

University of Dundee

DI32011

DI32011

Thomas Winyard

2026-04-18

Table of contents

DI32011: Mathematical Biology I 3
- Contact Hours . . . 3
- Lecture notes . . . 3
- Reading . . . 4
- Early weeks cover . . . 4
- Tutorials . . . 4
- Assessment . . . 4
- Python code . . . 4
- Schedule . . . 5
- References . . . 6

1 Introduction 7
- 1.1 Population Dynamics . . . 7
- 1.2 Exponential Growth . . . 7
- 1.3 Logistic Equation and Population Caps . . . 8
- 1.4 Nondimensionalisation . . . 10
  - 1.4.1 Dimensional analysis . . . 11

I Discrete time 12

2 Single species population dynamics 13
- 2.1 A general model for a single population in discrete time . . . 13
- 2.2 The Malthusian model . . . 13
- 2.3 A motivating example of a nonlinear model - The Ricker model . . . 15
  - 2.3.1 Model development . . . 16
  - 2.3.2 Computational solutions . . . 16
- 2.4 General techniques for analysing nonlinear difference equations . . . 17
  - 2.4.1 Computational solutions . . . 17
  - 2.4.2 Fixed points . . . 19
  - 2.4.3 Linear stability . . . 19
  - 2.4.4 Cobwebbing and linear stability . . . 20
  - 2.4.5 Bifurcation diagrams . . . 21
  - 2.4.6 Example of a qualitative analysis of the Malhusian model . . . 21

2.5 A nonlinear model of population dynamics in discrete time . . . 24
2.5.1 The per capita growth rate . . . 25
2.5.2 Numerical solution . . . 25
2.5.3 Fixed points . . . 27
2.5.4 Linear stability analysis . . . 27
2.5.5 Cobweb diagrams . . . 28
2.5.6 Bifurcation diagram . . . 28
2.5.7 Symbolic computation . . . 28
2.6 An application - how much harvesting can a population sustain? . . . 30
2.6.1 Direct simulation . . . 31
2.6.2 Fixed points . . . 34
2.6.3 Linear stability . . . 34
2.6.4 Stability boundaries in the $h\gamma$ plane . . . 35
2.7 Oscillations, n-cycles and chaos . . . 38
2.7.1 The harvesting model revisted . . . 39
2.8 A note on the modelling of real-world fish stocks . . . 41

3 Multi species population dynamics in discrete time 43
3.1 A general model of two interacting species in discrete time . . . 43
3.2 General techniques for analysing coupled first order difference equations . . . 43
3.2.1 Fixed points and linear stability . . . 43
3.2.2 Jury conditions . . . 44
3.2.3 Proof of the Jury conditions . . . 45
3.2.4 Complex roots . . . 46
3.2.5 Real roots . . . 46
3.3 Host Parasitoid infection . . . 47
3.3.1 Model equations . . . 47
3.3.2 Numerical solution . . . 47
3.3.3 Fixed points . . . 47
3.3.4 Linear stability . . . 50
3.3.5 Linear stability of the trivial fixed point . . . 50
3.3.6 Linear stability of the nontrivial fixed point . . . 50
3.3.7 Employing the Jury conditions . . . 51
3.3.8 Symbolic calculations in Python . . . 51

II Continuous time 52

4 Single species population dynamics 53
4.1 The Malthusian (linear) model . . . 53
4.2 Tools for analysing the dynamics of a single population in continuous time . . . 54
4.2.1 Numerical solution . . . 54
4.2.2 Steady-state . . . 54

4.2.3 Linear stability analysis . . . 55
4.2.4 Graphical solution . . . 56
4.2.5 Bifurcation diagrams . . . 56
4.3 The logistic growth model . . . 56
4.3.1 Model development . . . 56
4.3.2 Steady states and linear stability . . . 58
4.3.3 Graphical analysis . . . 58
4.3.4 An exact solution . . . 59
4.4 The spruce budworm model . . . 60
4.4.1 Model development . . . 60
4.4.2 Nondimensionalisation . . . 61
4.4.3 Numerical solutions . . . 62
4.4.4 Steady state analysis . . . 62
4.4.5 Linear stability analysis . . . 64
4.4.6 Bifurcation analysis . . . 64
4.4.7 Hysteresis . . . 67
4.5 Harvesting . . . 69
4.6 Delay differential equation models . . . 70
4.7 References . . . 71

5 Multi species population dynamics 72
5.1 General tools . . . 72
5.1.1 Steady states . . . 72
5.1.2 Linear stability analysis . . . 72
5.1.3 Nullclines . . . 75
5.1.4 Poincaire-Bendixson theorem . . . 76
5.1.5 Dulac criterion . . . 76
5.2 The Lotka-Voltera model . . . 76
5.2.1 Nondimensionalisation . . . 77
5.2.2 Numerical solutions . . . 77
5.2.3 Steady states . . . 77
5.2.4 Linear stability . . . 78
5.2.5 Solutions in the phase plane . . . 79
5.2.6 Direct integration . . . 79
5.3 Competition . . . 80
5.3.1 Nondimensionalisation . . . 81
5.3.2 Steady states . . . 81
5.3.3 Nullclines . . . 82
5.3.4 Linear stability . . . 83
5.3.5 Phase portrait . . . 85
5.3.6 Insight . . . 85
5.4 Symbiosis/Mutualism . . . 87
5.4.1 Nondimensionalisation . . . 87

5.4.2 Steady states . . . 87
5.4.3 Nullclines . . . 87
5.4.4 Linear stability . . . 88
5.4.5 Insight . . . 88

6 Biochemical kinetics **89**
6.1 The law of mass action . . . 89
6.1.1 Example . . . 90
6.2 Enzyme kinetics . . . 91
6.2.1 Deriving the model equations . . . 92
6.2.2 Numerical solutions . . . 92
6.2.3 Reducing the dimensions of the model . . . 92
6.2.4 The quasi-steady state approximation (QSSA) . . . 94
6.2.5 Enzyme kinetics: the Michaelis-Menten quasi-steady state approximation (QSSA) . . . 95
6.3 The Brusselator . . . 100
6.3.1 Deriving model equations . . . 100
6.3.2 Nondimensionalisation . . . 101
6.3.3 Steady states analysis . . . 101
6.3.4 Linear stability analysis . . . 102
6.3.5 Applying the Poincaire-Bendixson theorem . . . 102

III Appendices **107**

7 Python **108**
7.1 Symbolic calculations . . . 108
7.2 Numerical solution of difference equations . . . 108
7.3 Numerical integration of ODEs . . . 108
7.4 Plotting . . . 108

8 Curve sketching **109**

DI32011: Mathematical Biology I

Lecturer: Thomas Winyard

Email: twinyard001@dundee.ac.uk

Website: twinyard.co.uk

Office: DIICSU 618

Office Hour: Wednesday 14:00 – 15:00, [Office 618]

Online Office Hour: Thursday 14:00 – 15:00, teams

Contact Hours

- Mondays 10:00 – 12:00, A206 (Lecture)
- Fridays 16:00 – 18:00, A206 (Lecture/Tutorial)

These will take the form of two roughly 45 minute lectures on Monday seperated by a break and a 30 to 45 minute lecture and 45 to 60 minute tutorial on Friday. Hence, the schedule is based on roughly 2 hours of lectures and 1 hour of tutorial a week.

Lecture notes

The lecture notes are based on ones originally written by Philip Murray, and are aviailable in HTML or PDF at my website. You can also generate the pdf by clicking on the pdf link at the top left of the webpage. Note the PDF version of the notes will not include interactive python elements. I will occasionally edit/update the notes as we proceed through lectures. If you spot any errors, typos or omissions please let me know via email.

Reading

- Mathematical Biology I: An Introduction, Murray (2002)
- Essential Mathemtical Biology Britton and Britton (2003)
- Mathematical models in Biology Edelstein-Keshet (2005)

We will follow Murray as the course text book while the other two sources are recomended reading.

Early weeks cover

Due to visa issues I will not be present for the first few weeks of the course and Chris Jefferson has kindly agreed to cover. You can still reach me via email and I will hold electronic office hours until I can do them in person (see above).

Tutorials

Tutorials will take place in the Friday slot each week with the tutorial sheet provided in advance. To get the most out of tutorials read through the tutorial sheet in advance and attept the simpler questions. This will allow you to focus on (and discuss) the most salient questions in the tutorial. Tutorials are also an oportunity to practice good written mathematical presentation and how to communicate mathematics with each other.

Assessment

- Final exam (80 %)
- 2 class tests (10 % each), approximately week 7 and 11 of term

Details of final exam and class test format TBA.

Python code

Python code is provided for most of the figures in the notes (you can expand the code section by clicking 'Code'). Note that the Python code does not appear in the pdf.

Many of you have taken the Introduction to Programming module at Level 2 and therefore have some experience installing and using Python. You may also be taking Fundamentals of Scientific Computing alongside this course for which Python will play a part. I strongly

encourage you to use the provided codes as a tool to play around with numerical solutions of the various models that we will be working on. The codes should run as standalone Python codes.

> **Note**
>
> To use Python on your own computer we recomend Anaconda. Instructions on how to install it were provided in Introduction to Programming and are available here.
> To use it:
>
> 1. Launch Anaconda
> 2. When a folder opens, double click on *Spyder*.
> 3. Paste a code from lecture notes into the editor on the left-hand side.
> 4. Click on the green arrow to run the code.
> 5. The plots should appear in the plots tab on the right-hand side.
> 6. Experiment with the code. When you change a model parameter, does the solution change in an expected way?

The notes also provide some examples of how to use Python as a symbolic calculator. This uses a Python library called *sympy* and is quite similar to Maple.

Schedule

Table 1: Projected delivery

Week	Lecture	Section	Tutorial sheet	Activity
4	1 – 2	1.0 – 2.4	1	
5	3 – 4	2.4 – 2.8	2	
6	5	3.0 – 3.3	3	Holiday (Mon)
7	6 – 7	3.3 – 4.2	4	
8	8 – 9	4.2 – 4.4	-	Class Test 1 (20th)
9	10	4.4 – 4.5	5	Holiday (Fri)
10	11 – 12	4.5 – 5.1	6	Holiday (Mon)*
11	13 – 14	5	-	Class Test 2 (TBA)
12	15 – 16	6	7	
13	Revision	Revision	Exam Revision	Exam Revision

*This lecture is expected to be rescheuled either as part of a make up day or independently, however the details of this are yet to be confirmed.

References

1 Introduction

While biology is the study of living organisms, mathematical biology is the application of mathematical tools to give enhanced understanding of biological systems. In particular, we will study equations that capture the key features of a given system. Constructing such models requires stripping away the systems complex nature and identifying a handfull of key quantities required to describe how the system changes.

The key quantities we consider broadly fall into two categories: fixed quantities that do not change in time, called **constants**, and quantities that evolve in time, called **dynamical variables**. Quantities whose values are specified a priori are called **parameters**, and are typically constant in time (though can be dynamic with clear defined behaviour), while quantities whose values are determined by the model are called **variables** or **degrees of freedom**.

When we say that a quantity changes in time, an important consideration is whether time is modeled as continuous, $t \in \mathbb{R}^+$, such that changes occur infinitesimally, or discrete, $t \in \mathbb{Z}$, such that changes occur in finite steps (e.g., yearly updates).

1.1 Population Dynamics

A key problem in biology is modelling mathematically how the population of various species changes over time (tracking births, deaths and migration). This might be quite abstract when studying, for example, the population of a chemical. As with our general approach we must identify the salient dynamical degrees of freedom (variables that change over time), the most obvious of which is,

$$N(t) - \text{Population change as a function of time,} \tag{1.1}$$

though there may be other variables involved or multiple competing populations.

1.2 Exponential Growth

If we assume the simplest population model with fixed birth rate and death rate, then every member of the species has the same fixed probability of giving birth and dying. For a change

in time Δt the number of births is $b\,\Delta t$ and the number of total deaths is $d\,\Delta t$, where we call b the **birth rate** and d the **death rate**, such that,

$$N(t+\Delta t) = N(t) + (b-d)N(t)\Delta t. \tag{1.2}$$

If Δt is finite then this is a discrete exponential model (called the Malthusian model) and if it is infinitesimal $\Delta t \to 0$ then we have the first order continous differential equation,

$$\frac{dN}{dt} = (b-d)N = rN. \tag{1.3}$$

For convenience we will define the constant $r = b - d$. The solution follows from previous courses on ODEs,

$$N = N_0\, e^{rt} \tag{1.4}$$

where N_0 is the initial population at time $t = 0$. Note that this model predicts that population grows or shrinks (depending on the sign of r) indefinitely. Unsurprisingly such a simplistic model is rarely accurate.

It is important to note that in everyday language the word exponential is often used not to refer to a system with such behaviour, for example you will have no doubt heard people refer to the exponential growth of the world population, which can be seen in Figure 1.1. For most of our history (until the 1960's) we have experienced super-exponential growth (where the exponent r increases with time) and since then r has started to decrease. It is even predicted that the exponent may become negative in the future leading to population decrease.

1.3 Logistic Equation and Population Caps

To modify the above simplistic approach we might consider a variable birth and death rate that depends on population,

$$N_{t+1} = (b(N_t) - d(N_t))\, N_t - \text{Discrete model}, \tag{1.5}$$

$$\frac{dN}{dt} = (b(N) - d(N))\, N - \text{Continous model}, \tag{1.6}$$

which is hardly a model without understanding how the general functions $b(N)$ or $d(N)$ change in time.

The simplest extension of the above exponential growth is to make d and b linear in N such that for a continous system we have the quadratic,

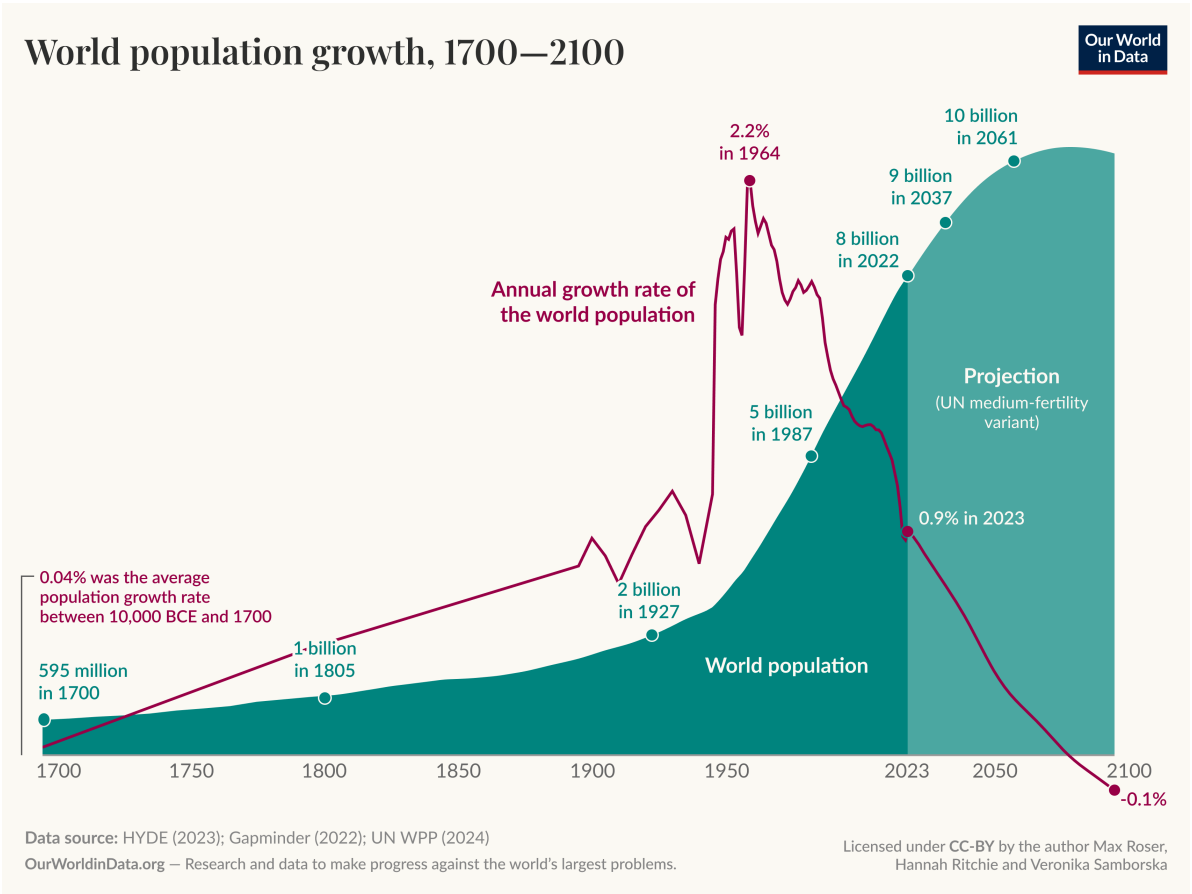


Figure 1.1: World population taken from our world in data. Population to date is in dark green and predicted trends in light green, including the associated annual change in red. Note, a constant red line would correspond to exponential growth.

$$\frac{dN}{dt} = rN - \lambda N^2 \tag{1.7}$$

where $r, \lambda > 0$ are constants. This continous ODE now has a population cap as small populations will grow and large populations shrink. It is easier to see this if we rewrite such that,

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N, \qquad \text{where} \quad K = \frac{r}{\lambda}, \tag{1.8}$$

here K is often refered to as a **carrying capacity**. This is called the **logistic equation**. It exhibits logarithmic solutions and we will study this system later in the course (both continous and discrete).

