

# MA32009 Lecture slides

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# Lecture 1

# Malthusian model - derivation and qualitative analysis

## A general model

$$\frac{dN}{dt} = f(N)N = H(N),$$

# Numerical solution

# Dimensions and nondimensionalisation

As an example, consider the linear ODE

$$\frac{dN}{dt} = rN.$$

## Introducing dimensionless variables

## Steady-state analysis



# Lecture 10

- ▶ Recap
- ▶ Techniques for single first order ODE (ctd)
- ▶ Example model 1: Logistic growth
- ▶ Example model 2: Spruce budworm

# Linear stability analysis

## Linear stability analysis (ctd)

## Graphical solution

# Bifurcation diagrams

## Example model 1: the logistic growth equation

$$\frac{dN}{dt} = rN(t) \left( 1 - \frac{N(t)}{K} \right).$$

## Numerical solution

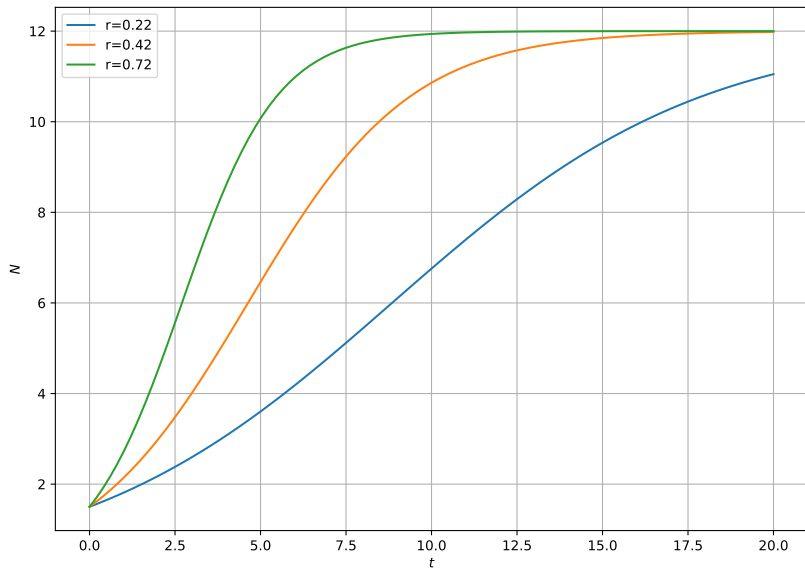


Figure 1: Numerical solution of the logistic growth model

## Steady states and linear stability



# Graphical analysis

An exact solution of the logistic growth equation

## Example model 2: the spruce budworm model

$$\frac{dN}{dt} = r_B N \left( 1 - \frac{N}{K_B} \right) - \frac{BN^2}{A^2 + N^2}, \quad (1)$$

## Nondimensionalisation

$$\frac{dn}{d\tau} = rn \left( 1 - \frac{n}{q} \right) - \frac{n^2}{1 + n^2} = H(n),$$

