentrations of mRNA and protein and $\gamma_{m,p}$ are their degradation constants.

See e.g. Landman *et al.* BioRxiv https://doi.org/10.1101/2021.12.01.470700

Oscillations in gene circuits – Delay Differential Equations



It takes time to synthesise mRNA after the moment of transcription initiation. Finished mRNA is only 'released' into the pool after some time τ

Differential equations of the form

$$\dot{x} = f(x(t-\tau))$$

are **Delay Differential Equations** (DDEs)

Explicity time delay

Modelling the circuit

$$\dot{m} = -\gamma_m m + \gamma_m \Phi(p(t-\tau))$$
$$\dot{p} = -\gamma_p p + \gamma_p m(t)$$

Group question:

- Does this model have a stationary point?
- Where is the stationary point?

A stationary point exists at $m^* = p^* = \Phi(p^*)$

Here, m, p are normalised concentrations of mRNA and protein and $\gamma_{m,p}$ are their degradation constants.

See e.g. Landman *et al.* BioRxiv https://doi.org/10.1101/2021.12.01.470700

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Linear stability analysis of Delay Differential Equations

Yes, it's still possible to do linear stability analysis and find eigenvalues.

If we linearise, then solutions have the form $\boldsymbol{v} = \binom{a}{b}\exp(\lambda t)$.

The matrix equation to solve then becomes

$$\lambda \binom{a}{b} \exp(\lambda t) = \begin{pmatrix} -\gamma_m & \dfrac{\gamma_m \partial\Phi(p^*)}{\partial t}\exp(-\lambda\tau) \\ \gamma_p & -\gamma_p \end{pmatrix} \binom{a}{b} \exp(\lambda t)$$

Just a constant, independent of time

Evaluated at $t - \tau$ we get

$$\boldsymbol{v}(t-\tau) = \binom{a}{b}\exp(\lambda t)\boxed{\exp(-\lambda\tau)}$$

$$\dot{m} = -\gamma_m m + \gamma_m \Phi(p(t-\tau))$$
$$\dot{p} = -\gamma_p p + \gamma_p m(t)$$

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How to solve [illegible]? Almost an eigenvalue equation.

with your original derivation

Evaluated at $t-\tau$ we get

$$\boldsymbol{v}(t-\tau) = \binom{a}{b}\exp(\lambda t)\exp(-\lambda\tau)$$

$$\begin{aligned} \dot{m} &= -\gamma_m m + \gamma_m \Phi(p(t-\tau)) \\ \dot{p} &= -\gamma_p p + \gamma_p m(t) \end{aligned}$$