1.4 Nondimensionalisation

In mathematical biology we are intrested in studying trends and comparing different models without focussing imediately on direct measurement. A useful way of abstracting our models so we can easily compare for example population models of bacteria and elephants on very different scales is **nondimensionalisation**, where we make variables (both dependent and independent) dimensionless. In general this will be the population N

In general this will involve rewriting the population and time as the dimensionless variables,

$$n = \frac{N}{\tilde{N}}, \qquad \tau = \frac{t}{\tilde{T}}. \tag{1.9}$$

such that a general ODE transforms as,

$$\frac{dN}{dt} = H(N(t)) \qquad \longrightarrow \qquad \frac{dn}{d\tau} = \frac{\tilde{T}}{\tilde{N}} H\left(\right). \tag{1.10}$$

A good example is the logistic equation in Equation 1.8, where we absorb the constants by choosing $\tilde{N} = K$ and $\tilde{T} = 1/r$ such that we define,

$$n = \frac{N}{K}, \qquad \tau = rt, \tag{1.11}$$

which we call the **dimensionless variables**. The equation then becomes significantly simpler,

$$\frac{dn}{d\tau} = n(1 - n). \tag{1.12}$$

So we have now stripped away all the parameters that are unnecessary for studying the features of behaviours of the model. It is easy to revert back to the original equation by simply substituting back in for n and τ.

Note, be careful with absorbing signs e.g. for Equation 1.3, the exponential growth model, if we defined $\tau = rN$ we get the dimensionless solution,

$$N(\tau) = N_0\, e^{\tau}. \tag{1.13}$$

This may be suggestive that population always grows, but if $d > b \Leftrightarrow r < 0$ then the rescaling has reversed time.

1.4.1 Dimensional analysis

The dimensions/units of each term in a model must be consistent. This observation helps to determine the units of different parameters in a model.

For example, we can deduce that the units of the parameter r in Equation 1.4

$$\frac{dN}{dt} = rN. \tag{1.14}$$

The units of the left-hand term are

$$\frac{\#popdensity}{\#time}, \tag{1.15}$$

thus the units of the right-hand side must match. This means that r must have the units,

$$\#r = \frac{1}{\#time}, \tag{1.16}$$

for dimensional consistency. This is a useful technique for making sure equations are correct and also gives some physical intuition as to what different parameters represent. In the above example r is inverse in time, so it is describing a rate of change, which matches our intuiton that it is the difference in birth and death rate.

Part I

Discrete time

2 Single species population dynamics

We first consider models of a single population defined at discrete times. Discrete (rather than continuous) time is used in population models where, for example, there are strong annual trends in the underlying animal behaviour (e.g. fish eggs hatching at a fixed time of the year), there are not overlapping generations and the population size at the next time step can be written as a function of the current population size (e.g. a mutation that evolves from one generation to the next).

2.1 A general model for a single population in discrete time

Let N_t be a dependent variable, representing the population size of a single species, at the discrete time $t \in \mathbb{Z}$. We write the change in population as the first order difference equation,

$$N_{t+1} = H(N_t) = N_t f(N_t), \tag{2.1}$$

where the function $H : \mathbb{R} \to \mathbb{R}$ is the population update (or transition) function with units of population. Alternatively, $f(N_t)$ defines the *per capita* growth factor and is dimensionless.

Note, *per capita* is Latin for *per person* and hence is used to express something averaged over the population.

The goal of this section is to develop a range of techniques that allow us to analyse the behaviour of Equation 2.1 for a given function H and initial condition N_0 (population at $t = 0$).

Finally, note that many of you were introduced to difference equations in the module Discrete Mathematics. It is recommended that you revisit the section on Discrete Difference Equations in your notes.

2.2 The Malthusian model

The simplest form for Equation 2.1 is a *constant per capita growth factor*. Let b be the per capita birth rate and d the per capita death rate where $b, d \in \mathbb{R}^+$ (b and d are both positive real constants). This gives us that $b - d$ is the constant net per capita growth rate. We write the corresponding difference equations as,

$$N_{t+1} = N_t + bN_t - dN_t = rN_t, \tag{2.2}$$

where the parameter $r = 1 + b - d$ is the *per capita growth factor*. Note that $d \leq 1 + b$ as you can't have more deaths than current population plus births, which implies that $r \geq 0$.

Given the initial condition N_0, Equation 2.2 can be solved recursively,

$$N_1 = rN_0, \tag{2.3}$$
$$N_2 = rN_1 = r^2 N_0, \tag{2.4}$$
$$N_3 = rN_2 = r^3 N_0, \tag{2.5}$$
$$\ldots \tag{2.6}$$
$$N_t = r^t N_0. \tag{2.7}$$

Hence for the case of Malthusian growth, the size of the population can be explicitly calculated for all t. In Figure 2.1 we present a numerical solution of the model where we have simply iterated through solutions for different values of the parameter r.

Exercise: Use python to simulate the solution of a general difference equation $N_{t+1} = H(N_t)$. This should be modular so you can pass it different models in the form of different functions H. Test it with the Malthusian model and compare with Figure 2.1.

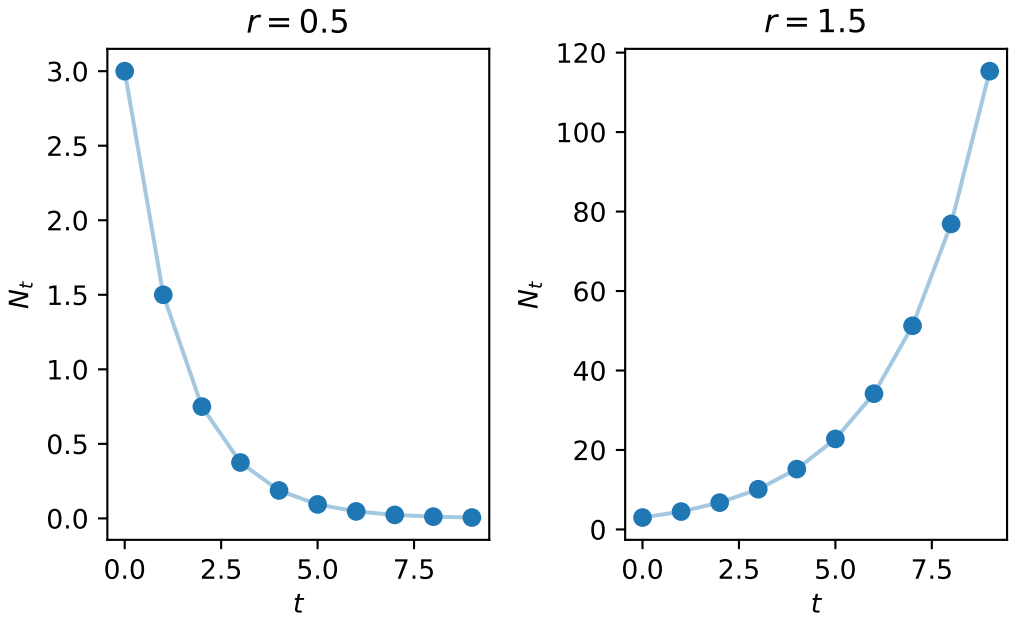


Figure 2.1: A plot of the Malthusian model solution when (a) r=0.5 and (b) r=1.5.

Note, I have included connecting (straight) lines between the points to make the trend clear. However, this is a discrete system and N_t is only evaluated at the natural numbers (points).

Exercise: Describe how the behaviour of the Malthusian model changes with r. What are the critical values of r that split the Malthusian model into qualitatively different behaviour? How does this compare with the continous exponential ODE in Equation 1.3? Are the parameters r in the two equations describing the same thing, how do they differ?

Qualitative analyses categorise solution behaviours into different cases based on their parameters. The behaviour of the Malthusian model changes at the critical value of $r = 1$ for which $N_t = N_0$ is constant. For $r > 1$ ($r < 1$) the solution is monotonically increasing (decreasing). Similarly the behaviour of the population at large t also changes,

$$\lim_{t\to\infty} N_t = \begin{cases} \infty & r > 1, \\ N_0 & r = 1, \\ 0 & r < 1. \end{cases} \tag{2.8}$$

Whilst the simplicity of the Malthusian model allows us to calculate explicit solutions that yield insight into how the processes of birth and death combine to give either net growth or net reduction in population size, an obvious flaw with this model is that it displays unbounded growth for $r > 1$. In most biological systems, other effects, such as competition for resources or predation, will tend to limit a population's size. In single species population models, these effects are accounted for phenomenologically by introducing nonlinear terms into the function f.

2.3 A motivating example of a nonlinear model - The Ricker model

Many models of population dynamics in discrete time were initially developed to study fisheries. Well-studied examples include the Beverton Holt model

$$N_{t+1} = \frac{rN_t}{1 + \frac{N_t}{K}}, \tag{2.9}$$

the Hassell model

$$N_{t+1} = \frac{rN_t}{(1 + \frac{N_t}{K})^b}, \tag{2.10}$$

and the Ricker model

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})}. \tag{2.11}$$

where $r, K, n \in \mathbb{R}^+$ are positive parameters. Below we consider the Ricker model which was initially used to study Canadian sockeye salmon population dynamics.

2.3.1 Model development

One way to capture a decreased growth rate at high densities, is to assume that the per capita growth rate is an exponentially decreasing function of population density, i.e.

$$f(N_t) = e^{r(1-\frac{N_t}{K})}, \tag{2.12}$$

where r is a growth rate and K a carrying capacity (both positive constants). Hence the governing equation is

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})}. \tag{2.13}$$

Note that as the population size gets large ($N_t \gg K$), the growth rate tends to zero but that for small populations $N_t \ll K$ the growth rate is approximately constant. This is the Ricker model.

Note that the model is nonlinear and does not have an explicit solution.

2.3.2 Computational solutions

After directly computing numerical solutions of the Ricker model for different values of the parameter r, the data in Figure 2.2 were obtained.

Note that model behaviour changes drastically as the parameter r varies. For instance,

- when $r = 0.5$ (Figure 2.2 (a)), the solution monotonically approaches the value 2,
- when $r = 1.5$ (Figure 2.2 (b)) it approaches two in an oscillatory manner; and
- when $r = 2.5$ (Figure 2.2 (c)) it oscillates around two.

The above numerical results raise the following questions:

- can we develop tools that allow us to qualitatively describe how the model solutions depend on model parameters?
- are the there certain families of solutions with qualitatively similar behaviours?
- how do such families of solutions depend on model parameters?

The remainder of this chapter is focussed on these questions. We will apply the techniques to the Ricker model to understand the above behaviour (for all of r) in future tutorials.

In Figure 2.3 you can explore simulations of the Ricker model.

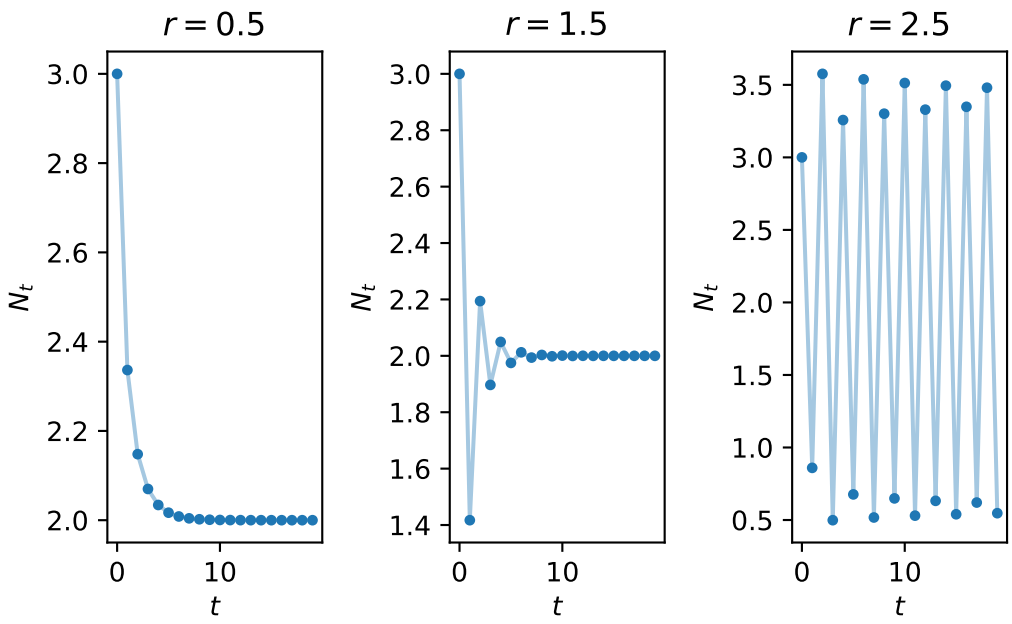


Figure 2.2: Numerical solutions of the Ricker model for (a)r=0.5, (b) r=1.5, (c) r=2.5.

2.4 General techniques for analysing nonlinear difference equations

In this section we develop techniques that will be used to analyse first order, discrete-time models of the form

$$N_{t+1} = N_t f(N_t) = H(N_t). \tag{2.14}$$

In most cases, unlike the Malthusian model, difference equations cannot be solved analytically. In such cases studying general properties can help us to catagorise the behaviour of different models.

2.4.1 Computational solutions

Perhaps the most obvious way to investigate an equation of the form of Equation 2.14 is to iteratively compute N_t over a prescribed time range.

Hence given some initial population N_0, the solution set $\{N_0, N_1, N_2, ..., N_T\}$ is computed up to some end time T. Such an approach provides a numerical solution for a given parameter set and initial condition. However, it does not provide much insight into the general behaviour of model.

```
#| '!! shinylive warning !!': |
#|   shinylive does not work in self-contained HTML documents.
#|   Please set `embed-resources: false` in your metadata.
#| standalone: true
#| components: [viewer]
#| viewerHeight: 500


from shiny import App, Inputs, Outputs, Session, render, ui
from shiny import reactive

import numpy as np
from pathlib import Path
import matplotlib.pyplot as plt
from scipy.integrate import odeint

app_ui = ui.page_fluid(
    ui.layout_sidebar(
        ui.sidebar(
    ui.input_slider(id="r",label="r",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="u0",label="N_0 (Initial condition)",min=0.0,max=4.0,value=0.5,step=0
    ui.input_slider(id="T",label="Number of iterations",min=0.0,max=60.0,value=20.0,step=1.0)

        ),

        ui.output_plot("plot"),
    ),
)

def server(input, output, session):

    @render.plot
    def plot():
        fig, ax = plt.subplots(2,1)
        #ax.set_ylim([-2, 2])
        # Filter fata


        r=float(input.r())
        u0=float(input.u0())
        T=int(input.T())

        def rickerrhs(x,par):
          r=par
          K=1.0
          f=x*np.exp(r*(1-x/K))
          return f
        # Define rhs of logistic map

        # this function computes the solutio to the difference equation. It also stores solu
        def SolveSingleDiffAndCobweb(t,rhs,N_0,r):
          # Initialise solution vector
          N = np.zeros_like(t,dtype=float)
```

2.4.2 Fixed points

We define N^* to be a fixed point of Equation 2.14 if and only if

$$N^* = N^* f(N^*) = H(N^*). \tag{2.15}$$

Hence the fixed points can be identified by solving an algebraic equation. Hence for any given time t^* if $N_{t^*} = N^*$ then $\forall t \geq t^*$, $N_t = N^*$. An interesting question is, how does the model behave when the population is close to a given critical point.