## Plotting the RHS

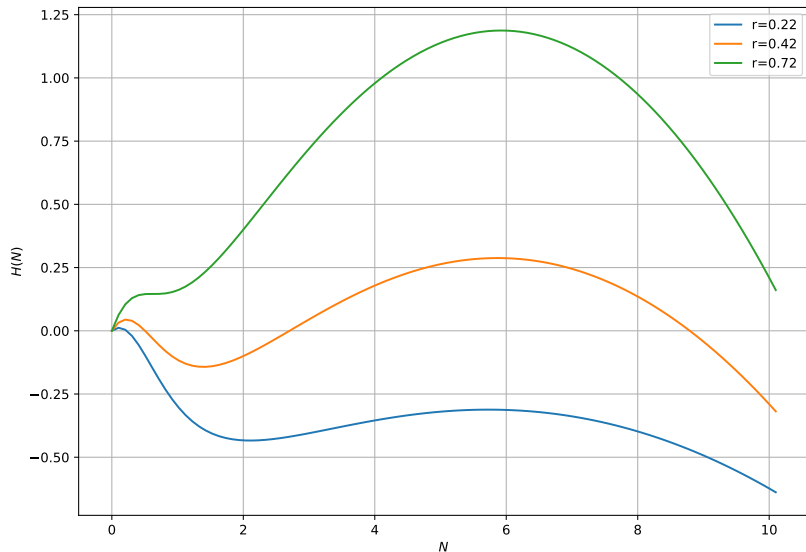
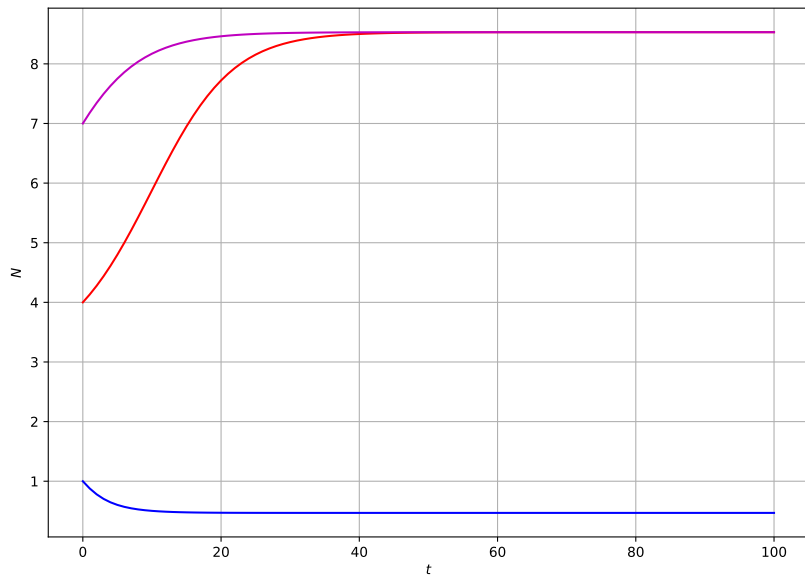


Figure 2: RHS of spr. budworm model

## Numerical solution



## Steady state analysis

$$rn^*(1 - \frac{n^*}{q}) - \frac{n^{*2}}{1 + n^{*2}} = 0.$$

# Linear stability analysis



## Lecture 12

### **i** Recap - Spruce budworm model

$$\frac{dn}{d\tau} = rn \left( 1 - \frac{n}{q} \right) - \frac{n^2}{1 + n^2} = H(n),$$

Steady states:  $n^* = 0$  or

$$rn^* \left( 1 - \frac{n^*}{q} \right) - \frac{n^{*2}}{1 + n^{*2}} = 0.$$

- ▶  $r$  small - one stable steady state
- ▶  $r$  large - one stable steady state (outbreak)
- ▶  $r$  intermediate - bistability (two stable steady states and one unstable)