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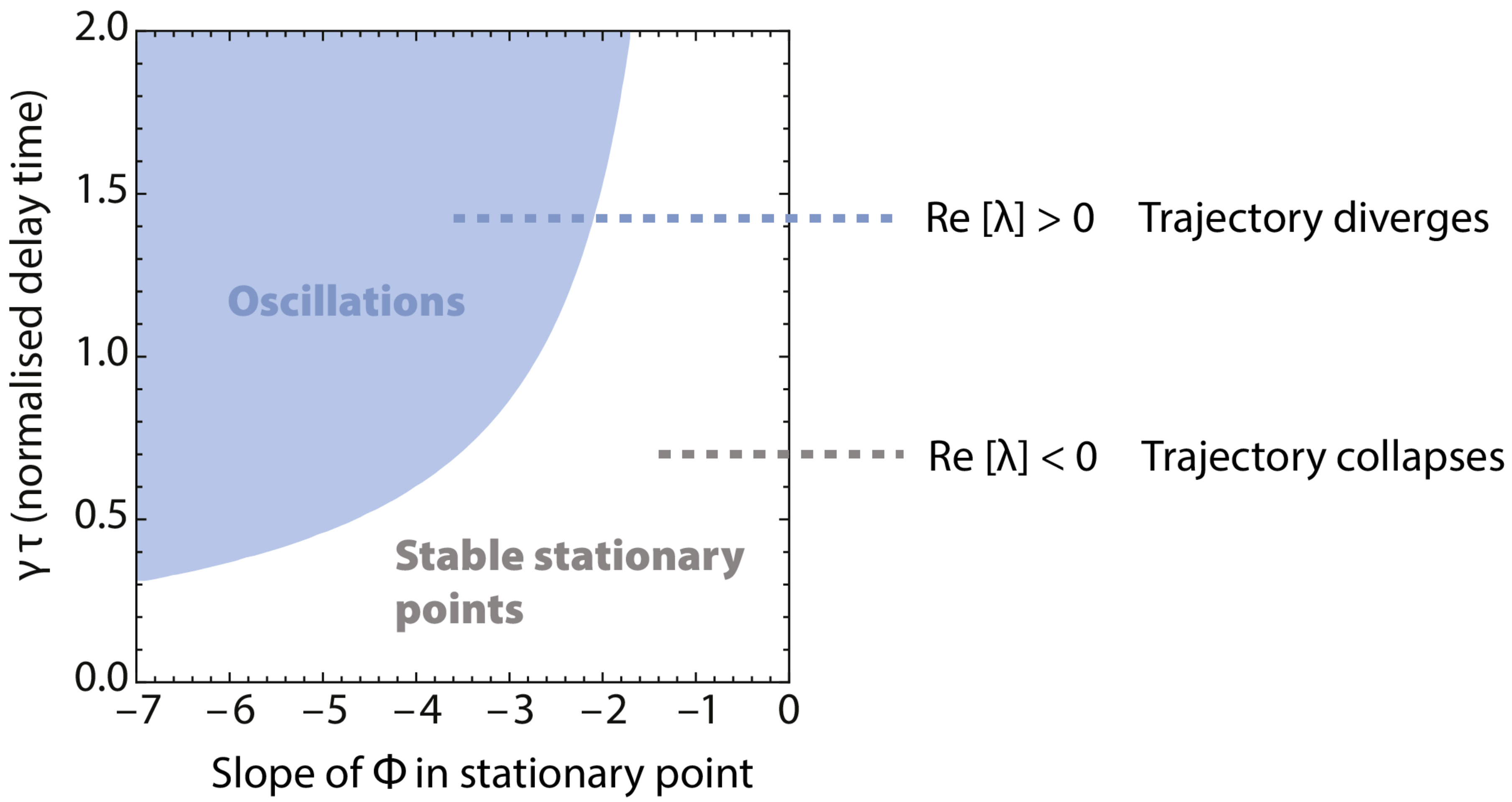
$$\begin{aligned} \dot{m} &= -\gamma_m m + \gamma_m \Phi(p(t-\tau)) \\ \dot{p} &= -\gamma_p p + \gamma_p m(t) \end{aligned}$$