2.4.3 Linear stability

By linearising about the identified fixed points using a Taylor series expansion, it can be determined whether or not small perturbations grow or decay in subsequent iterations.

Making a change of dependent variables,

$$N_t = N^* + \hat{N}_t,$$

Equation 2.14 transforms upon substitution to

$$N^* + \hat{N}_{t+1} = H(N^* + \hat{N}_t), \tag{2.16}$$

where Taylor expanding the right-hand side yields

$$N^* + \hat{N}_{t+1} = H(N^*) + H'(N^*)\hat{N}_t + \mathcal{O}(\hat{N}_t^2). \tag{2.17}$$

Note that for a fixed point $N^* = H(N^*)$, which leads to a cancellation,

$$\hat{N}_{t+1} = H'(N^*)\hat{N}_t + \mathcal{O}(\hat{N}_t^2). \tag{2.18}$$

Hence, if we consider small perturbations about the fixed point ($\hat{N}$ is small), the leading order behaviour of the perturbation is governed by

$$\hat{N}_t = (H'(N^*))^t \hat{N}_0. \tag{2.19}$$

Hence the linear stability of the fixed point is governed by the sign and magnitude of the term $H'(N^*)$,

- $|H'(N^*)| < 1$, **stable**, the perturbation shrinks geometrically to zero.
- $|H'(N^*)| > 1$, **unstable**, the perturbation grows exponentially in magnitude.
- $|H'(N^*)| = 1$, **marginal** or borderline case, linear analysis is inconclusive and higher order terms $\mathcal{O}(\hat{N}_t)$ need to be considered.

2.4.4 Cobwebbing and linear stability

A cobweb diagram allows solutions of a first order difference equation to be sketched without explicitly solving.

2.4.4.1 An algorithm for generating a cobweb diagram

The cobweb diagram consists of multiple curves with N_t on the horizontal azis and N_{t+1} on the vertical axis. In words we then,

1. Sketch the net growth rate function $H(N_t)$.
2. Sketch the line $N_{t+1} = N_t$.
3. Plot the first point $(N_0, H(N_0))$ on the cobweb diagram.
4. Plot a horizontal line between $(N_0, H(N_0))$ and $(H(N_0), H(N_0))$. Note $N_1 = H(N_0)$.
5. Plot a vertical line between (N_1, N_1) and $(N_1, H(N_1))$.
6. Repeat steps 4 and 5.

It should not be hard to convince yourself that iterating at right angles between the $N_{t+1} = N_t$ straight line and the graph of $H(N_t)$ performs succesive iterations of the map. In addition, a key observation is that any **intersections** between the straight line and the graph of $H(N_t)$ are **fixed points**.

The above list is an algorithm, that we often display in a convenient or campact form using pseudo-code,

```
#| label: algo-quicksort
#| html-indent-size: "1.2em"
#| html-comment-delimiter: "//"
#| html-line-number: true
#| html-line-number-punc: ":"
#| html-no-end: false
#| pdf-placement: "htb!"
#| pdf-line-number: true

\begin{algorithm}
\caption{Quicksort}
\begin{algorithmic}
\Procedure{Quicksort}{$A, p, r$}
  \If{$p < r$}
    \State $q = $ \Call{Partition}{$A, p, r$}
    \State \Call{Quicksort}{$A, p, q - 1$}
    \State \Call{Quicksort}{$A, q + 1, r$}
  \EndIf
```

```
\EndProcedure
\Procedure{Partition}{$A, p, r$}
  \State $x = A[r]$
  \State $i = p - 1$
  \For{$j = p, \dots, r - 1$}
    \If{$A[j] < x$}
      \State $i = i + 1$
      \State exchange
      $A[i]$ with     $A[j]$
    \EndIf
    \State exchange $A[i]$ with $A[r]$
  \EndFor
\EndProcedure
\end{algorithmic}
\end{algorithm}
```

Plotting cobweb diagrams in the vicinity of a fixed point N^* (intersections) for different values of $H'(N^*)$ allows us to see graphically how the derivative of the right-hand side affects linear stability of a fixed point (see Figure 2.4). In particular,

- when $H'(N^*) > 1$, the fixed point is monotonically unstable;
- when $0 < H'(N^*) < 1$, the fixed point is monotonically stable;
- when $-1 < H'(N^*) < 0$, the fixed point is oscillatory stable;
- when $H'(N^*) = -1$, the fixed point is oscillatory; and
- when $H'(N^*) < -1$, the fixed point is oscillatory unstable.

2.4.5 Bifurcation diagrams

A bifurcation is a qualitative change in solution behaviour as a function of the models parameters (either a change in the number of fixed points or their stability). A bifurcation diagram is a compact means of displaying bifurcations.

The simplest bifurcation digaram is a plot of the fixed point value of the population (which we have often denoted N^*) against a model parameter of interest. From this diagram one can immediately see how the number of fixed points and their stability changes as a given parameter increases.

2.4.6 Example of a qualitative analysis of the Malhusian model

Let's work through the various concepts introduced above using the Malthusian model (Equation 2.2).

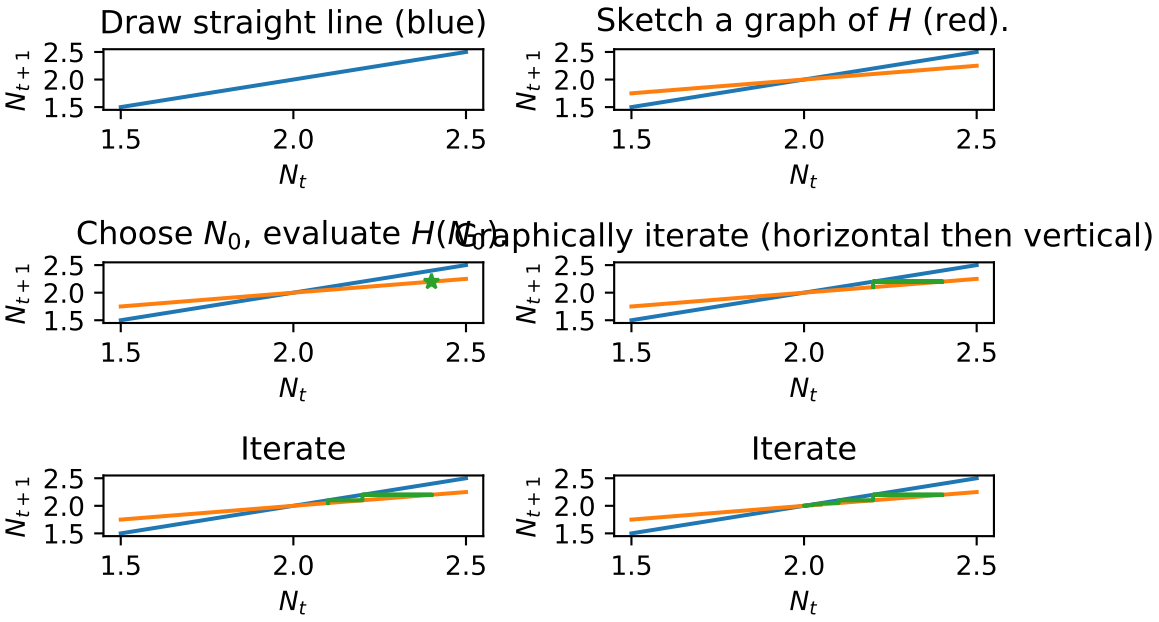


Figure 2.4: Generating a cobweb plot.

```
<IPython.core.display.HTML object>
```

Figure 2.5: Animation of a cobweb diagram for the Malthusian model with $N_0 = 0.2$ and $r = 1.5$.

The fixed points satisfy

$$N^* = rN^*. \tag{2.20}$$

As $r > 0$ the only solution is $N^* = 0$.

In this case

$$H'(N_t) = r. \tag{2.21}$$

Hence the linear stability of the solution depends on the value of the parameter r For $r > 1$ the fixed point $N^* = 0$ is monotonically unstable. For $r < 1$ the fixed point $N^* = 0$ is monotonically stable. As expected this result is consistent with the simulation results in Figure 2.1.

For the cobweb diagram:

- Label the axes with N_t and N_{t+1}.
- From linear stability analysis note there are two qualitatively distinct cases ($r < 1$ and $r > 1$). We will need a cobweb diagram for each case.
- Case 1: graph the function $H(N_t)$. In this case it is the straight line $N_{t+1} = rN_t$ with $r < 1$ (final plot in Figure 2.6).
- Case 2: graph the function $H(N_t)$. In this case it is the straight line $N_{t+1} = rN_t$ with $r > 1$ (final plot already shown in Figure 2.5).
- Fill in the cobwebbed trajectories with some arbitrarily chosen initial condition.
- Establish that behaviour of the cobweb is consistent with linear stability analysis.

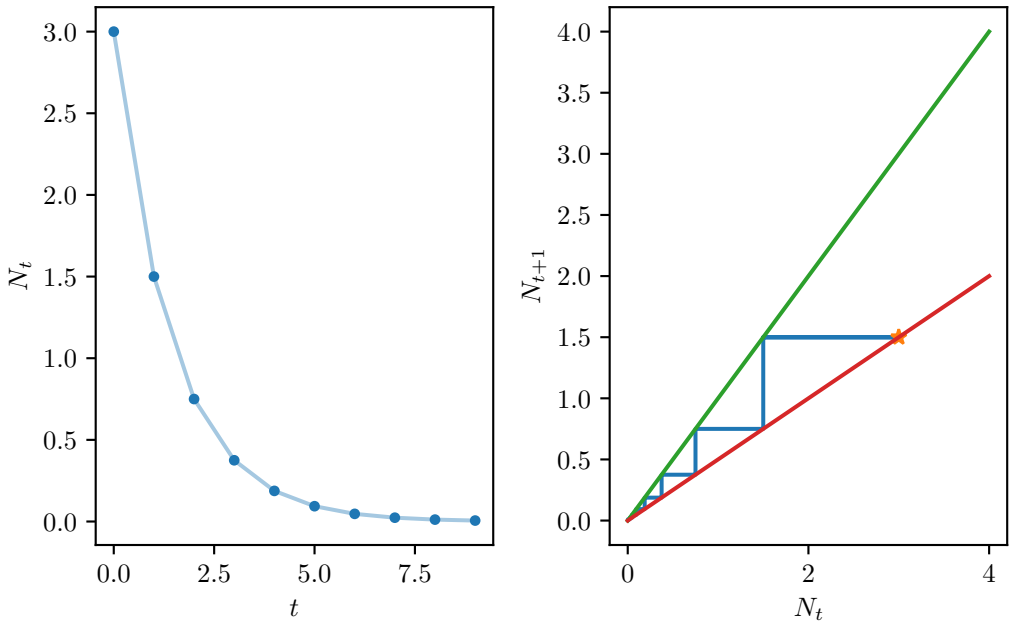


Figure 2.6: A cobweb plot of the Malthusian model solution when r=0.5. (a) Time series and (b) Cobweb diagrams.

For bifurcation diagram:

- We will plot the value of fixed point against a parameter of interest. In this case N^* against r.
- Deduce from fixed point and linear stability analysis whether there are any changes in solution behaviour as r varies (e.g. number of solution or their linear stability).
- In this case the value of the fixed point is independent of r but the linear stability changes at $r = 1$. This is a bifurcation.
- Use annotation to represent qualitative solution behaviour.

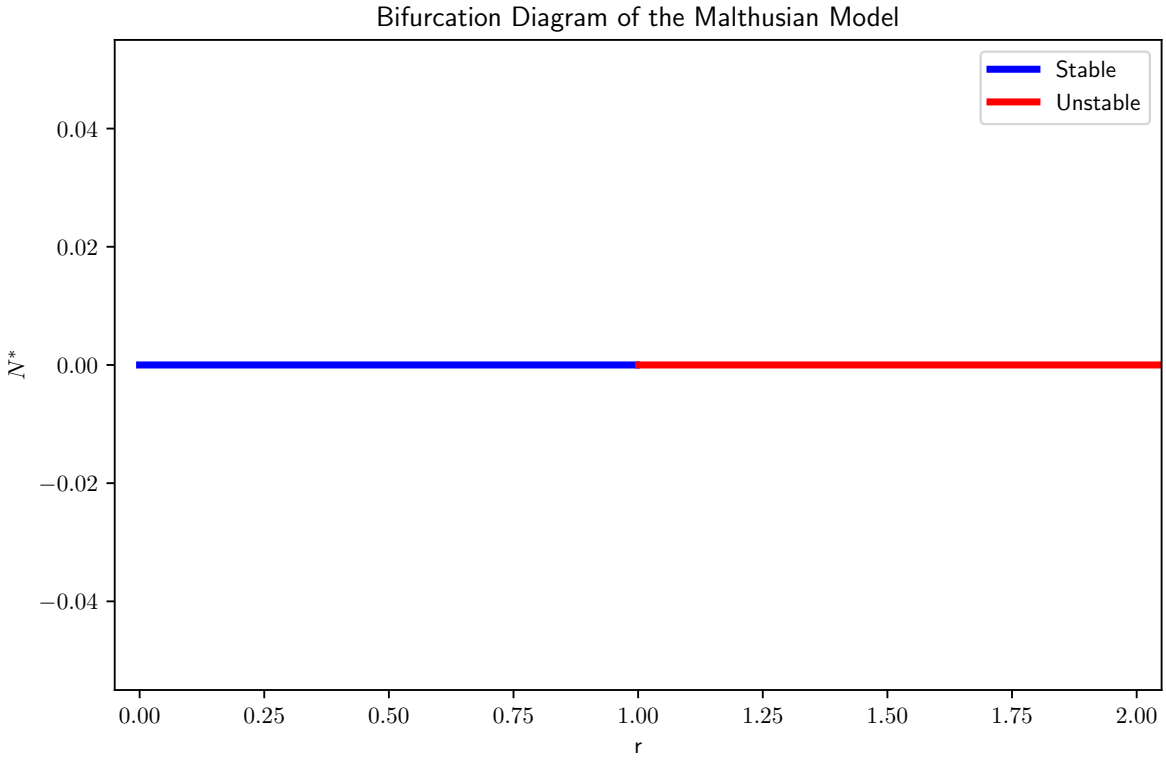


Figure 2.7: A bifurcation plot of the Malthusian model as the growth rate r changes.

2.5 A nonlinear model of population dynamics in discrete time

Consider a model of population growth given by

$$N_{t+1} = \frac{\gamma N_t}{1 + N_t^2}, \tag{2.22}$$

where $\gamma \in \Re^+$ is the linear growth rate.

2.5.1 The per capita growth rate

Note that the per capita growth rate is described by the function

$$f(N_t) = \frac{\gamma}{1 + N_t^2}. \tag{2.23}$$

Hence at large populations the per capita growth rate tends to zero whilst for small populations it tends to γ. Hence so long as $\gamma > 1$ we will have net growth for small populations and net removal for large populations. The net growth rate is given by

$$H(N_t) = \frac{\gamma N_t}{1 + N_t^2}. \tag{2.24}$$

2.5.2 Numerical solution

In Figure 2.8 time series solution of the model are plotted for parameter values $\gamma = 0.5$, $\gamma = 1.5$, $\gamma = 2.5$. Note qualitative changes in model behaviour in the different parameter regimes. Can you identify the fixed points? Are the solutions oscillatory?