Today: bifurcation analysis, hysteresis, harvesting

## Tangent bifurcations in $rq$ space

## Plotting stability regions in the $rq$ plane

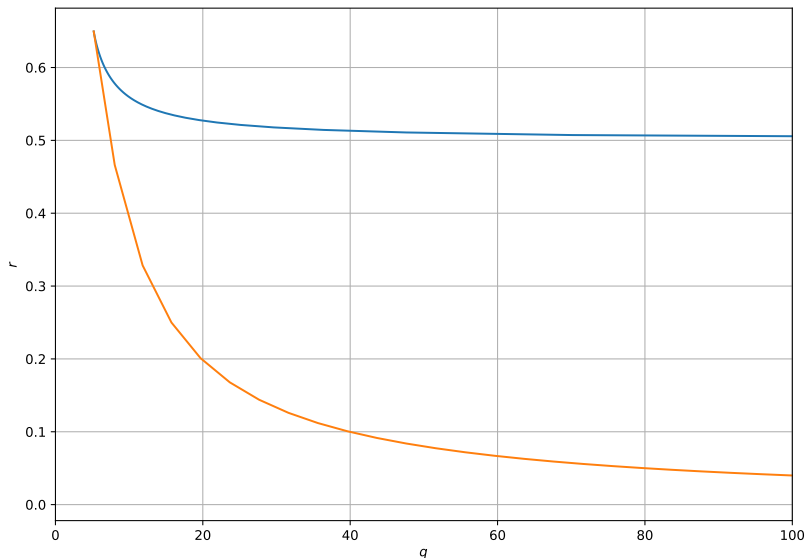


Figure 3: Bifurcations in the  $rq$  plane

Hysteresis - irreversible transitions in solution behaviour

# Hysteresis

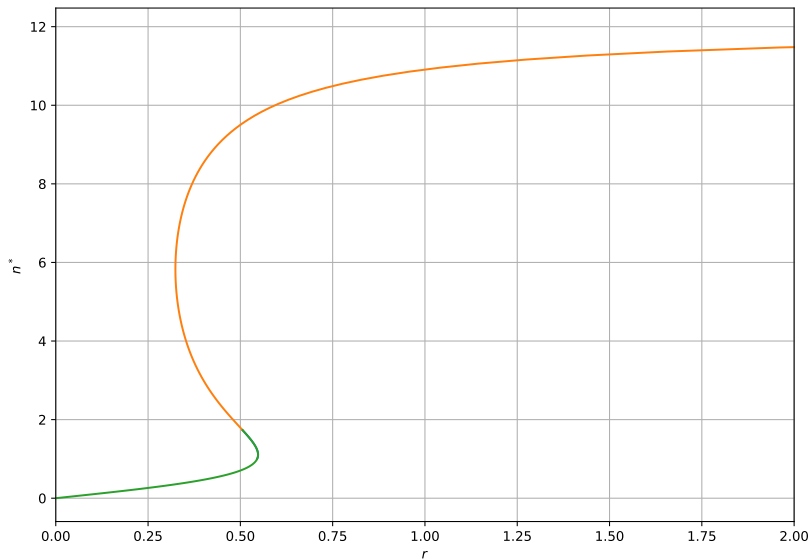


Figure 4: Bifurcations in the  $r$  $q$  plane

## Harvesting

- ▶ use models to simulate how much resource can be extracted?
- ▶ approach: take model without harvesting and add in harvesting terms

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - EN.$$

where  $E$  is the harvesting rate.

Question: what value of  $E$  maximises the long term yield?