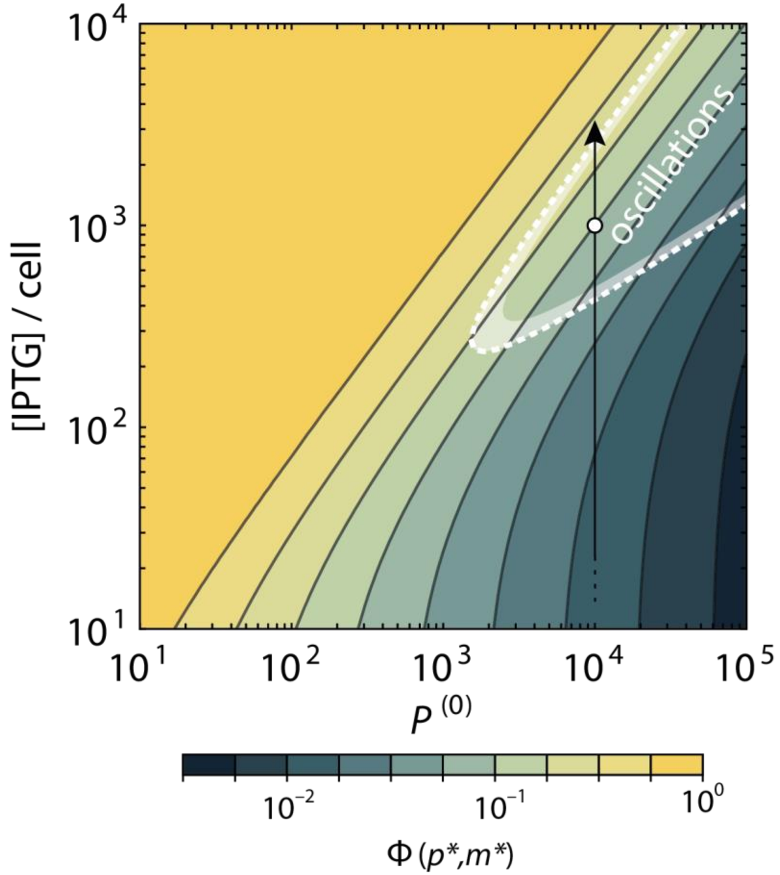
Write down the characteristic equation

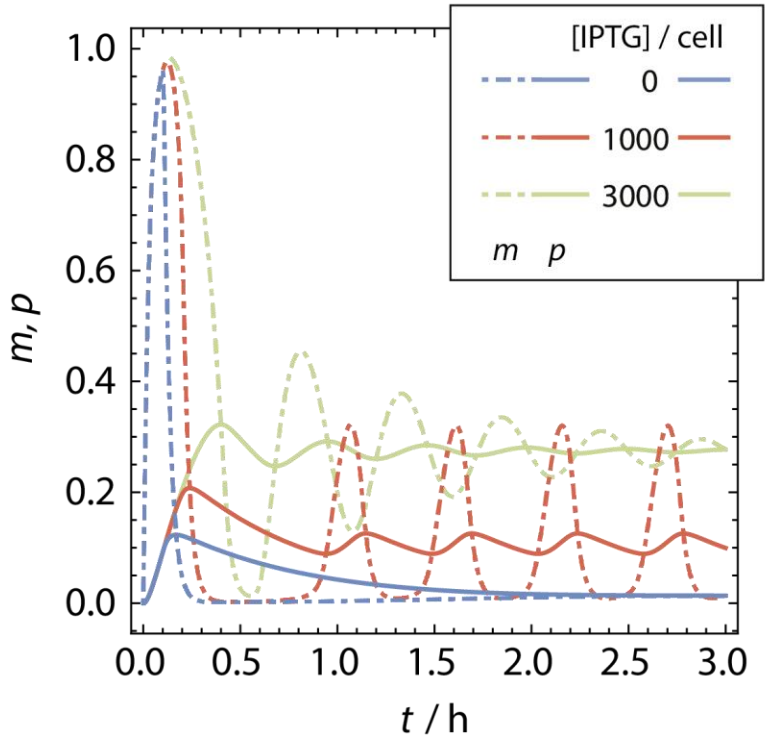
$$\det \begin{pmatrix} -\gamma_m - \lambda & \dfrac{\gamma_m \partial \Phi(p^*)}{\partial t} \exp(-\lambda \tau) \\ \gamma_p & -\gamma_p - \lambda \end{pmatrix} = 0$$

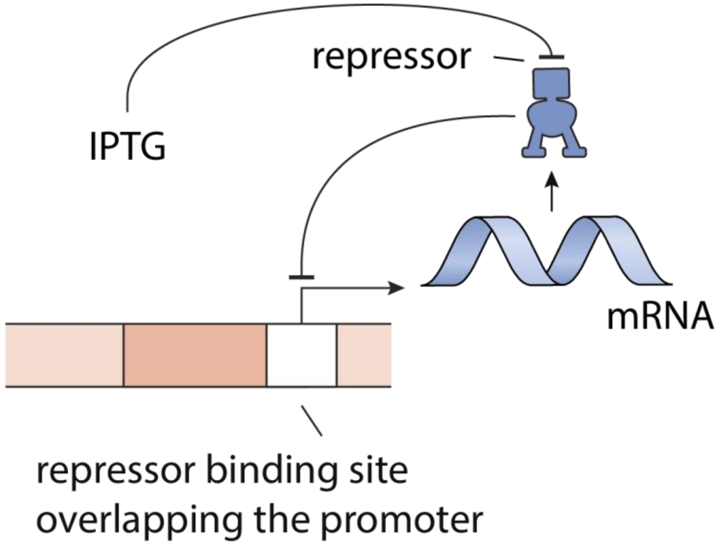
This has numerical solutions only



2.0
1.5
1.0
0.5
0.0
−7
−6
−5
−4
−3
−2
−1
0
γ τ (normalised delay time)
Slope of Φ in stationary point
Oscillations
Stable stationary points
Re [λ] > 0
Trajectory diverges
Re [λ] < 0
Trajectory collapses