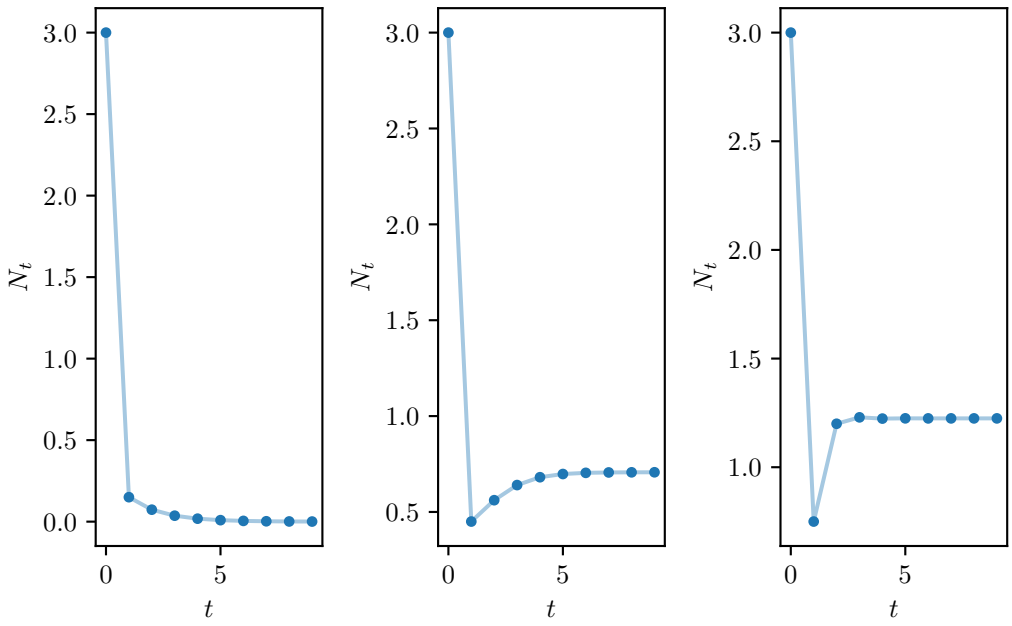


Figure 2.8: Time series solution for (a) γ=0.5 and (b) γ=1.5 and (c) γ=10.5.

```
#| '!! shinylive warning !!': |
#|   shinylive does not work in self-contained HTML documents.
#|   Please set `embed-resources: false` in your metadata.
#| standalone: true
#| components: [viewer]
#| viewerHeight: 500


from shiny import App, Inputs, Outputs, Session, render, ui
from shiny import reactive

import numpy as np
from pathlib import Path
import matplotlib.pyplot as plt
from scipy.integrate import odeint

app_ui = ui.page_fluid(
    ui.layout_sidebar(
        ui.sidebar(
    ui.input_slider(id="r",label="gamma",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="u0",label="N_0 (Initial condition)",min=0.0,max=4.0,value=0.5,step=0
    ui.input_slider(id="T",label="Number of iterations",min=0.0,max=60.0,value=20.0,step=1.0)
    ui.input_slider(id="max_sol",label="Max. axis value",min=0.0,max=5.0,value=1.5,step=0.1)


        ),

        ui.output_plot("plot"),
    ),
)

def server(input, output, session):

    @render.plot
    def plot():
        fig, ax = plt.subplots(2,1)
        #ax.set_ylim([-2, 2])
        # Filter fata


        r=float(input.r())
        u0=float(input.u0())
        T=int(input.T())
        max_sol=float(input.max_sol())

        def rickerrhs(x,par):
          r=par
          K=1.0
          f=r*x/(1+x**2)
          return f
        # Define rhs of logistic map

        # this function computes the solutio to the difference equation. It also stores solu
```

2.5.3 Fixed points

The fixed points of Equation 2.22 satisfy the algebraic equation

$$N^* = \frac{\gamma N^*}{1 + {N^*}^2} \tag{2.25}$$

which has solutions

$$N^* = 0 \quad \text{and} \quad N^* = \sqrt{\gamma - 1}. \tag{2.26}$$

2.5.3.1 Parameter restrictions for biological validity

If $\gamma < 1$, there is only one biologically relevant fixed point. If $\gamma > 1$ there are two fixed-points, $N^* = 0$ and $N^* = \sqrt{\gamma - 1}$. Hence the value of the model parameter γ qualitatively affects the behaviour and number of solutions.

2.5.4 Linear stability analysis

For the given model we compute

$$H'(N_t) = \frac{\gamma}{1 + N_t^2} + \frac{-2\gamma N_t^2}{(1 + N_t^2)^2}. \tag{2.27}$$

The stability of the fixed point $N^* = 0$ is determined by

$$H'(0) = \gamma. \tag{2.28}$$

Hence if $\gamma < 1$ the first fixed point is monotonically stable as $0 < H'(0) < 1$. When $\gamma > 1$ the first fixed point becomes monotonically unstable, also the second fixed point becomes biologically relevant.

The stability of the second fixed point, $N^* = \sqrt{\gamma - 1}$, is determined by

$$H'(\sqrt{\gamma - 1}) = \frac{\gamma}{1 + \gamma - 1} + \frac{-2\gamma(\gamma - 1)}{(1 + (\gamma - 1))^2}, \tag{2.29}$$

$$= \frac{2}{\gamma} - 1. \tag{2.30}$$

Hence the critical point is unstable when,

$$|H'(\sqrt{\gamma - 1})| = |\frac{2}{\gamma} - 1| > 1 \tag{2.31}$$

We can show this by considering the two inequalities,

$$\frac{2}{\gamma} - 1 > 1 \quad \text{OR} \quad \frac{2}{\gamma} - 1 < -1,$$

where the first inequality is the condition for montonic unstable and the second oscillatory unstable. The second is never satisfied for $\gamma > 0$ while the first is satisfied for $\gamma < 1$. However, a necessary condition for the biological relevance of N^* is that $\gamma > 1$. Hence N^*, if it is biologically relevant, cannot be unstable.

While N^* is stable for $\gamma > 1$, is it montonic or oscillatory? Consider $H'(N^*)$ and look for sign changes,

$$H'(\sqrt{\gamma - 1}) = \frac{2}{\gamma} - 1,$$

which has a sign change at $\gamma = 2$ as $H'(1) = 0$ and the sign changes from positive to negative. Hence N^* is monotonically stable for $1 < \gamma < 2$ and is oscillatory stable for $\gamma > 2$.

Hence, the parameters γ splits the model into three key regimes $\gamma \in (0, 1)$, $\gamma \in (1, 2)$, $\gamma \in (2, \infty)$.

2.5.5 Cobweb diagrams

In Figure 2.10 cobweb diagrams illustrate model behaviour in the three different parameter regimes. Note that the cobweb diagrams can be sketched by hand, given an accurate enough sketch of the right-hand side function $H(N_t)$. Note also that the cobweb diagrams are consistent with the linear stability analysis but that the linear approximation is only valid close to the equilibrium point.

2.5.6 Bifurcation diagram

Bifurcations at the critical values $\gamma = 1$ and $\gamma = 2$ are highlighted in the bifurcation diagram presented in Figure 2.11. Note that the bifurcation diagram allows classification of the different model behaviours in a single plot without explicitly calculating the solution to the model.

2.5.7 Symbolic computation

We can use symbolic calculators to aid many of computations performed above. Below is an example using the Python library sympi,

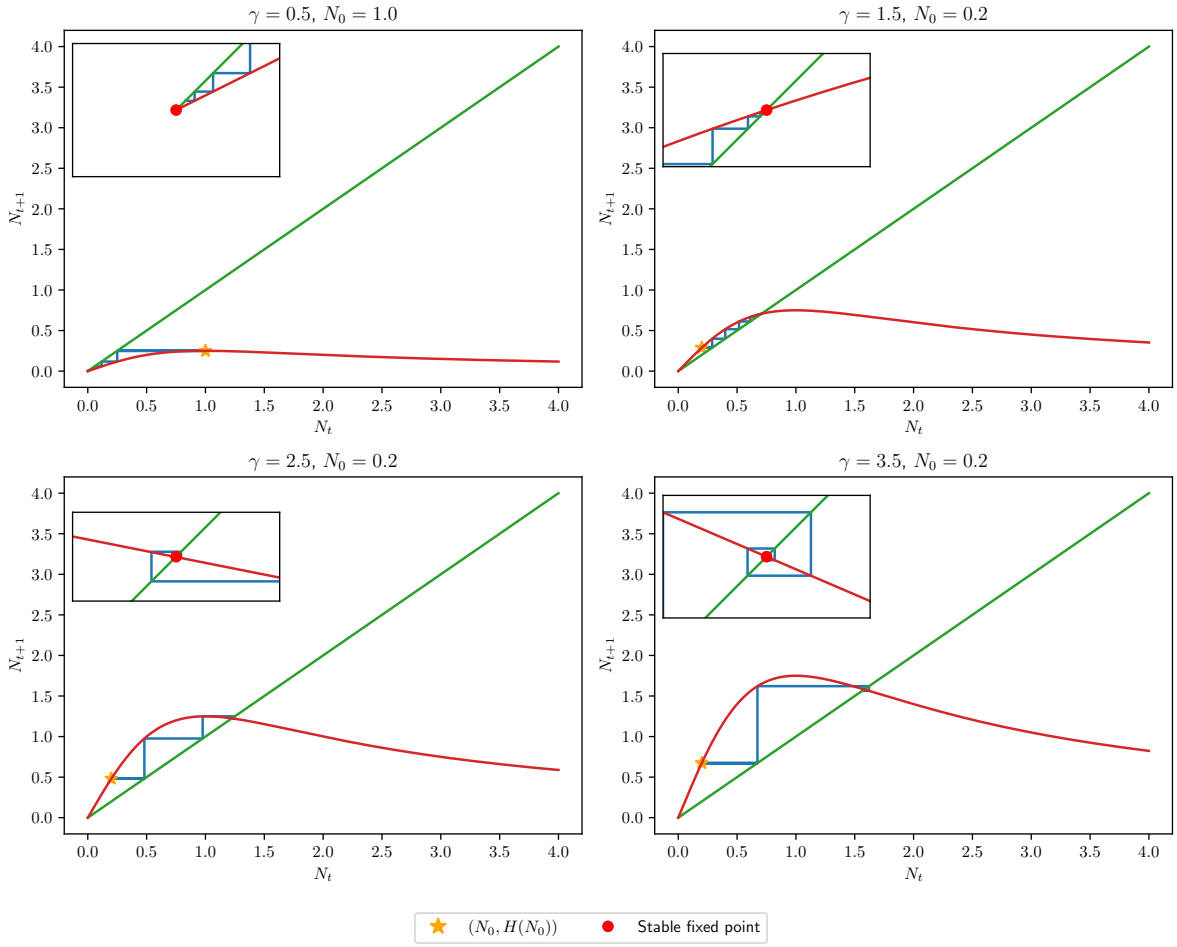


Figure 2.10: Cobweb diagrams for different values of γ, along with insets that zoom in on the stable critical point.

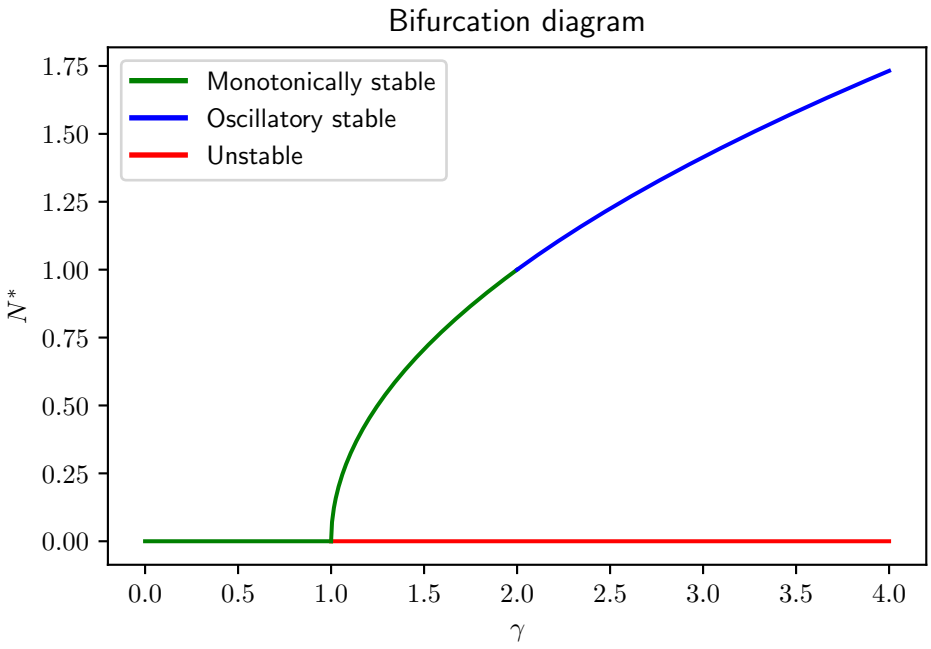


Figure 2.11: A bifiurcation diagram showing how the critical points change.

```
The FPs are:
[{N: 0}, {N: -sqrt(gamma - 1)}, {N: sqrt(gamma - 1)}]
The derivative of H is:
gamma*(1 - N**2)/(N**2 + 1)**2
The derivative evaluated at FP 1 is:
gamma
The derivative evaluated at FP 2 is:
(2 - gamma)/gamma
```

2.6 An application - how much harvesting can a population sustain?

Models of population dynamics can be used to study how interventions will affect population dynamics. Extending from the model developed in the previous example, a valid question might be what is the maximal rate of harvesting a fish stock can sustain without becoming extinct? Introducing a harvesting term at per capita harvesting rate h, the governing model equation becomes

$$N_{t+1} = \frac{\gamma N_t}{1 + N_t^2} - hN_t, \tag{2.32}$$

which suggests two fundamental questions: (i) does the introduction of harvesting change the dynamics of the system?; and (ii) what rate of harvesting such a population could withstand?

2.6.1 Direct simulation

Based on the previous analysis we consider the system in a parameter regime where without harvesting there is a stable fixed point ($\gamma > 1$).

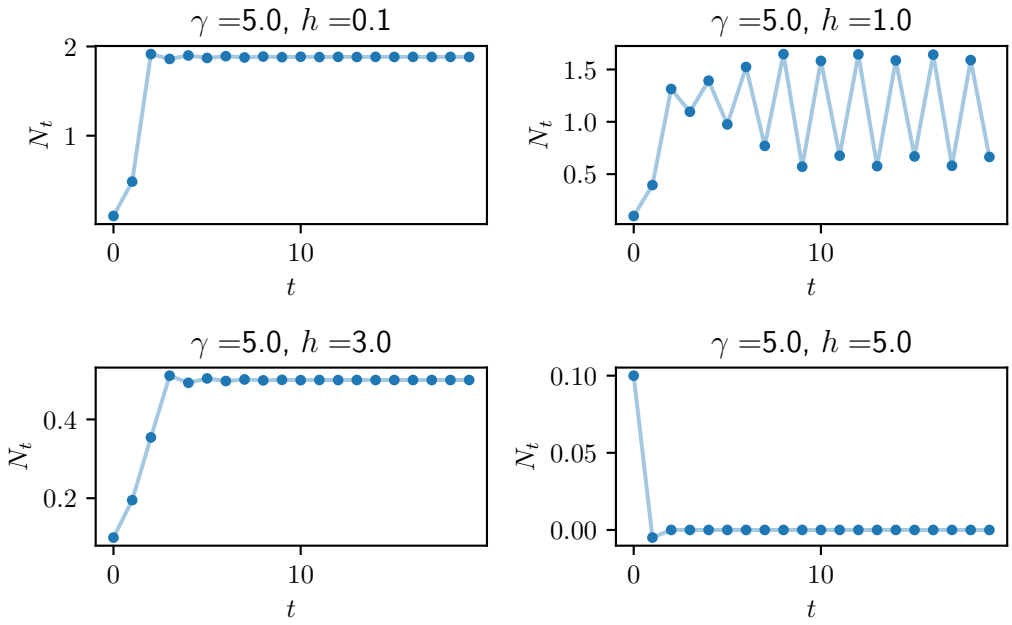


Figure 2.12: Time series solution for different values of h.

In Figure 2.12 time series solutions at increasing harvesting rates ($h = 0.1$, $h = 1$, $h = 3$, $h = 5$) are presented, and their corresponding cobweb diagrams in Figure 2.13. For low harvesting rates the system behaves almost identically to the no harvesting case but with an expected reduction in the fixed point value. For intermediate harvesting the population undergoes oscillations. However, for further increased harvesting rates there appears again to be a stable fixed point. Eventually we harvest too many fish and the population collapses.

Can analysis of the model help us understand how/why changes in the form of solutions occur?

