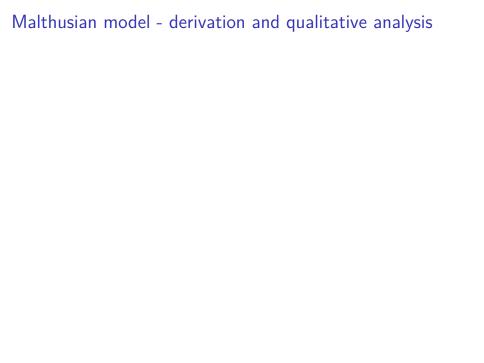
#### MA32009 Lecture slides

Philip Murray

#### Lecture 1



#### A general model

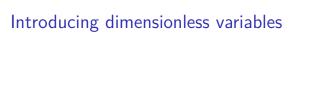
$$\frac{dN}{dt} = f(N)N = H(N),$$

# Numerical solution

#### Dimensions and nondimensionalisation

As an example, consider the linear ODE

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

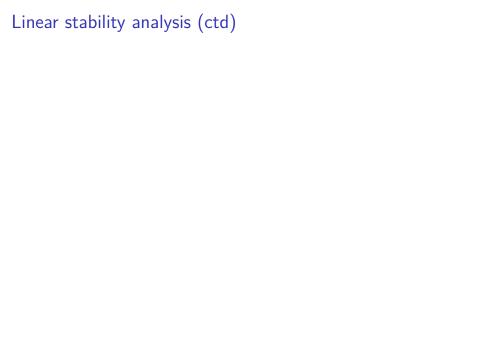


# Steady-state analysis

#### Lecture 10

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





# 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

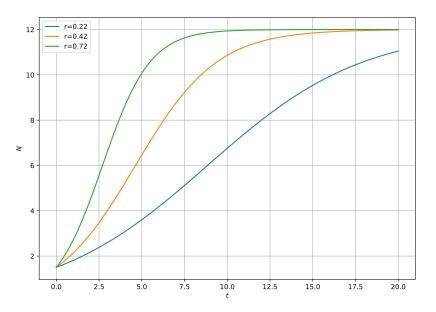
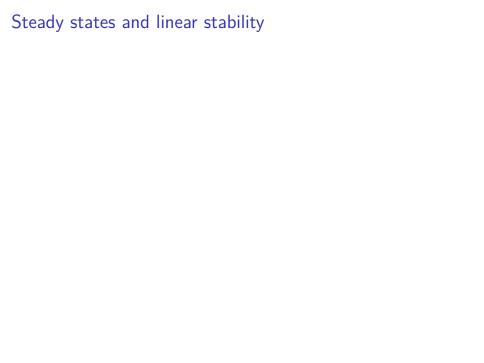
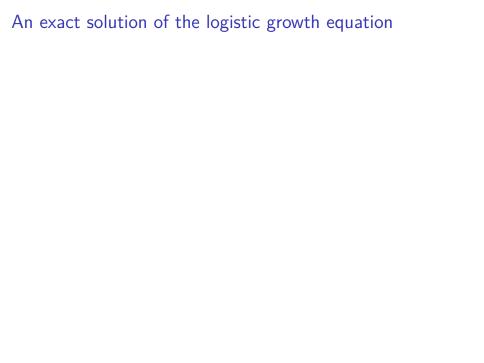


Figure 1: Numerical solution of the logistic growth model



# Graphical analysis



#### Example model 2: the spruce budworm model

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

#### Nondimensionalisation

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

# Plotting the RHS

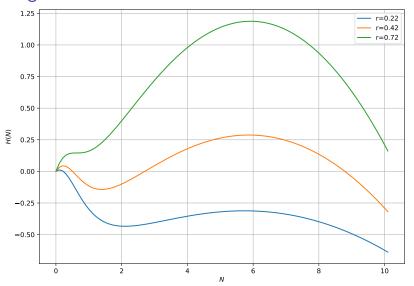
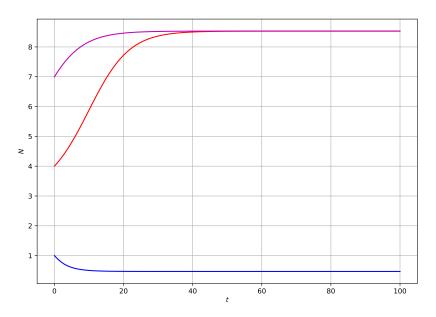