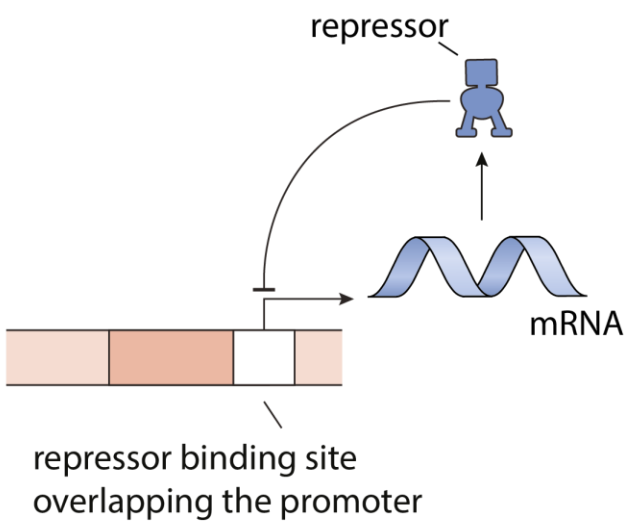


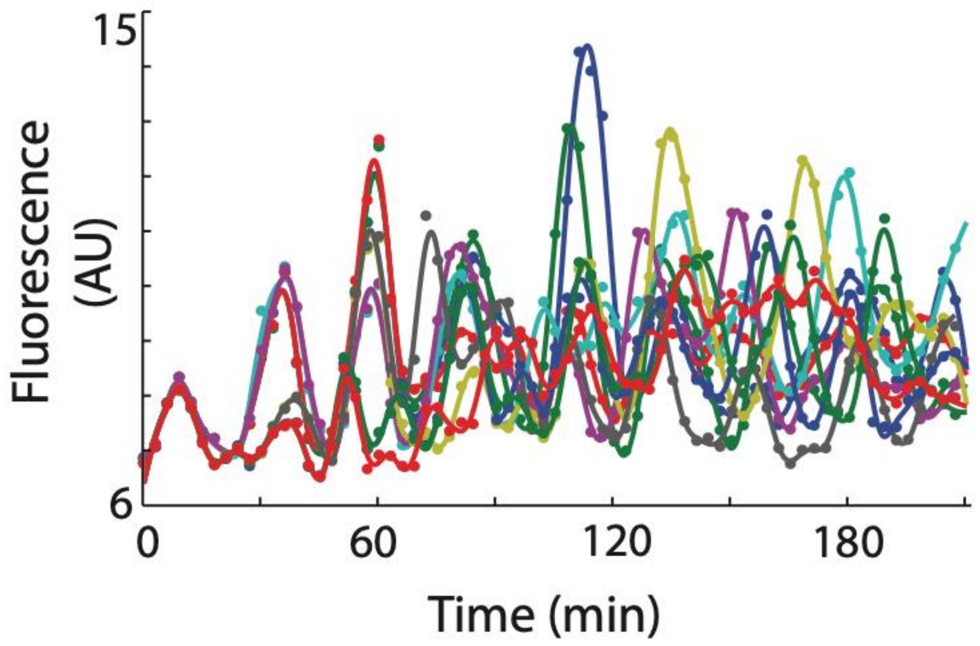


See e.g. Landman *et al.* BioRxiv https://doi.org/10.1101/2021.12.01.470700

The bad news...