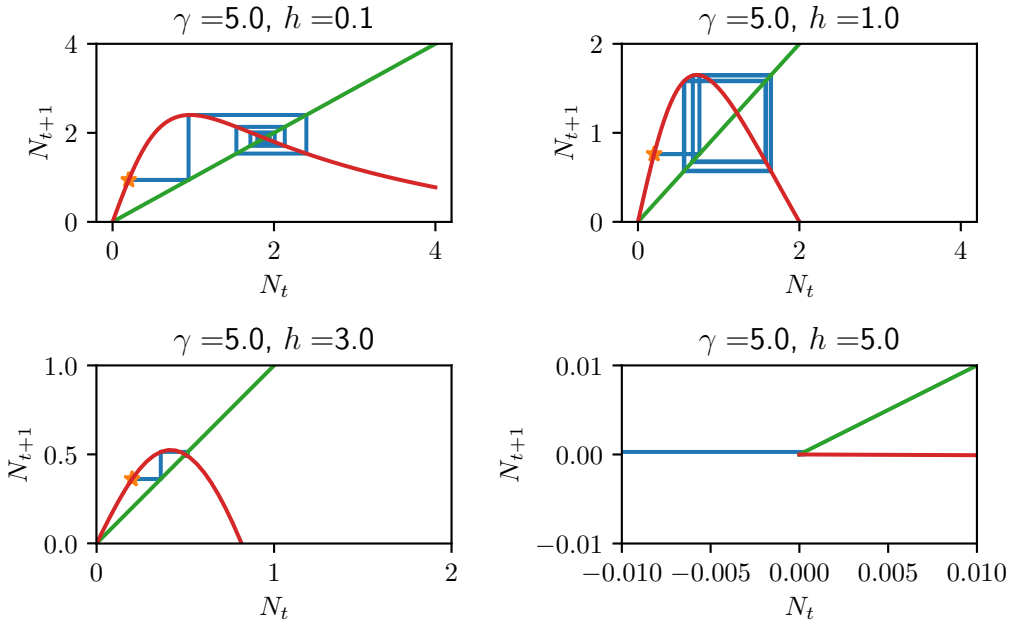


Figure 2.13: Cobweb diagrams for different values of h and $\gamma = 5$. These are the same values as in Figure 2.12. Note that the scales of the axes are very different in each plot and for $h = 5$ $N_1 < 0$ making the cobweb diagram non-physical

```
#| '!! shinylive warning !!': |
#|   shinylive does not work in self-contained HTML documents.
#|   Please set `embed-resources: false` in your metadata.
#| standalone: true
#| components: [viewer]
#| viewerHeight: 500


from shiny import App, Inputs, Outputs, Session, render, ui
from shiny import reactive

import numpy as np
from pathlib import Path
import matplotlib.pyplot as plt
from scipy.integrate import odeint

app_ui = ui.page_fluid(
    ui.layout_sidebar(
        ui.sidebar(
    ui.input_slider(id="r",label="gamma",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="h",label="h",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="u0",label="N_0 (Initial condition)",min=0.0,max=4.0,value=0.5,step=0
    ui.input_slider(id="T",label="Number of iterations",min=0.0,max=60.0,value=20.0,step=1.0)
    ui.input_slider(id="max_sol",label="Max. axis value",min=0.0,max=5.0,value=1.5,step=0.1)


        ),

        ui.output_plot("plot"),
    ),
)

def server(input, output, session):

    @render.plot
    def plot():
        fig, ax = plt.subplots(2,1)
        #ax.set_ylim([-2, 2])
        # Filter fata


        r=float(input.r())
        h=float(input.h())
        u0=float(input.u0())
        T=int(input.T())
        max_sol=float(input.max_sol())

        def rickerrhs(x,r,h):
          f=r*x/(1+x**2)-h*x
          return f
        # Define rhs of logistic map

        # this function computes the solutio to the difference equation. It also stores solu
```

2.6.2 Fixed points

The fixed points of the system satisfy

$$N^* = \frac{\gamma N^*}{1 + {N^*}^2} - hN^*. \tag{2.33}$$

Hence the fixed points are

$$N_1^* = 0 \qquad \text{and} \qquad N_2^* = \sqrt{\frac{\gamma}{1+h} - 1}. \tag{2.34}$$

Note that harvesting lowers the population size of the non-zero fixed point (N_2^*) when it exists. The condition on the parameters γ and h in order that there is a non trivial biologically relevant fixed point ($N_2^* > 0$) is given by,

$$\frac{\gamma}{1+h} - 1 > 0 \qquad \Rightarrow \qquad \gamma > 1 + h. \tag{2.35}$$

2.6.3 Linear stability

Linear stability is determined by,

$$H'(N_t) = \frac{\gamma}{1 + {N_t}^2} - \frac{2\gamma N_t^2}{(1 + {N_t}^2)^2} - h. \tag{2.36}$$

At $N_1^* = 0$ we obtain,

$$H'(0) = \gamma - h. \tag{2.37}$$

Hence if $\gamma > 1 + h$, $N^* = 0$ is unstable. Note that this is the condition that determines whether the non-zero fixed point N_2^* exists or not. For the other fixed point $N_t = N_2^*$ we get,

$$H'\left(\sqrt{\frac{\gamma}{1+h} - 1}\right) = \frac{\gamma}{1 + \frac{\gamma}{1+h} - 1} - \frac{2\gamma\frac{\gamma}{1+h} - 1}{(1 + \frac{\gamma}{1+h} - 1)^2} - h. \tag{2.38}$$

Hence, unsurprisingly, linear stability is now a function of two parameters γ and h. A bit of algebra produces a simpler form as a polynomial in h,

$$H'(N_2^*) = h^2\frac{2}{\gamma} + h\frac{2}{\gamma}(2 - \gamma) + \frac{2}{\gamma} - 1, \tag{2.39}$$

hence when $h = 0$ we retrieve the stability condition from the previous model.

2.6.4 Stability boundaries in the $h\gamma$ plane

We want to understand the critical points for different parameters choices (h, γ). We can break up the (h, γ) plane into regions by the contours that determine a change in the linear stability of the critical points. To this end, we want to find the three fundamental contours $H'(N_2^*) = -1,\ 0,\ 1$ which we do by substituing those values into Equation 2.39, which for our chosen values gives the contours,

$$\begin{aligned} H'(N_2^*) = -1 \quad &\Rightarrow \quad \gamma = \frac{(1+h)^2}{h}, \\ H'(N_2^*) = 0 \quad &\Rightarrow \quad \gamma = \frac{2(h+1)^2}{2h+1}, \\ H'(N_2^*) = 1 \quad &\Rightarrow \quad \gamma = 1 + h, \end{aligned} \tag{2.40}$$

All the above analysis can now be summarised by fixing h where we have the following regions in order of increasing γ,

1. $\gamma < h - 1 \ \Rightarrow\ H'(0) < -1,\ N_1^*$ is oscillatory unstable $\rightarrow$ population collapse,
2. $h - 1 < \gamma < h \ \Rightarrow\ -1 < H'(0) < 0,\ N_1^*$ is oscillatory stable $\rightarrow$ population collapse,
3. $h < \gamma < h + 1 \ \Rightarrow\ 0 < H'(0) < 1,\ N_1^*$ is monotonically stable $\rightarrow$ population collapse,
4. $h + 1 < \gamma < \frac{2(h+1)^2}{2h+1} \ \Rightarrow\ 0 < H'(N_2^*) < 1,\ \$,\ N_2^*$ is monotonically stable $\rightarrow$ population stable,
5. $\frac{2(h+1)^2}{2h+1} < \gamma < \frac{(1+h)^2}{h} \ \Rightarrow\ -1 < H'(N_2^*) < 0,\ N_2^*$ is oscillatory stable $\rightarrow$ population stable,
6. $\gamma > \frac{(1+h)^2}{h} \ \Rightarrow\ H'(N_2^*) < -1,\ N_2^*$ is oscillatory unstable $\rightarrow$ don't have the tools to know!

In Figure 2.15 we plot the contours of the hypersurface $H'(N^*)$ at the critical values of -1, 0 and 1. Note, that as $h \to 0$ we retain the behaviour of the previous model with no harvesting. Also for $h \gg 3$ the contours all become linear with gradient 1. We now understand the long time behaviour of the population unless $\gamma > \frac{(1+h)^2}{h}$, where N_2^* is unstable.

Exercise: Consider where in the parameter space the plots in Figure 2.12 and Figure 2.13 are and use this to explain the behaviour of the plots.

In Figure 2.16 we have plotted the time series solution for parameters where N_2^* is unstable for fixed γ. As h increases the long-time behaviour jumps between 2-values, then jumps between 4-values in a cycle, then it becomes chaotic and finally it returns to a 2-cycle. The next section will attempt to understand this mysterious region.

Many of the above calculations can be aided using a symbolic calculator:

```
The FPs are:
{N: 0}
{N: -sqrt(gamma - h - 1)/sqrt(h + 1)}
{N: sqrt(gamma - h - 1)/sqrt(h + 1)}
```

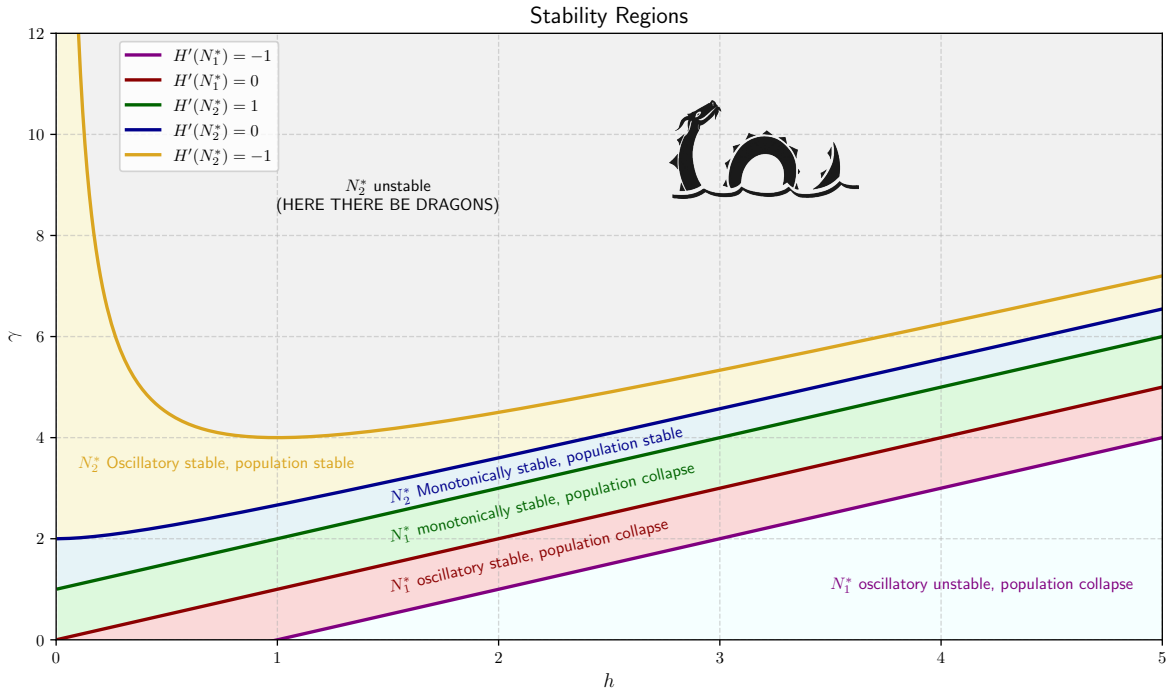


Figure 2.15: Stability regions from studying the linear stability of the fixed points of the harvesting model. This is not enough to understand population stability/collapse for the grey region, as can be seen in Figure 2.16

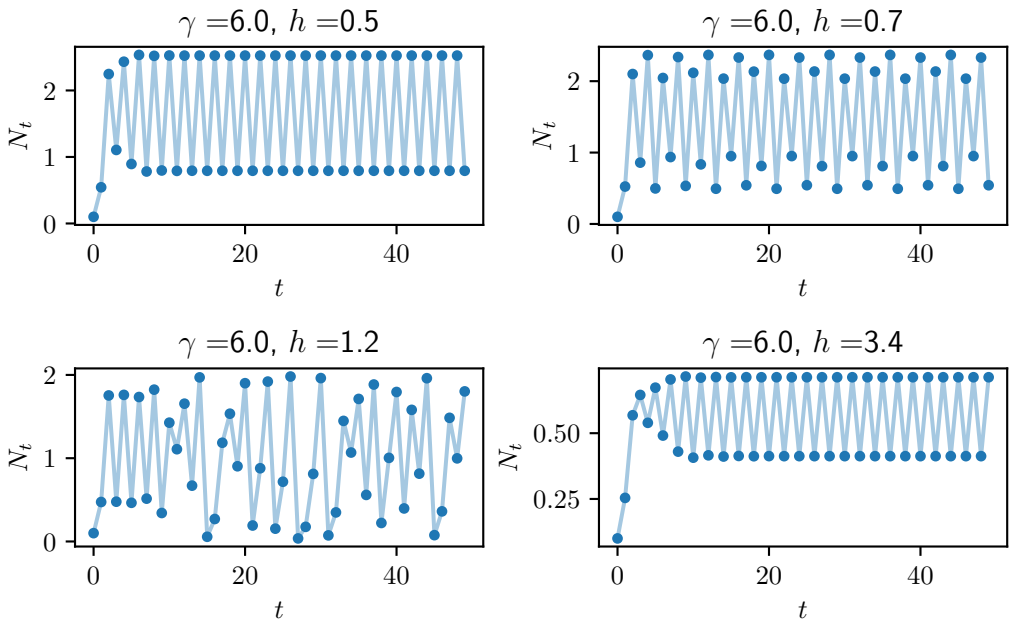


Figure 2.16: Time series solution for $\gamma = 6$ and values of h inside the grey region of the phase diagram in Figure 2.15 above (where N_2^* is unstable), demonstrating very different behavour.

```
The derivative of H is:
-N**2*gamma/(N**2 + 1)**2 + gamma/(N**2 + 1)**2 - h
The derivative evaluated at FP 0 is:
gamma - h
The derivative evaluated at FP 2 is:
(gamma + 2*(h + 1)*(-gamma + h + 1))/gamma
```

2.7 Oscillations, n-cycles and chaos

Linear stability analysis describes the evolution of small perturbations close to a fixed point. But far from a fixed point the nonlinear terms that were dropped in a Taylor expansion are no longer negligible. In particular, in the case where $H'(N^*) < -1$, it can be the case that regions of parameter space in which a fixed point is oscillatory unstable can give rise to periodic and chaotic solutions.

Consider a general difference equation of the form,

$$N_{t+1} = H(N_t) \tag{2.41}$$

A solution to Equation 2.41 is defined to be **periodic** with period T if and only if,

$$\begin{aligned} N_{t+T} &= N_t \quad \forall t, \\ N_{t+\tau} &\neq N_t \quad \forall t, \end{aligned} \tag{2.42}$$

where $\tau < T$.

Period 2 solutions or **2-cycles** can be identified by looking for solutions that repeat after two iterations, hence a population $\bar{N}$ defines a 2-cycle if and only if,

$$\bar{N} = H(H(\bar{N})) = H^2(\bar{N}), \quad \text{where } \bar{N} \neq H(\bar{N}), \tag{2.43}$$

Hence, we can define a general n-cycle as $\bar{N}$ such that,

$$\bar{N} = H^n(\bar{N}), \quad \text{where } \bar{N} \neq H^k(\bar{N}) \ \forall\, k \in \mathbb{N},\ k < n. \tag{2.44}$$

Hence, n-cycles are fixed points of the problem,

$$N_{t+n} = H^n(N_t). \tag{2.45}$$

Note that finding a fixed point of Equation 2.45 is not sufficient to show it is an n-cycle as it must also not be a fixed point of $N_{t+k} = H^k(N_t)$ where $0 < k < n$. For example, fixed points of $H(N_t)$ are all fixed points of $H^n(N_t)\ \forall\, n \in \mathbb{N}$.

We have already developed the tools to find such fixed points and study their stability. Note that as the period of the solutions increases the right hand side of the function becomes increasingly complicated to tackle algebraically.

2.7.1 The harvesting model revisted

In many systems, such as the harvesting model and the logistic equation, increasing the growth rate parameter leads initially to the fixed point becoming unstable and the emergence of period two solutions, then period 4 solutions and so on until eventually there is a transition to chaotic solutions.

Consider period 2 solutions $\bar{N}$ of Equation 2.32, namely solutions of,

$$\bar{N} = H^2(\bar{N}) = \frac{\gamma\frac{\gamma\bar{N}}{1+\bar{N}^2} - h\bar{N}}{1 + \left(\frac{\gamma\bar{N}}{1+\bar{N}^2} - h\bar{N}\right)^2} - h\frac{\gamma\bar{N}}{1+\bar{N}^2} - h\bar{N}. \tag{2.46}$$

This is certainly solvable by hand but is easier using SymPy which we do below. We simplified Equation 2.46 so it became a degree 9 polynomial in $\bar{N}$. We already know some of the roots however, as all 1-cycles (fixed points of H) will be fixed points of H^2. So we can divide by these three roots simplifying to a sextic but with even powers only. Hence we end up with a cubic in $\bar{n} = \bar{N}^2$, which we can solve. We then select only positive cycles $(\bar{N}_1, \bar{N}_2)$ such that,

$$\bar{N}_1 = H(\bar{N}_2), \quad \text{and } \bar{N}_2 = H(\bar{N}_1). \tag{2.47}$$

Note that the pair $(-\bar{N}_1, -\bar{N}_2)$ will always exist due to the symmetry of the polynomial.