Figure 2: RHS of spr. budworm model

#### Numerical solution



# Steady state analysis

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



#### Lecture 12

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

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

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

Today: bifurcation analysis, hysteresis, harvesting

# Tangent bifurcations in $\emph{rq}$ space

# Plotting stability regions in the rq plane

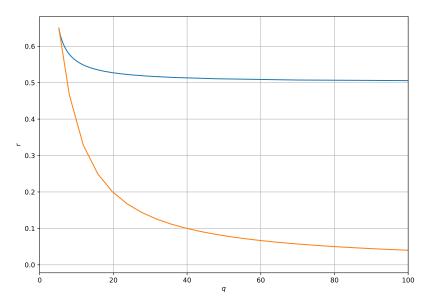
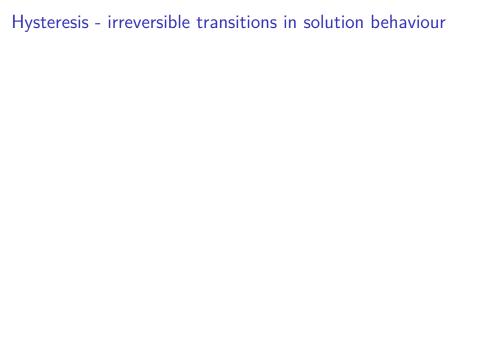


Figure 3: Bifurcations in the rq plane



#### Hysteresis

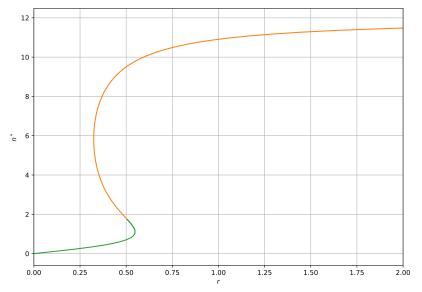


Figure 4: Bifurcations in the rq plane

#### 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  ${\cal E}$  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.)

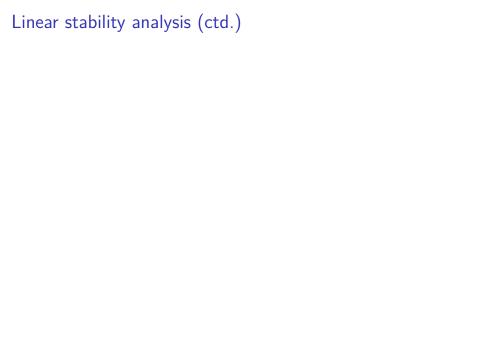
$$\frac{dN}{dt} = -N(t-T),$$

#### Two dependent variable ODE models

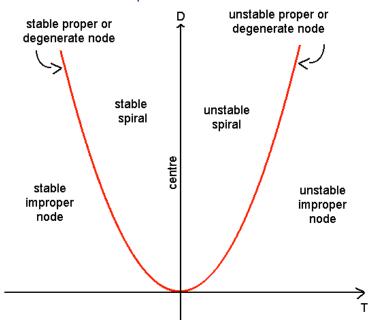
$$\begin{split} \frac{du}{dt} &= f(u,v),\\ \frac{dv}{dt} &= g(u,v). \end{split}$$

# Steady states





#### The trace determinant plane

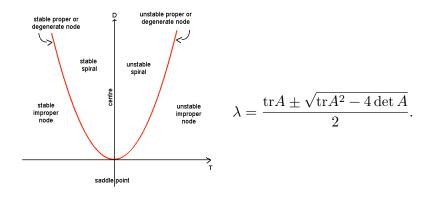


eaddlalnaint

#### Lecture 14

Recap

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



# **Nullclines**

# Periodic solutions (Poincaire-Bendixson theorem)

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

# No periodic soltutions - (Dulac criterion)

- ▶ D simply connected region in the plane
- ightharpoonup 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

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

#### Nondimensionalisation

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

#### Lecture 15 - recap

Lotka-Volterra model - predator prey interaction n - prey p - predator

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

#### Strategy:

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

#### Numerical solutions

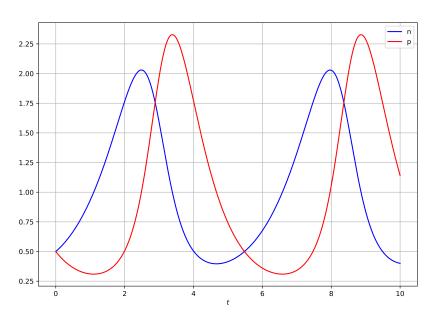


Figure 6

# Steady states

# **Nullclines**

# The phase plane

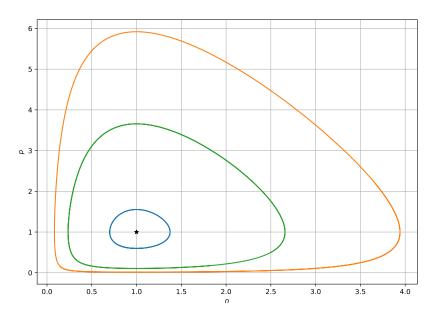


Figure 7



# Integration



# Lecture 16 Competition

- i Recap: Lotka-Volterra model
  - predator prey interaction
  - n prey
  - p predator