There are 2 problems with this approach

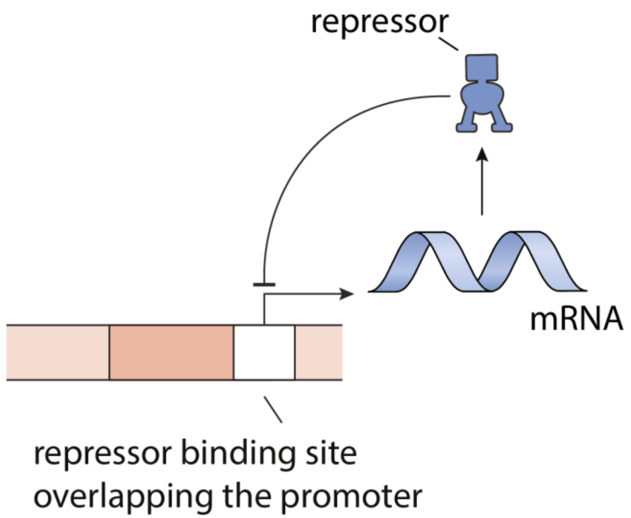




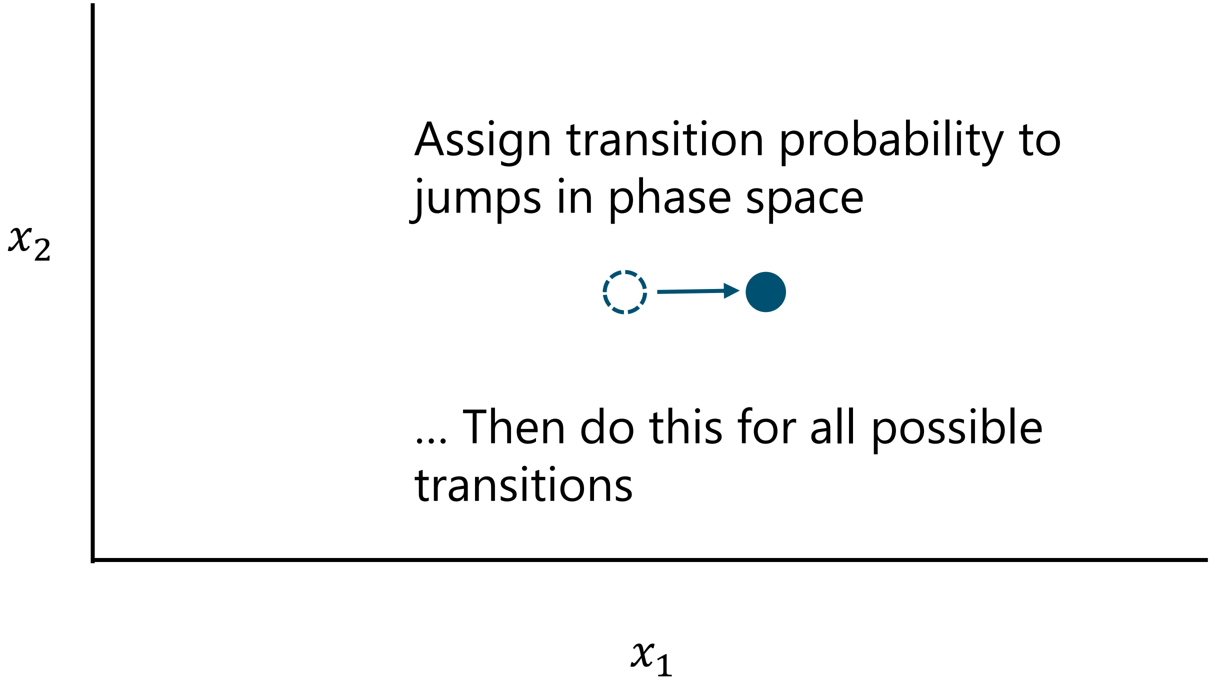
Gene regulation is bursty – stochastic

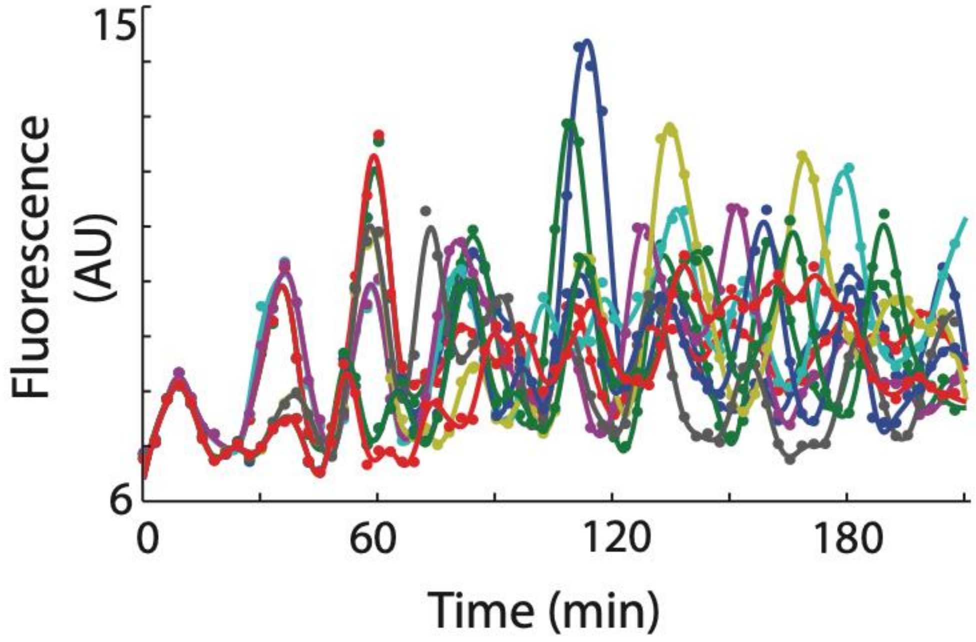
There are 2 problems with this approach

1) Gene production is noisy
2) Gene production is discrete



One way forward: chemical master equations





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Gene regulation is bursty – stochastic

There are 2 problems with this approach

1) Gene production is noisy
2) Gene production is discrete

One way forward: chemical master equations

x_2

Assign transition probability to jumps in phase space

… Then do this for all possible transitions

x_1