Finally we now consider the stability of each fixed point, which is given by $(H^2)'(\bar{N}_1)$ which is simply given by the chain rule to be,

$$(H^2)'(\bar{N}_1) = H'(H(\bar{N}_1))H'(\bar{N}_1) = H'(\bar{N}_2)H'(\bar{N}_1), \tag{2.48}$$

which is equivalent for $(H^2)'(\bar{N}_2)$. In Figure 2.17 we then plot three regions in the (h, γ) plane,

- discriminant of the quadratic $\Delta(\bar{n}) < 0$, hence no real solutions and no physical 2-cycle (grey),
- $0 < H'(\bar{N}_1)H'(\bar{N}_2) < 1$, hence the 2-cycle is monotonically stable (blue),
- $-1 < H'(\bar{N}_1)H'(\bar{N}_2) < 0$, hence the 2-cycle is oscillatory stable (green),
- $H'(\bar{N}_1)H'(\bar{N}_2) < -1$, hence the 2-cycle is oscillatory unstable (red).

```
The FPs are:
{N: 0}
{N: -sqrt(gamma - h - 1)/sqrt(h + 1)}
{N: sqrt(gamma - h - 1)/sqrt(h + 1)}
The derivative of H is:
-N**2*gamma/(N**2 + 1)**2 + gamma/(N**2 + 1)**2 - h
The derivative evaluated at FP 0 is:
gamma - h
```

```
The derivative evaluated at FP 2 is:
(gamma + 2*(h + 1)*(-gamma + h + 1))/gamma
The 2-cycle polynomial is:
(h + 1)*(-gamma + h*n + h - n - 1)*(-gamma*h*n + h**2*n**2 + h**2*n + n + 1)
with solutions:
(gamma*h - h**2 - sqrt(gamma**2*h**2 - 2*gamma*h**3 - 2*gamma*h + h**4 - 2*h**2 + 1) - 1)/(2
(gamma*h - h**2 + sqrt(gamma**2*h**2 - 2*gamma*h**3 - 2*gamma*h + h**4 - 2*h**2 + 1) - 1)/(2
(gamma - h + 1)/(h - 1)
solutions with non-physical 2-cycles:
(gamma - h + 1)/(h - 1)
Discriminant of the physical 2-cycle polynomial:
gamma**2/h**2 - 2*gamma/h - 2*gamma/h**3 + 1 - 2/h**2 + h**(-4)
```

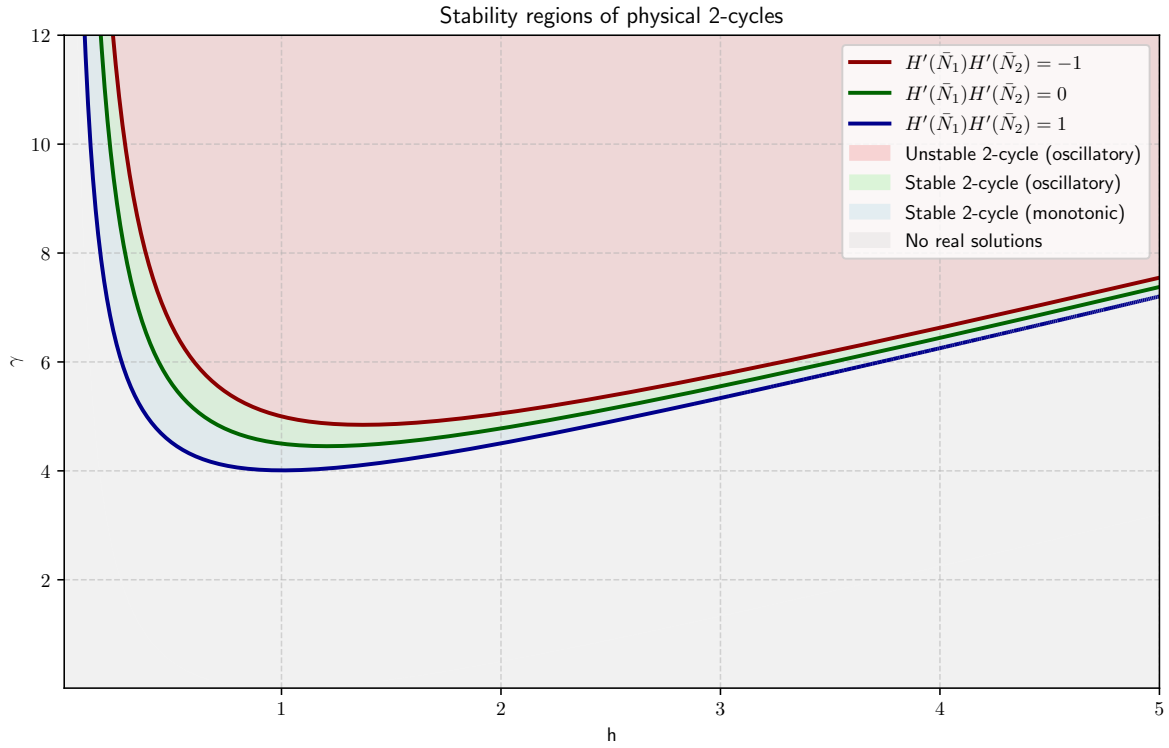


Figure 2.17: The regions of stability of fixed points of period 2 or 2-cycles.

(see, for example, Figure 2.18).

We could repeat the above process for 4-cycles and then 8-cycles though it will get progressively harder. To get a feel for what happens as the harvesting rate increases in this region we could instead do some numerics to simulate a bifurcation diagram. Here we plot all possible final populations for each h, namely all N_t for $300 < t < 800$. The results of this are shown in

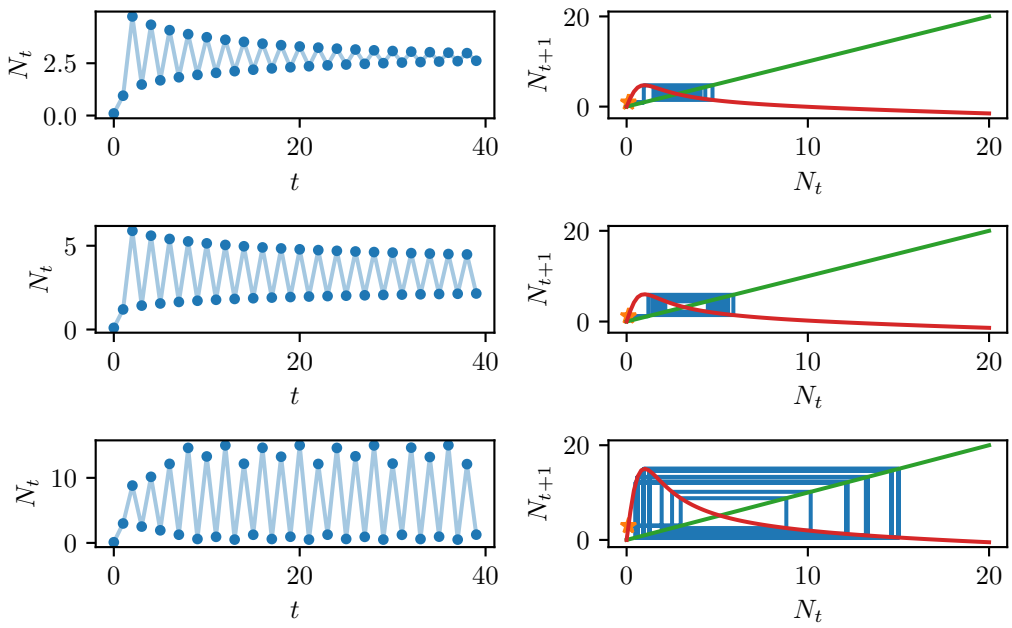


Figure 2.18: Transition form period 2 to period 4 solutions in the harvesting model

Figure 2.19, where we can see for $\gamma = 6$ as h increases from 0 and decreases from 4 the period of the solution doubles with decresing interval and then becomes chaotic. There are also large white regions amonst the chaos, where ordered dynamics returns before becoming chaotic again. These kind of features appear in many non-linear population models.

2.8 A note on the modelling of real-world fish stocks

You can find reports on fish stocks (measurements and modelling work) from the International Council for the Exploration of the Sea at the link. Here's a link to the data for Atlantic salmon. Note that although the models we have worked on are not detailed enough to accurately model real fish population dynamics, many of the principles we have covered arise in the cutting edge models.

3 Multi species population dynamics in discrete time

In this chapter we generalise the previous approach by considering the population dynamics of two interacting populations.

3.1 A general model of two interacting species in discrete time

Let N_t and P_t represent population densities at time t where t is a discrete variable. We will consider systems that can be written as a system of 2 difference equations of the form,

$$N_{t+1} = f(N_t, P_t),$$
$$P_{t+1} = g(N_t, P_t).$$

where the population dynamics of the species are coupled to one another via the functions f and g.

The precise form for f and g will be defined by the biological system we study. Typical inter-population interactions that are studied are: predator prey models, competition and cooperation.

3.2 General techniques for analysing coupled first order difference equations

3.2.1 Fixed points and linear stability

The fixed points of Equation 3.15 (N^*, P^*) satisfy

$$N^* = g(N^*, P^*)$$
$$P^* = f(N^*, P^*).$$

To consider the linear stability of a steady state we consider the change of variables,

$$N_t = N^* + \hat{N}_t,$$
$$P_t = P^* + \hat{P}_t,$$

where we can collect the perturbations into a vector,

$$\hat{\phi}_t = \begin{pmatrix} \hat{N}_t \\ \hat{P}_t \end{pmatrix}. \tag{3.1}$$

After substitution into Equation 3.15 and performing a Taylor expansion about (N^*, P^*),

$$\hat{\phi}_{t+1} = J\hat{\phi}_t + \mathcal{O}\left(\|\hat{\phi}_t\|^2\right). \tag{3.2}$$

If we assume that $\hat{N}$ and $\hat{P}$ are both small then we can consider this equation to linear (leading) order,

$$\hat{\phi}_{t+1} = J\hat{\phi}_t, \tag{3.3}$$

where the matrix J is the familiar Jacobian matrix,

$$J = \left(\begin{array}{cc} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{array} \right)\Bigg|_{(N^*,P^*)}. \tag{3.4}$$

By solving this linear system we can investigate whether small perturbation about the fixed point grow or decay in magnitude as time evolves and hence determine the linear stability of the fixed point.

The solution of Equation 3.3 takes the form,

$$\hat{\phi}_t = \sum_{i=1}^{2} C_i \lambda_i^t \mathbf{c}_i, \tag{3.5}$$

where the C_i's are constants determined by initial conditions and the λ_i's and $\mathbf{c}_i$'s are the eigenvalues and eigenvectors of J, respectively. From this form we can split into three cases:

- $|\lambda_i| < 1 \quad \forall i$, the fixed point is *linearly stable*,
- $\exists\, i \; s.t. \; |\lambda_i| > 1$, the fixed point is **linearly unstable** to perturbations,
- $\exists\, i \; s.t. \; |\lambda_i| = 1 \wedge |\lambda_i| \leq 1 \quad \forall i$, the fixed point is **marginal**, linear analysis is inconclusive and higher order terms $\mathcal{O}\left(\|\hat{\phi}_t\|^2\right)$ need to be considered.

3.2.2 Jury conditions

In many cases it is not useful to explicitly compute the eigenvalues of the Jacobian matrix. In such cases we can employ the Jury conditions in order to determine when a fixed point is linearly stable.

Recall that for a two dimensional matrix A, the eigenvalues satisfy the quadratic characteristic equation

$$\lambda^2 - trA\lambda + detA = 0. \tag{3.6}$$

The stability of the fixed is guaranteed if $|\lambda_i| < 1 \ \forall i$.

Consider the characteristic equation,

$$P(\lambda) = \lambda^2 + a\lambda + b = 0, \tag{3.7}$$

where $a, b \in \Re$. Note that $a = -trA$ and $b = \det A$.

The Jury conditions state that $|\lambda_i| < 1 \ \forall i$ if, and only if,

- $b < 1$,
- $1 + a + b > 0$,
- $1 - a + b > 0$.

See Figure 3.1 for a schematic diagram.

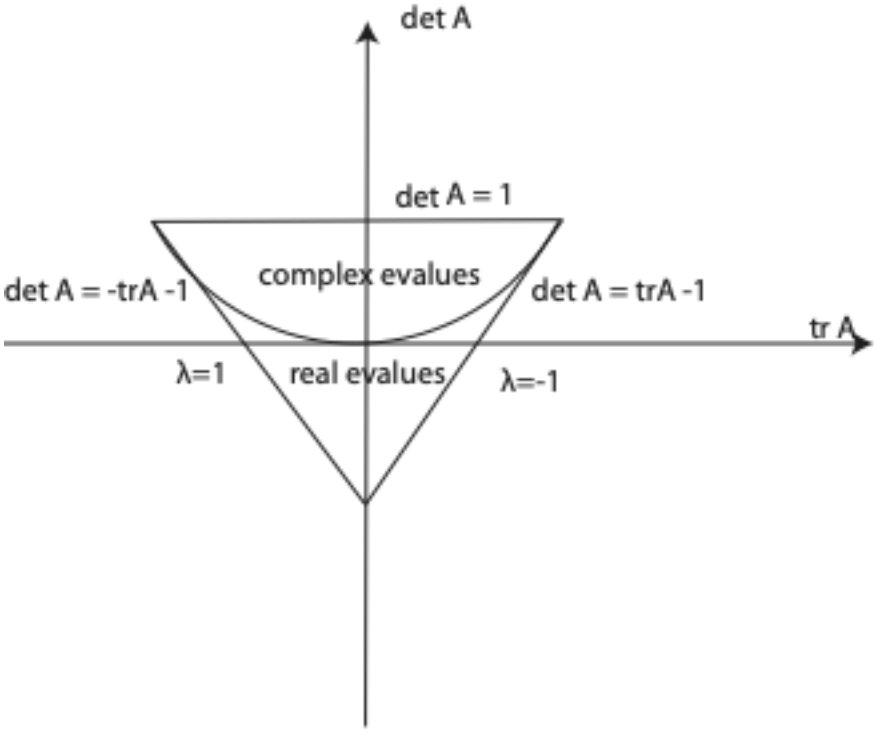


Figure 3.1: Jury conditions

3.2.3 Proof of the Jury conditions

The roots of $P(\lambda)$ are

$$\lambda_{1,2} = \frac{-a \pm \sqrt{a^2 - 4b}}{2}. \tag{3.8}$$

3.2.4 Complex roots

Suppose $a^2-4b<0$, then the roots $\lambda_{1,2}$ are complex conjugates. Since b is equal to the product of the roots (and they have the magnitude), we find that

$$|b| = |\lambda_1\lambda_2| = |\lambda_1|^2 = |\lambda_2^2|. \tag{3.9}$$

Hence $|\lambda_i| < 1 \ \forall \ \ i$ if and only if $|b|<1$.

For the other conditions we introduce the identity:

$$a^2 - 4b = (|a|-2)^2 - 4(1+b-|a|). \tag{3.10}$$

Therefore, when $a^2-4b<0$, the inequality requires

$$(|a|-2)^2 - 4(1+b-|a|) < 0. \tag{3.11}$$

This can only occur if

$$1+b-|a|>0 \implies 1+b-a>0 \ \text{ and } \ 1+b+a>0. \tag{3.12}$$

Note that the above inequality also gives us,

$$1+b>|a|\geq 0 \quad \Rightarrow \quad b>-1,$$

Hence, rather than stating $|b|<1$ from the start of the proof it is sufficient to use the simpler $b<1$, as the last two Jury conditions imply $b>1$ regardless.