## Delay differential equation models

$$\frac{dN}{dt} = H(N(t), N(t - T)),$$

## A linear delay differential equation model

$$\frac{dN}{dt} = -N(t - T),$$



## Linear stability analysis (ctd.)

$$\frac{dN}{dt} = -N(t - T),$$

## Two dependent variable ODE models

$$\frac{du}{dt} = f(u, v),$$

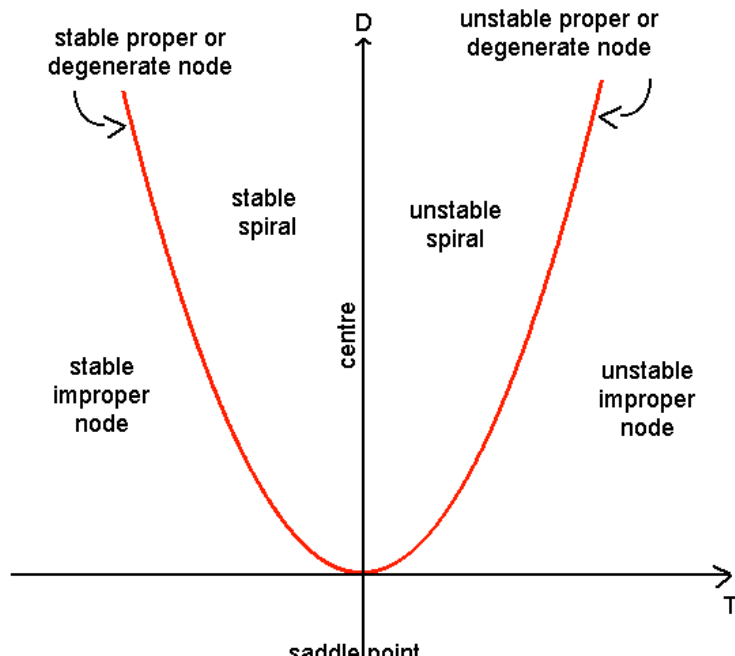
$$\frac{dv}{dt} = g(u, v).$$

## Steady states

# Linear stability analysis

## Linear stability analysis (ctd.)

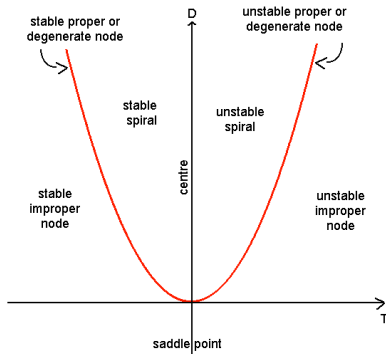
## The trace determinant plane



# Lecture 14

## Recap

$$\begin{aligned}\frac{du}{dt} &= f(u, v), \\ \frac{dv}{dt} &= g(u, v).\end{aligned}$$



$$\lambda = \frac{\text{tr} A \pm \sqrt{\text{tr} A^2 - 4 \det A}}{2}.$$

# Nullclines



## Periodic solutions (Poincaré-Bendixson theorem)

- ▶ System of two ODEs
- ▶ Confined set containing unstable node or spiral
- ▶ as  $t \rightarrow \infty$ , the trajectory will tend towards a limit cycle.

## No periodic solutions - (Dulac criterion)

- ▶  $D$  simply connected region in the plane
- ▶  $B(x, y)$ , continuously differentiable on  $D$ , with

$$\frac{\partial}{\partial u}(Bf) + \frac{\partial}{\partial v}(Bg)$$

not identically zero and does not change sign in  $D$ .

# Lotka Volterra

$$\frac{dN}{dt} = aN - bNP,$$

$$\frac{dP}{dt} = cNP - dP,$$

## Nondimensionalisation

$$\frac{dn}{d\tau} = n(1 - p) = f(n, p),$$

$$\frac{dp}{d\tau} = \alpha p(n - 1) = g(n, p),$$

## Lecture 15 - recap

Lotka-Volterra model - predator prey interaction

$n$  - prey  $p$  - predator

$$\begin{aligned}\frac{dn}{d\tau} &= n(1 - p) = f(n, p), \\ \frac{dp}{d\tau} &= \alpha p(n - 1) = g(n, p),\end{aligned}$$

Strategy:

- ▶ numerical solution
- ▶ steady states
- ▶ nullclines
- ▶ linear stability

# Numerical solutions

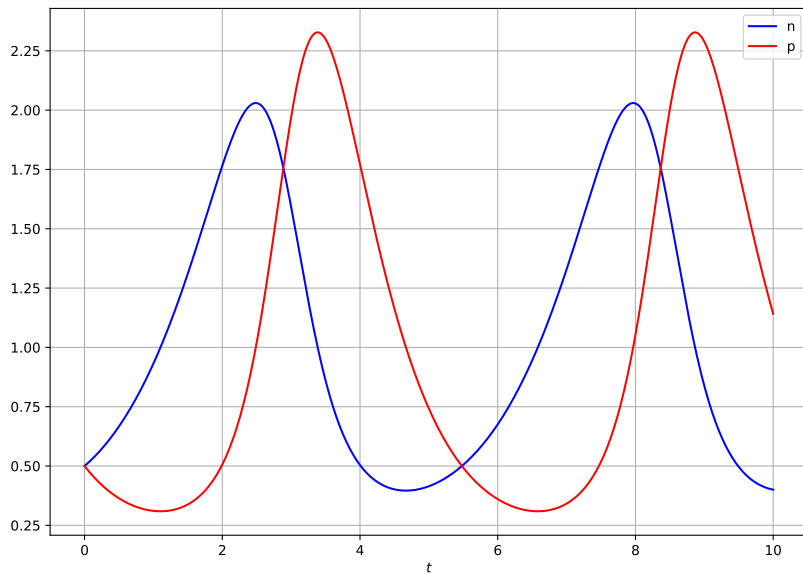


Figure 6

## Steady states

# Nullclines



# The phase plane

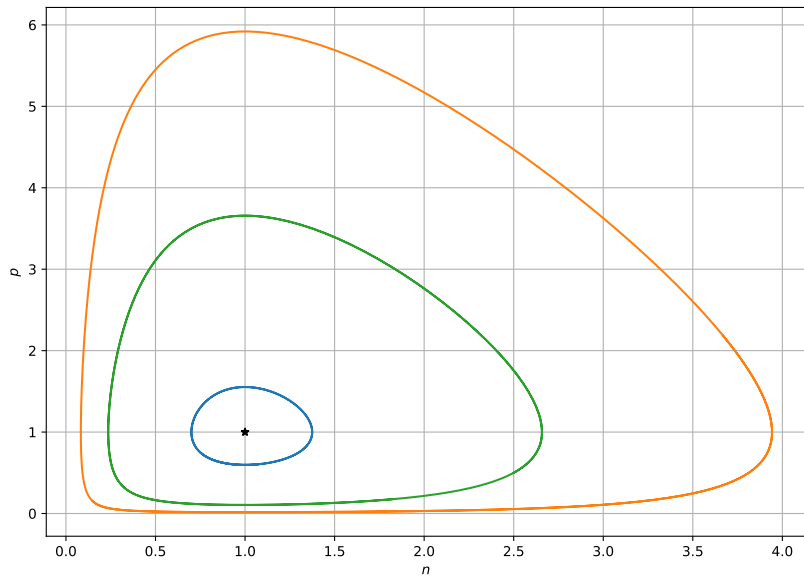


Figure 7

# Linear stability

# Integration

...

# Lecture 16 Competition

## **i** Recap: Lotka-Volterra model

- ▶ predator prey interaction
- ▶  $n$  - prey
- ▶  $p$  - predator

$$\begin{aligned}\frac{dN}{dt} &= aN - bNP, \\ \frac{dP}{dt} &= cNP - dP,\end{aligned}$$

## **i** Aim - introduce and analyse a model of competition

## Competition model

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left( 1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right), \\ \frac{dN_2}{dt} &= r_2 N_2 \left( 1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right),\end{aligned}$$

- ▶ Justify why this is a model for competition
- ▶ Define model parameters
- ▶ Explain the meaning of each of the terms in the model

# Nondimensionalisation

$$\frac{dn_1}{d\tau} = n_1 (1 - n_1 - a_{12}n_2) = f(n_1, n_2),$$
$$\frac{dn_2}{d\tau} = \rho n_2 (1 - n_2 - a_{21}n_1) = g(n_1, n_2),$$

► Define  $\rho$ ,  $a_{12}$  and  $a_{21}$

## Nondimensionalisation (ctd.)



## Steady states

## Steady states (ctd)

# Nullclines

## Lecture 17 Competition

$$\begin{aligned}\frac{dn_1}{d\tau} &= n_1 (1 - n_1 - a_{12}n_2) = f(n_1, n_2), \\ \frac{dn_2}{d\tau} &= \rho n_2 (1 - n_2 - a_{21}n_1) = g(n_1, n_2),\end{aligned}$$

Steady states:

$$(0, 0), (1, 0), (0, 1)$$

and

$$\left( \frac{1 - a_{12}}{1 - a_{12}a_{21}}, \frac{1 - a_{21}}{1 - a_{12}a_{21}} \right).$$