Then, the probability distribution of the system in phase space changes as

$$\frac{\partial P(\boldsymbol{x}, t | \boldsymbol{x}', t')}{\partial t} = \sum_{\text{all transitions}} W(x_i, x_i')$$

Direct Stochastic Simulation

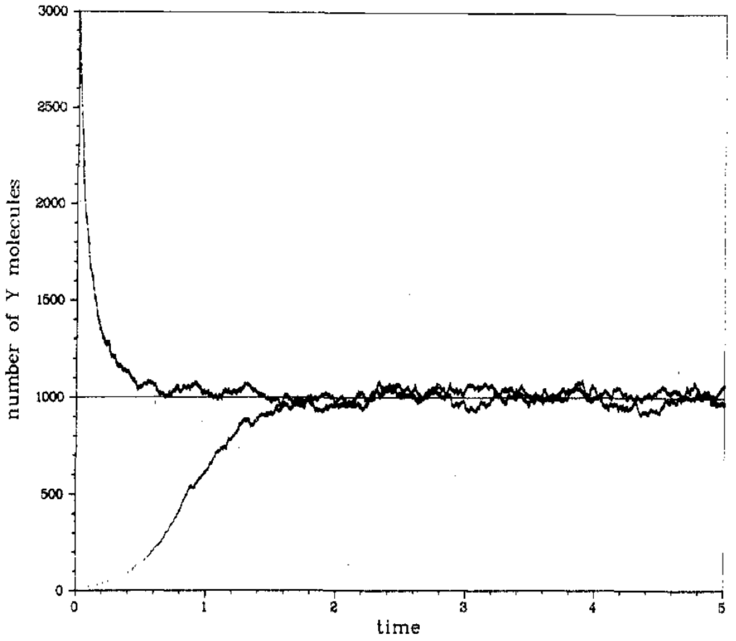
2340 Daniel T. Gillespie

Exact Stochastic Simulation of Coupled Chemical Reactions

Daniel T. Gillespie*

Research Department, Naval Weapons Center, China Lake, California 93555 *(Received May 12, 1977)*

Publication costs assisted by the Naval Weapons Center



Solving chemical master equations usually numerical only.

One way is direct stochastic simulation
- Gillespie's algorithm

Computer practical – Gillespie algorithm

Stochastic simulation of population of foxes and rabbits in the same ecosystem.