3.2.5 Real roots

Suppose $a^2-4b\geq 0$ such that the roots $\lambda_{1,2}\in\mathbb{R}$ and take R to be the largest of their absolute values,

$$R = \max\{|\lambda_1|,|\lambda_2|\} = \frac{|a|+\sqrt{a^2-4b}}{2}. \tag{3.13}$$

This is an increasing function of $|a|$. Thus we can bound a by considering $R=1$,

$$\begin{aligned} R=1 \ &\Rightarrow \ \frac{|a|+\sqrt{a^2-4b}}{2} = 1, \\ &\Rightarrow \ |a|-2 = -\sqrt{|a|^2-4b}, \\ &\Rightarrow \ |a|^2-4|a|+4 = |a|^2-4b, \\ &\Rightarrow \ |a| = b+1. \end{aligned} \tag{3.14}$$

Hence $0\leq R<1$ if and only if $0\leq|a|<1+b$. Also, since $|\lambda_i|<1\forall i$ implies that $|\lambda_1\lambda_2|<1$, it follows that $|b|<1$ must hold. Similar to the argument for complex roots $b>-1$ is already implied by the last two Jury conditions thus it is sufficent to take $b<1$.

3.3 Host Parasitoid infection

Parasitoids are creatures that have a free living and parasitic stage. The free-living adult lays eggs in a host that later hatch and develop after eating the host. The discrete stages of the parasitoids life cycle and the dependence on its reproduction on the availability of host suggest a discrete time, multi species models. Let N_t and P_t represent the number of hosts and parasitoids at time t, respectively. Let R_0 represent the reproductive ratio of host in the absence of parasites and C the average number of viable eggs laid by each parasite on a host.

3.3.1 Model equations

We consider equations of the form

$$\begin{aligned} N_{t+1} &= R_0 N_t f(N_t, P_t), \\ P_{t+1} &= C N_t (1 - f(N_t, P_t)). \end{aligned}$$

The justification for this form is that at a given time t there are N_t hosts. A total of $N_t f(N_t, P_t)$ escape the parasite and are able to reproduce whilst a total of $N_t(1 - f(N_t, P_t))$ do not escape the parasite and lead to parasitic reproduction at the next time step.

Choosing

$$f(N_t, P_t) = e^{-aP_t}, \tag{3.15}$$

yields the Nicholson Bailey model

$$\begin{aligned} N_{t+1} &= R_0 N_t e^{-aP_t}, \\ P_{t+1} &= C N_t (1 - e^{-aP_t}). \end{aligned}$$

3.3.2 Numerical solution

3.3.3 Fixed points

The fixed points satisfy

$$\begin{aligned} N^* &= R_0 N^* e^{-aP^*}, \\ P^* &= C N^* (1 - e^{-aP^*}). \end{aligned}$$

The first equation yields

$$N^* = 0. \tag{3.16}$$

Suppose $N^* \neq 0$

$$1 = R_0 e^{-aP^*}. \tag{3.17}$$

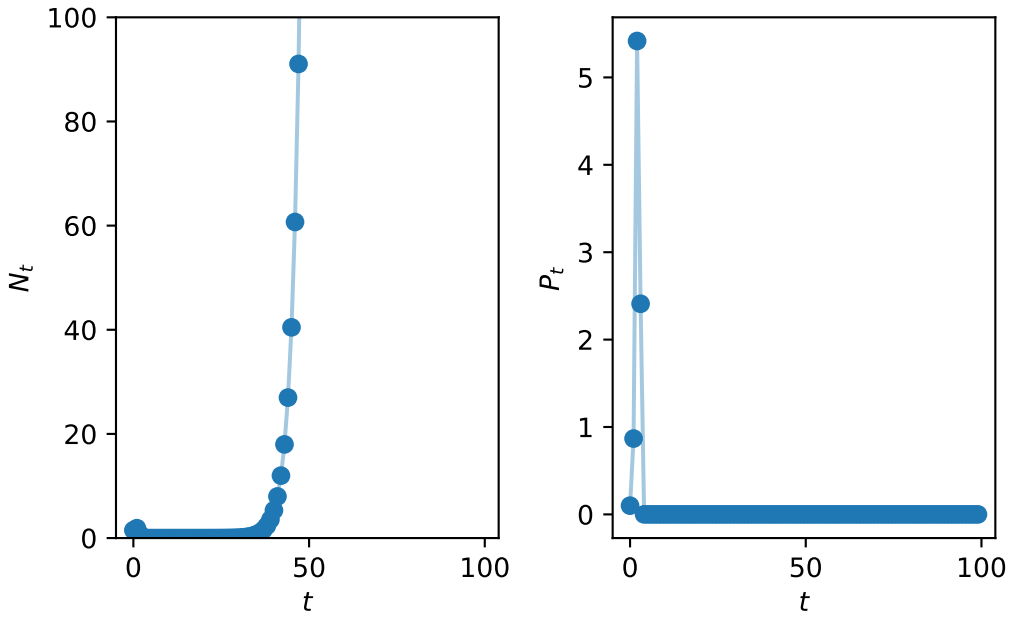


Figure 3.2: A plot of the Nicholson Bailey model solution.

Hence

$$P^* = \frac{1}{a} \ln R_0. \tag{3.18}$$

Consider the second equation. Suppose $N^* = 0$. We obtain

$$P^* = 0. \tag{3.19}$$

Hence one fixed point is $(0, 0)$.

Suppose $P^* = \frac{1}{a} \ln R_0$.

$$\frac{1}{a} \ln R_0 = CN^*(1 - \frac{1}{R_0}). \tag{3.20}$$

Hence

$$N^* = \frac{\frac{1}{a} \ln R_0}{C(1 - \frac{1}{R_0})} = \frac{R_0 \ln R_0}{aC(R_0 - 1)}. \tag{3.21}$$

Hence the second fixed point is

$$\left(\frac{R_0 \ln R_0}{aC(R_0 - 1)}, \frac{1}{a} \ln R_0 \right). \tag{3.22}$$

We can verify by substitution that

$$\left(\frac{R_0 \ln R_0}{aC(R_0 - 1)}, \frac{1}{a} \ln R_0 \right). \tag{3.23}$$

```
#| '!! shinylive warning !!': |
#|   shinylive does not work in self-contained HTML documents.
#|   Please set `embed-resources: false` in your metadata.
#| standalone: true
#| components: [viewer]
#| viewerHeight: 750


from shiny import App, Inputs, Outputs, Session, render, ui
from shiny import reactive

import numpy as np
from pathlib import Path
import matplotlib.pyplot as plt
from scipy.integrate import odeint

app_ui = ui.page_fluid(
    ui.layout_sidebar(
        ui.sidebar(
    ui.input_slider(id="R_0",label="R_0",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="a",label="a",min=0.0,max=5.0,value=1.2,step=0.001),
     ui.input_slider(id="C",label="C",min=0.0,max=5.0,value=1.2,step=0.001),
    ui.input_slider(id="N_0",label="N_0 (Initial condition)",min=0.0,max=4.0,value=0.5,step=0
    ui.input_slider(id="P_0",label="P_0 (Initial condition)",min=0.0,max=4.0,value=0.5,step=0
    ui.input_slider(id="T",label="Number of iterations",min=0.0,max=60.0,value=20.0,step=1.0)


        ),

        ui.output_plot("plot"),
    ),
)

def server(input, output, session):

    @render.plot
    def plot():
        fig, ax = plt.subplots()
        #ax.set_ylim([-2, 2])
        # Filter fata


        R_0=float(input.R_0())
        a=float(input.a())
        C=float(input.C())
        T=int(input.T())
        N_0=float(input.N_0())
        P_0=float(input.P_0())

        par=[R_0,a,C]
        init_cond=[N_0,P_0]

        def nicholsonbaileyrhs(x,par):
```

is a fixed point. We can then deduce a condition on the model parameters that must hold in order that the fixed point is biologically relevant.

To verify by substitution we substitute the proposed solution into the governing equations. Note that

$$e^{-aP^*} = \frac{1}{R_0}. \tag{3.24}$$

In this case

$$\frac{R_0 \ln R_0}{aC(R_0-1)} = R_0 \frac{R_0 \ln R_0}{aC(R_0-1)} \frac{1}{R_0},$$
$$\frac{1}{a} \ln R_0 = C \frac{R_0 \ln R_0}{aC(R_0-1)} (1 - \frac{1}{R_0}).$$

Cancellation shows that both equations hold. Hence the fixed point is a valid fixed point. To be biologically relevant we require that both components of the solution are real and positive. In this case this leads to the condition $R_0 > 1\}$.

3.3.4 Linear stability

The Jacobian matrix is given by

$$A_{(N_t,P_t)} = \begin{pmatrix} R_0 e^{-aP_t} & -R_0 a N_t e^{-aP_t} \\ c(1-e^{-aP_t}) & aCN_t e^{-aP_t} \end{pmatrix}. \tag{3.25}$$

3.3.5 Linear stability of the trivial fixed point

Evaluating at (0,0) yields

$$A = \begin{pmatrix} R_0 & 0 \\ 0 & 0 \end{pmatrix}. \tag{3.26}$$

Hence the eigenvalues are R_0 and 0. If $0 < R_0 < 1$ (0,0) is stable whilst if $R_0 > 1$ (0,0) is unstable.

3.3.6 Linear stability of the nontrivial fixed point

We can show that the Jacobian matrix evaluated at the nontrivial fixed point can be written as

$$A = \begin{pmatrix} 1 & -\frac{R_0 \ln R_0}{c(R_0-1)} \\ c(1-\frac{1}{R_0}) & \frac{\ln R_0}{R_0-1} \end{pmatrix}. \tag{3.27}$$

and deduce that the eigenvalues of A satisfy the characteristic polynomial

$$\lambda^2 - \lambda \left(1 + \frac{\ln R_0}{R_0 - 1}\right) + \frac{R_0 \ln(R_0)}{R_0 - 1} = 0. \tag{3.28}$$

3.3.7 Employing the Jury conditions

To proceed with linear stability analysis we employ the Jury conditions. Consider the polynomial

$$\lambda^2 + a\lambda + b = 0, \tag{3.29}$$

In our case

$$a = -(1 + \frac{\ln R_0}{R_0 - 1}) \tag{3.30}$$

and

$$b = \frac{R_0 \ln(R_0)}{R_0 - 1}. \tag{3.31}$$

The third Jury condition ($b < 1$) implies that for linear stability

$$\ln R_0 < 1 - \frac{1}{R_0}. \tag{3.32}$$

To demonstrate that this inequality is not true for $R_0 > 1$, let $f_1 = \ln R_0$ and $f_2 = 1 - 1/R_0$. When $R_0 = 1$, $f_1 = f_2 = 0$. However,

$$f_1' = \frac{1}{R_0} \quad \text{and} \quad f_2' = \frac{1}{R_0^2}, \tag{3.33}$$

implies

$$f_1' > f_2' \ \ \forall \ R_0 > 1. \tag{3.34}$$

Hence

$$\ln R_0 > 1 - \frac{1}{R_0}. \tag{3.35}$$

Hence the fixed point is unstable if $R_0 > 1$.

3.3.8 Symbolic calculations in Python

Below sympy is used to identify the fixed points. The Jacobian matrix is then computed and evaluated at the fixed points.

```
The FPs are:
{N: 0, P: 0}
{N: R_0*log(R_0)/(C*a*(R_0 - 1)), P: log(R_0)/a}
The Jacobian of H is:
[[R_0*exp(-P*a), -N*R_0*a*exp(-P*a)], [C - C*exp(-P*a), C*N*a*exp(-P*a)]]
The Jacobian evaluated at FP 0 is:
[[R_0, 0], [0, 0]]
The Jacobian evaluated at FP 1 is:
[[1, -R_0*log(R_0)/(C*(R_0 - 1))], [C*(1 - 1/R_0), log(R_0)/(R_0 - 1)]]
```

Part II

Continuous time

4 Single species population dynamics

In this chapter we define time, t, to be a continuous variable and the population density, $N(t)$, to represent the size of a given population.

4.1 The Malthusian (linear) model

As time is now a continuous variable, we consider an interval of time δt. Consider a population of size $N(t)$. If the per capita production rate is b, then in time δt the increase in population size will be

$$bN(t)\delta t. \tag{4.1}$$

Similarly, if the per capita death rate is d, the decrease in population size in time δt will be

$$dN(t)\delta t. \tag{4.2}$$

Hence

$$N(t+\delta t) = N(t) + (bN(t) - dN(t))\delta t. \tag{4.3}$$

Rearranging and taking the limit as $\delta t \to 0$ yields

$$\frac{dN}{dt} = (b-d)N = rN(t). \tag{4.4}$$

The solution can be found using seperation of variables,

$$N(t) = N_0 \exp(rt), \tag{4.5}$$

where N_0 is the initial population at time $t = 0$. We can describe qualitatively different solutions behaviours,

- $r > 0$, the solution increases exponentially,
- $r < 0$, the solution decreases exponentially,
- $r = 0$, the solution is constant.

Malthusian growth in the continuous time model leads to either a constant population, exponentially increasing or exponentially decreasing growth. As was the case for the discrete time model, such a model could account for biological system only in particularly limited circumstances.

The Malthusian model (constant per capita growth rate) can exhibit a limited range of behaviour. To account for limitation of population growth at large population densities due to, for example, limited resources, we consider nonlinear per capita growth rates.

4.2 Tools for analysing the dynamics of a single population in continuous time

Let $N = N(t)$. We consider the general form for a single species model defined in continuous time,

$$\frac{dN}{dt} = f(N)N = H(N), \tag{4.6}$$

where f is the per capita growth rate and H is the net growth rate.

4.2.1 Numerical solution

Although an equation of the form Equation 4.6 may not be explicitly integrable, so long as the right-hand side is sufficiently well behaved, we can numerically integrate the problem (e.g. using packages such as Python's odeint). Such a technique provides a numerical approximation to the exact solution, given specific values of model parameters and initial conditions (i.e. we can graph solutions).

4.2.2 Steady-state

We denote **steady-state solutions** or **equilibria** of Equation 4.6 using $N = N^*$. At a steady-state,

$$\frac{dN}{dt} = 0, \tag{4.7}$$

and hence steady-states can be obtained by solving the algebraic equation,

$$H(N^*) = 0. \tag{4.8}$$

Note, some texts may call these fixed points or critical points. The first is often used in dynamical systems, while the second is older and rarely used as it can be ambiguous.

4.2.3 Linear stability analysis

To perform a linear stability analysis near an equillibrium we make the change of variables,

$$N(t) = N^* + \hat{N}(t), \tag{4.9}$$

where the new dependent variable, $\hat{N}(t)$, is a perturbation about the steady state N^*. The time derivative on the left-hand side of Equation 4.6 transforms to,

$$\frac{dN}{dt} = \frac{d}{dt}(N^*) + \frac{d}{dt}(\hat{N}(t)) = \frac{d\hat{N}(t)}{dt}. \tag{4.10}$$

Hence Equation 4.6 transforms to

$$\frac{d\hat{N}(t)}{dt} = H(N^* + \hat{N}(t)). \tag{4.11}$$

Employing a Taylor expansion on the right-hand side of Equation 4.6 we get,

$$\frac{d\hat{N}(t)}{dt} = H(N^*) + H'(N^*)\hat{N}(t) + \frac{1}{2}H''(N^*)\hat{N}^2(t) + \mathcal{O}(\hat{N}^3), \tag{4.12}$$

where we use $H(N^*) = 0$ and assume the perturbation $\hat{N}$ is small to neglect all terms quadratic and higher, which yields the linear ODE,

$$\frac{d\hat{N}(t)}{dt} = H'(N^*)\hat{N}(t) \tag{4.13}$$

with solution (by separation of variables),

$$\hat{N}(t) = \eta e^{H'(N^*)t} \tag{4.14}$$

where η is some initial perturbation about the steady-state. We now have 3 phases in this linear regime,

- $H'(N^*) > 0$, the pertubration grows exponentially fast and the steady-state is **unstable**.
- $H'(N^*) < 0$, the perturbation decays exponentially fast and the steady-state is **stable**.
- $H'(N^*) = 0$, the **marginal** case where linearisation is inconclusive and higher-order terms determine stability.

Note that, for the discrete time case, our solutions could decay or grow montonically or oscillatory. This is no longer the case for the continous model (as it would require $H'(N^*)$ to change in time). So we only have monotonic decay or growth.

4.2.4 Graphical solution

We can graphically identify steady-states and their stability by plotting dN/dt against $N(t)$. Steady-states arise at the roots of $H(N)$. The sign of the derivative at a root determines its linear stability.

4.2.5 Bifurcation diagrams

Bifurcations arise when the number of solutions or their stability changes at a given value of a model parameter. By plotting the steady state solutions against a model parameter and using annotation to represent stability of solutions we can obtain a bifurcation diagram.

As an exercise perform a qualitative analysis of the Malthusian model.