## Linear stability analysis

$$A_{(n_1^*, n_2^*)} = \begin{pmatrix} 1 - 2n_1 - a_{12}n_2 & -a_{12}n_1 \\ -\rho a_{21}n_2 & \rho(1 - 2n_2 - a_{21}n_1) \end{pmatrix}_{(n_1^*, n_2^*)}.$$

## Linear stability analysis (ctd)

# Phase portrait (one for each qualitatively distinct case)

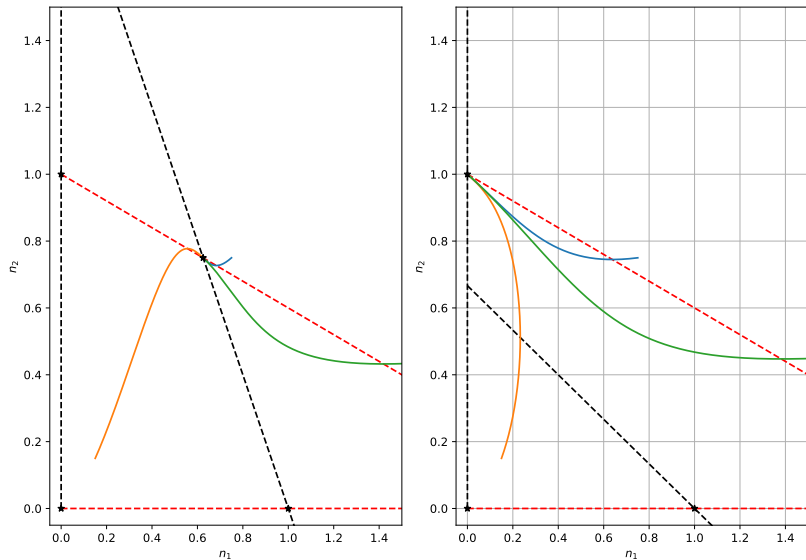


Figure 8

# Insight



## Mutualism/symbiosis

$$\begin{aligned}\frac{dn_1}{d\tau} &= n_1(1 - n_1 + a_{12}n_2) = f(n_1, n_2), \\ \frac{dn_2}{d\tau} &= \rho n_2(1 - n_2 + a_{21}n_1) = g(n_1, n_2).\end{aligned}$$

## Steady states

This model has steady-states  $(0, 0)$ ,  $(1, 0)$ ,  $(0, 1)$  and

$$(n_1^*, n_2^*) = \left( \frac{1 + a_{12}}{1 - a_{12}a_{21}}, \frac{1 + a_{21}}{1 - a_{12}a_{21}} \right).$$

## Coexistence steady state

# Summary

- ▶ Predator-prey, competition, mutualism
- ▶ techniques to analyse systems of nonlinear ODEs

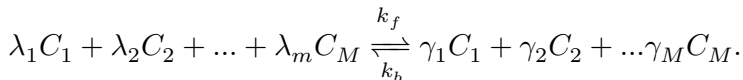
# Lecture 18 Biochemical kinetics

- ▶ Cells make proteins via gene transcription and translation
- ▶ Proteins can interact
- ▶ Molecular biology is the study of the molecules that underpin biological phenomena
- ▶ For example: the cell cycle regulated by changing concentrations of cyclin/CDKs

## **i** Our question

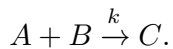
How do we mathematically describe networks of interacting chemical?