We will evaluate the behaviour deterministically and do a direct stochastic simulation

(using the GillesPy2 package for a Jupyter nb)

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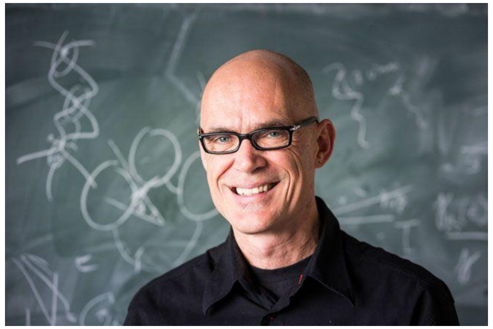
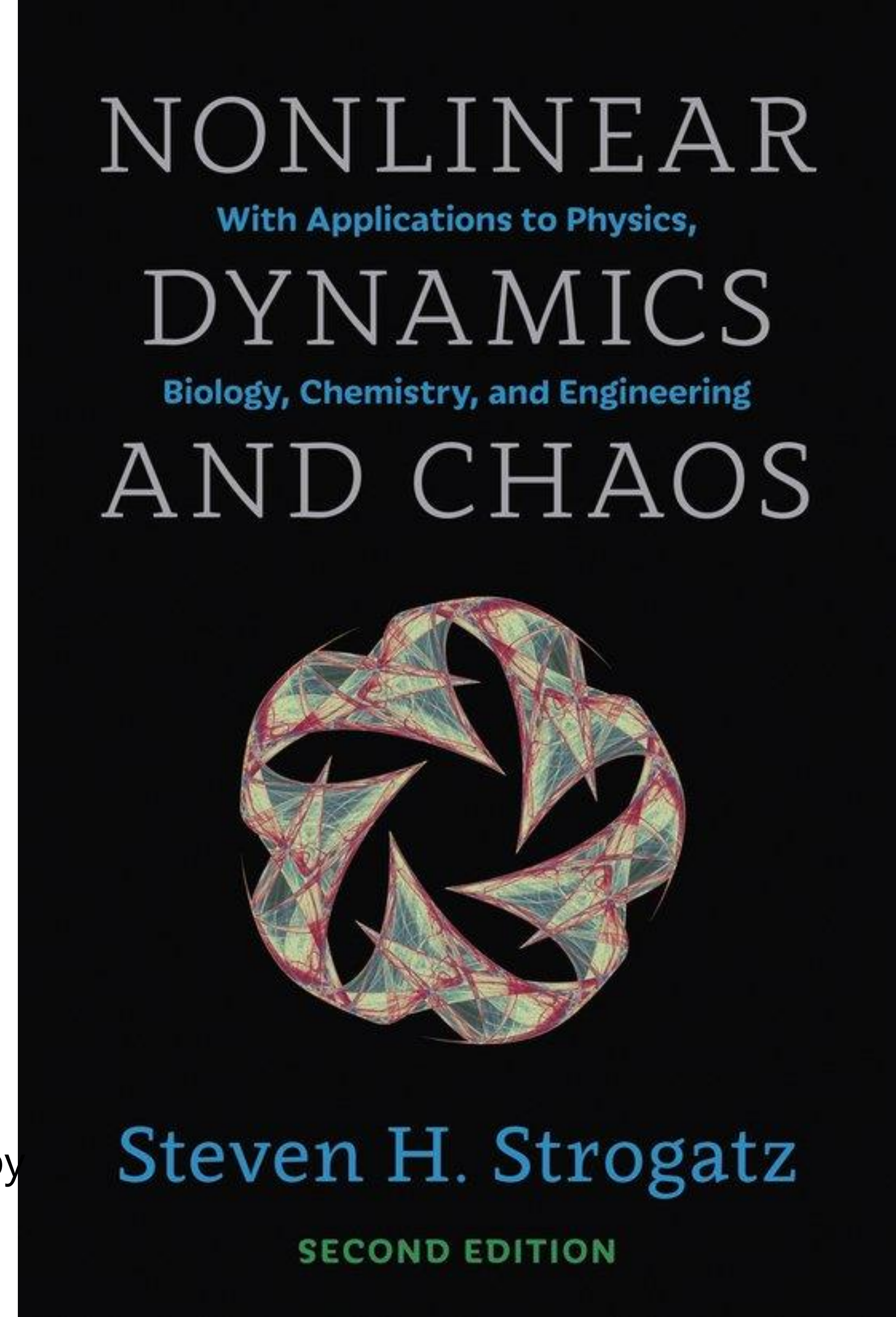
Thanks

Sjoerd Verduyn Lunel



Willem Kegel

These lectures are heavily influenced by the book by



Some self-promotion