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

i Aim - introduce and analyse a model of competition

#### Competition model

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

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

#### Nondimensionalisation

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

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

Nondimensionalisation (ctd.)

# Steady states



# **Nullclines**

# Lecture 17 Competition

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

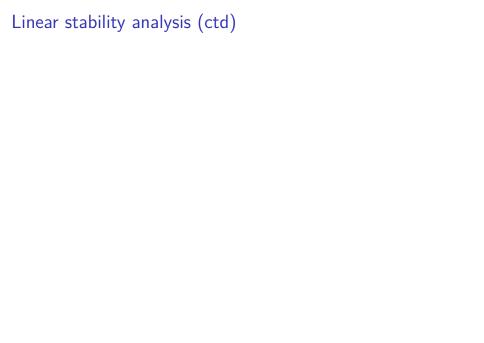
Steady states:

and

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

#### Linear stability analysis

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



# Phase portrait (one for each qualitatively distinct case)

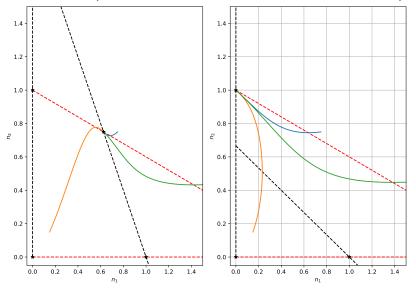


Figure 8



# Mutualism/symbiosis

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

#### Steady states

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

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



### 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

$$\lambda_1 C_1 + \lambda_2 C_2 + \ldots + \lambda_m C_M \rightleftharpoons_{\overrightarrow{k_b}} \gamma_1 C_1 + \gamma_2 C_2 + \ldots \gamma_M C_M.$$

# Conservation equation

# A forwards reaction

$$A + B \xrightarrow{k} C$$
.

#### A reversible reaction

$$A+B \overset{k_+}{\rightleftharpoons} C.$$

### General stochiometric constants

$$A + mB \xrightarrow{k_1} nB + pC.$$

## A reversible dimerisation

$$A + A \stackrel{k_+}{\rightleftharpoons} B.$$

## Enzyme kinetics

$$S+E \xrightarrow[k_{-1}]{k_1} C \xrightarrow{k_2} P+E.$$

#### Numerical solution

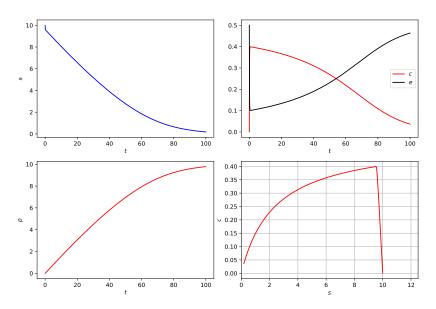


Figure 9: Numerical solutions of the Michaelis Menten model

## Dimension reduction



## Nondimensionalisation

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

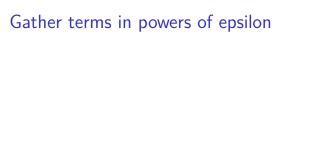
where

$$\lambda=\frac{k_2}{k_1s_0},\quad K=\frac{k_{-1}+k_2}{k_1s_0},\quad \epsilon=\frac{e_0}{s_0}.$$

## Propose asymptotic expansion: outer solution

$$\begin{split} u(\tau;\epsilon) &= u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + \ldots = \sum_{n=0}^\infty u_n(\tau) \epsilon^n, \\ v(\tau;\epsilon) &= v_0(\tau) + \epsilon v_1(\tau) + \epsilon^2 v_2(\tau) + \ldots = \sum_{n=0}^\infty v_n(\tau) \epsilon^n. \end{split}$$

#### Substitute:



## 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

$$rac{d}{d}$$

d

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

Seek series solutions

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

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

# Mathching inner and outer solutions