LOMA - reaction rate proportional to product of concentration of reactants

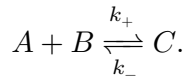


# Conservation equation

A forwards reaction

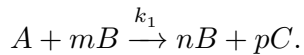


## A reversible reaction

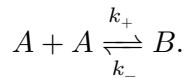




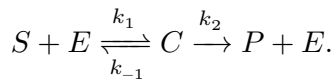
## General stoichiometric constants



## A reversible dimerisation



## Enzyme kinetics



## Numerical solution

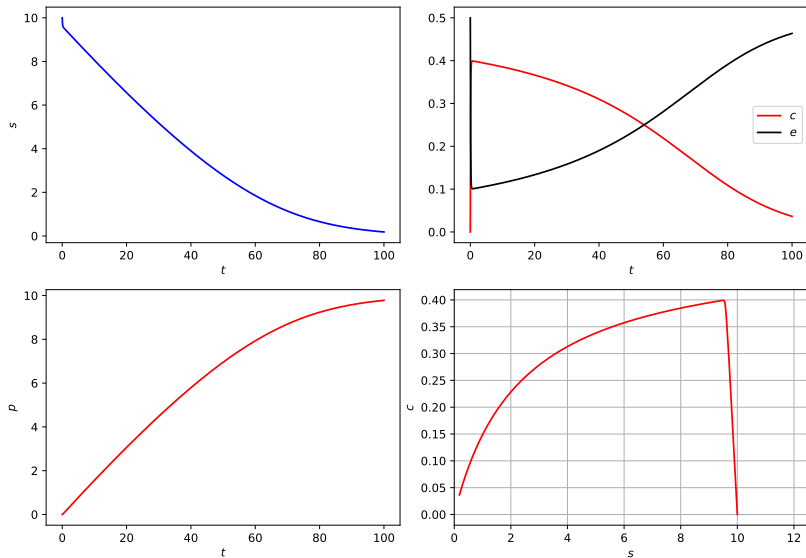


Figure 9: Numerical solutions of the Michaelis Menten model

# Dimension reduction

QSSA

## Nondimensionalisation

$$\begin{aligned}\frac{du}{d\tau} &= -u + (u + K - \lambda)v, \\ \epsilon \frac{dv}{d\tau} &= u - (u + K)v,\end{aligned}$$

where

$$\lambda = \frac{k_2}{k_1 s_0}, \quad K = \frac{k_{-1} + k_2}{k_1 s_0}, \quad \epsilon = \frac{e_0}{s_0}.$$

Propose asymptotic expansion: outer solution

$$u(\tau; \epsilon) = u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + \dots = \sum_{n=0}^{\infty} u_n(\tau) \epsilon^n,$$

$$v(\tau; \epsilon) = v_0(\tau) + \epsilon v_1(\tau) + \epsilon^2 v_2(\tau) + \dots = \sum_{n=0}^{\infty} v_n(\tau) \epsilon^n.$$

Substitute:



Gather terms in powers of epsilon

## Leading order solution

## An inner solution

Rescale time:

$$\sigma = \frac{\tau}{\epsilon}.$$

Define

$$u(\tau; \epsilon) = U(\sigma; \epsilon),$$

$$v(\tau; \epsilon) = V(\sigma; \epsilon).$$

## The inner problem

$$\begin{aligned}\frac{dU}{d\sigma} &= -\epsilon U + \epsilon(U + K - \lambda)V, \\ \frac{dV}{d\sigma} &= U - (U + K)V.\end{aligned}$$

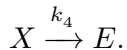
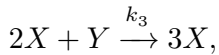
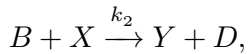
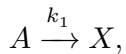
## Seek series solutions

$$U(\sigma; \epsilon) = U_0(\sigma) + \epsilon U_1(\sigma) + \epsilon^2 U_2(\sigma) + \dots = \sum_{n=0}^{\infty} U_n(\sigma) \epsilon^n,$$

$$V(\sigma; \epsilon) = V_0(\sigma) + \epsilon V_1(\sigma) + \epsilon^2 V_2(\sigma) + \dots = \sum_{n=0}^{\infty} V_n(\sigma) \epsilon^n.$$

## Mathching inner and outer solutions

# The Brusselator



## Nondimensional form

$$\begin{aligned}\frac{dx}{d\tau} &= a - bx + x^2y - x = f(x, y), \\ \frac{dy}{d\tau} &= bx - x^2y = g(x, y),\end{aligned}\tag{2}$$