4.3 The logistic growth model

4.3.1 Model development

Let $N = N(t)$. The logistic model, due to Verhulst, takes the form

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right), \tag{4.15}$$

where r is the linear growth rate and K is carrying capacity. We consider both $r, K \in \Re^+$.

Questions to ask of such a model are: what type of biologically realistic solutions does it possess? Are there steady-states? If so, are they stable or unstable? Are there bifurcations in solutions?

4.3.1.1 Numerical solutions

In Figure 4.1 we present numerical solutions of equation using different initial conditions. Note the limiting behaviour of solutions as $t \to \infty$. In Figure 4.1 it is clear that even though some solutions are initialised at $N_0 = 0.1$, much closer to $N^* = 0$ than $N^* = K$, they tend to the limit $N = K$. Why do solutions not tend to $N^* = 0$?

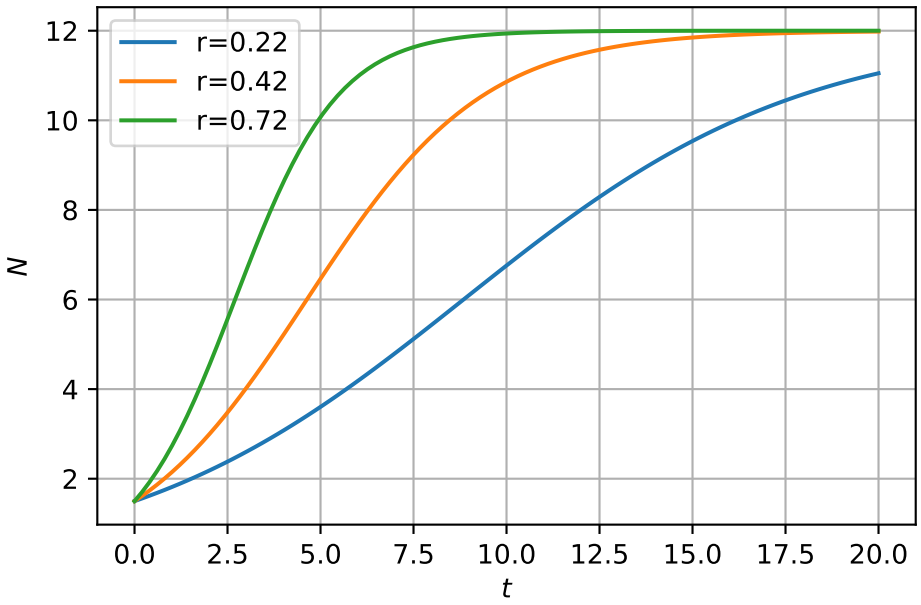


Figure 4.1: Numerical solution of the logistic growth model

4.3.1.2 Dimensional analysis and nondimensionalisation

N represents the population density and has units of one over area (say $1/m^2$) and t has units of time (say, seconds, s). Hence the left-hand side of Equation 4.15 has units of $1/(m^2 s)$. The first term on the right-hand side of Equation 4.15 is rN. N has units $1/m^2$ hence the parameter r must have units of $1/s$ for dimensional consistency. This is consistent as r represents the linear growth rate.

The second term has the form rN^2/K. Given the chosen units for r and N, the parameter K must have dimensions $1/m^2$. Again, this is consistent as K is a carrying capacity (i.e. it has units of population density).

We define the nondimensionalised variables

$$n = \frac{N}{\tilde{N}} \qquad \tau = \frac{t}{\tilde{T}} \tag{4.16}$$

where $\tilde{N}$ and $\tilde{T}$ are constants that have units of population density and time, respectively. Hence Equation 4.15 transforms, upon change of variables, to

$$\frac{\tilde{N}}{\tilde{T}} \frac{dn}{d\tau} = r\tilde{N} n (1 - \frac{n\tilde{N}}{K}). \tag{4.17}$$

In the case of the logistic equation there is only one time scale and density scale in the problem, hence we choose

$$\tilde{T} = \frac{1}{r} \quad and \quad \tilde{N} = K \tag{4.18}$$

and the dimensionless model is

$$\frac{dn}{d\tau} = n(1-n) \tag{4.19}$$

Note that we can retrieve the original equation by rescaling and calculating $N = \tilde{N}n$ and $t = \tilde{T}\tau$.

4.3.2 Steady states and linear stability

Steady states satisfy

$$n^*(1-n^*) = 0. \tag{4.20}$$

Hence

$$n^* = 0, \qquad n^* = 1. \tag{4.21}$$

To determine linear stability we compute

$$H'(n) = (1-2n). \tag{4.22}$$

When $n = n^* = 0$ we obtain

$$H'(n) = 1. \tag{4.23}$$

Hence the origin is an unstable steady-state.

At the steady-state $n^* = 1$

$$H'(n^*) = -1 \tag{4.24}$$

hence $n^* = 1$ is linearly stable.

Note that the linear stability analysis can explain the observations regarding the numeric solutions presented in Figure 4.1.

4.3.3 Graphical analysis

In Figure 4.2 we plot the right-hand side of Equation 4.19. We can qualitatively describe model solutions by considering the arrow along the x axis. Suppose we consider an initial condition with $0 < n_0 < 1$. Using the graph of $H(n)$, $dn/d\tau$ is positive, hence n increases as a function of time until $n(\tau) \to 1$.

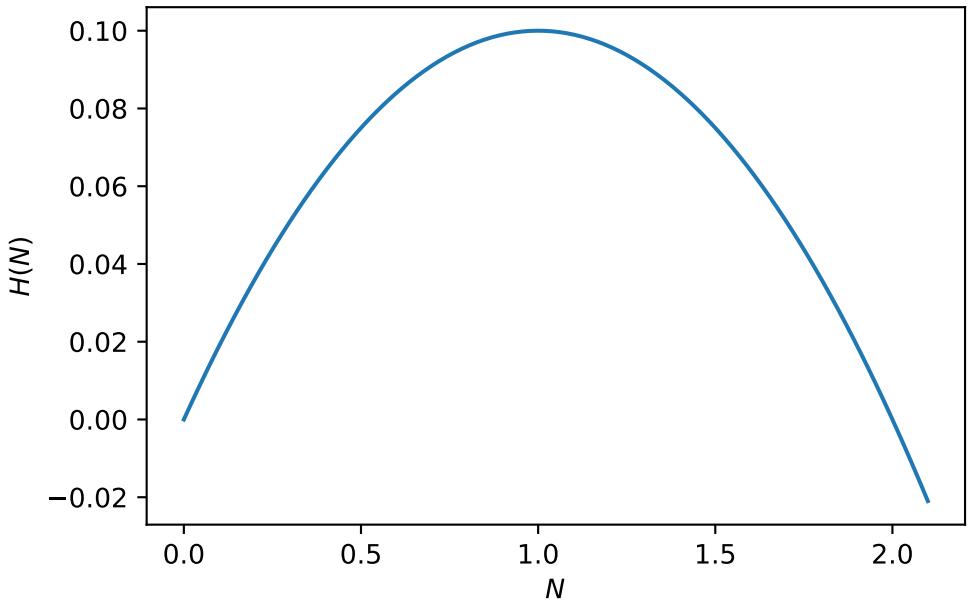


Figure 4.2: Right-hand side of the logistic ODE

4.3.4 An exact solution

Separation of variables yields

$$\int \frac{dN}{N(1-\frac{N}{K})} = r \int dt. \tag{4.25}$$

Using partial fractions

$$\int \frac{dN}{N} + \frac{1}{K} \int \frac{dN}{1-\frac{N}{K}} = r \int dt. \tag{4.26}$$

Integration yields,

$$\ln N - \ln\left(1 - \frac{N}{K}\right) = \ln \frac{N}{1-\frac{N}{K}} = rt + C. \tag{4.27}$$

Hence

$$N = \frac{De^{rt}}{1 + \frac{D}{K}e^{rt}} \tag{4.28}$$

Given an initial condition $N(0) = N_0$, we obtain

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)} \tag{4.29}$$

4.3.4.1 Qualitative analysis of the exact solution

As $t \to \infty$, $N \to K$. At $t = 0$, $N = N_0$ and that for small $N_0 \ll K$ the initial growth phase is exponential, i.e.

$$N(t) \sim N_0 e^{rt} \quad N_0 \ll K, t \ll \frac{1}{r}. \tag{4.30}$$

Note that in almost all the models that we will consider the above method is not an usually an option as the ODE is not explicitly integrable.

4.4 The spruce budworm model

The spruce budworm is a destructive and widely distributed forest defoliator in North America. Massive outbreaks occur periodically and can destroy large quantities of valuable spruce and fir. To understand the outbreak behaviour and develop and management strategies, a series of mathematical models have been developed, beginning with Ludwig et al. (1978). The goal of the models is to explain the qualitative pattern of sudden outbreaks and then a sudden collapse.

4.4.1 Model development

Letting $N(t)$ represent the population size at time t, it is assumed that budworm exhibits logistic growth and is subject to predation at rate $p(N)$. A governing ordinary differential equation is given by

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B}\right) - p(N), \tag{4.31}$$

where

$$p(N) = \frac{BN^2}{A^2 + N^2}, \tag{4.32}$$

r_B is the linear growth rate, K_B is the carrying capacity, B is the maximum rate of predation and A is a measure of budworm population where predation switches on (specifically, A represents the budworm density at which predation is half its maximum value).

It is informative to graph the predation term

$$p(N) = \frac{BN^2}{A^2 + N^2}, \tag{4.33}$$

and annotate the parameters A and B.

There is a root at $N = 0$. In the limit $N \to \infty$, $p \to B$. Note that for $N = A$, $p(A) = B/2$. The derivative is

$$p'(N) = \frac{2BN}{A^2 + N^2} - \frac{2BN^3}{(A^2 + N^2)^2} = \frac{2BA^2N}{(A^2 + N^2)^2} \tag{4.34}$$

Thus there is a turning point at $N = 0$ and $p' > 0 \forall N > 0$.

4.4.2 Nondimensionalisation

Introducing the (as yet unspecified) dimensional scalings $\tilde{N}$ and $\tilde{T}$, the model is nondimensionalised as follows

$$n = \frac{N}{\tilde{N}} \qquad \tau = \frac{t}{\tilde{T}}. \tag{4.35}$$

Changing variables in Equation 4.31 yields

$$\frac{\tilde{N}}{\tilde{T}} \frac{dn}{d\tau} = r_B \tilde{N} n \left(1 - \frac{\tilde{N} n}{K_B}\right) - \frac{B\tilde{N}^2 n^2}{A^2 + \tilde{N}^2 n^2}. \tag{4.36}$$

After some tidying

$$\frac{dn}{d\tau} = r_B \tilde{T} n \left(1 - \frac{\tilde{N} n}{K_B}\right) - \frac{B\tilde{N}\tilde{T}}{A^2} \frac{n^2}{1 + \frac{\tilde{N}^2}{A^2} n^2}. \tag{4.37}$$

A natural scale for cell density in the model is given by the parameter A, as it determines the density of budworm at which predation is half its maximal value. Hence we choose the scaling on the budworm density

$$\tilde{N} = A. \tag{4.38}$$

Similarly, a natural time scale for the model is given by

$$\tilde{T} = A/B. \tag{4.39}$$

Substituting for $\tilde{N}$ and $\tilde{T}$ yields

$$\frac{dn}{d\tau} = rn \left(1 - \frac{n}{q}\right) - \frac{n^2}{1 + n^2} = H(n), \tag{4.40}$$

where we define the nondimensional parameters

$$r = \frac{r_B A}{B} \quad \text{and} \quad q = \frac{K_B}{A}. \tag{4.41}$$

Note that Equation 4.40 has two nondimensional parameters and all variables are dimensionless. See Figure 4.3 for a plot of right-hand side of equation Equation 4.40. What kind of behaviours do you expect to see from the model?

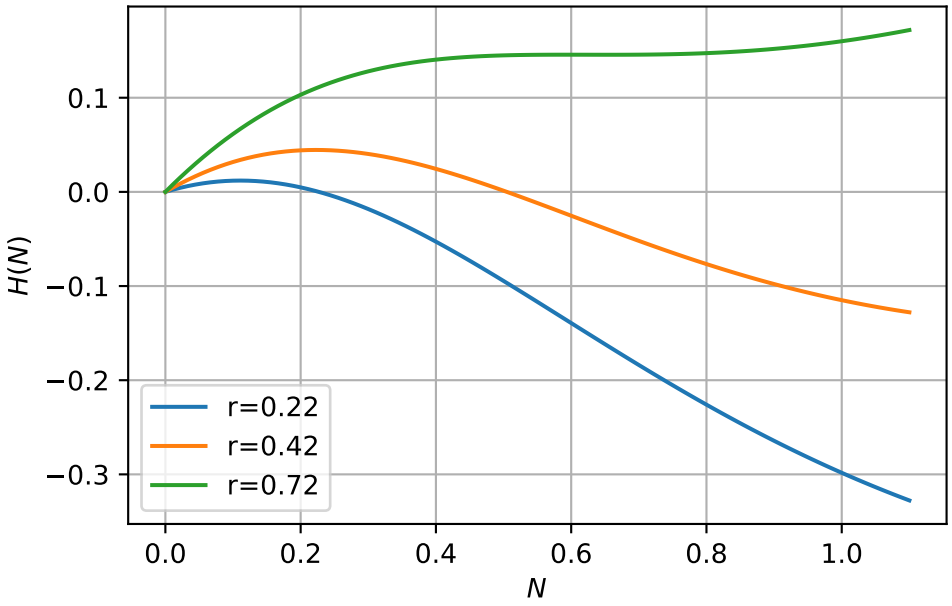


Figure 4.3: RHS of spr. budworm model

4.4.3 Numerical solutions

In Figure 4.4 we plot some numerical solutions of Equation 4.40 at different values of the parameter r.

Numerical solutions of Equation 4.40 indicate that there is a single stable steady state when r is both small and large but for intermediate values of r there are two stable steady states.

Our goal is to analyse the model and understand why different parameter values yield these strikingly different model behaviours.

4.4.4 Steady state analysis

Letting n^* represent steady states of Equation 4.40 yields

$$rn^*(1-\frac{n^*}{q})-\frac{n^{*2}}{1+n^{*2}}=0. \tag{4.42}$$

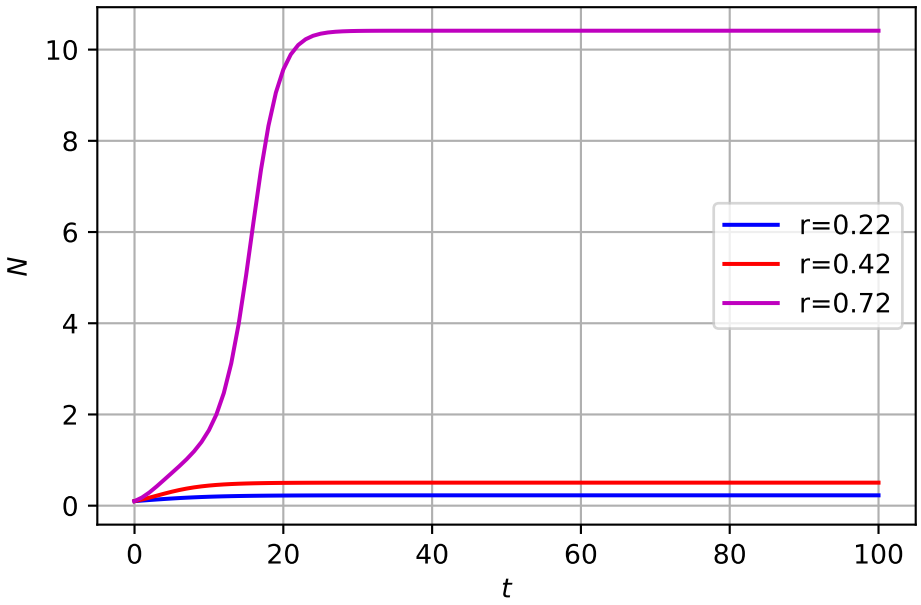


Figure 4.4: Numerical solution of spr. budworm model

Hence either

$$n^* = 0, \tag{4.43}$$

or n^* satisfies the cubic equation

$$r\left(1 - \frac{n^*}{q}\right) - \frac{n^*}{1 + n^{*2}} = 0. \tag{4.44}$$

Explicit solutions to such a cubic can be immediately written down but they are cumbersome to work with. We proceed using a graphical/qualitative approach.

Define

$$f(n^*) = r\left(1 - \frac{n^*}{q}\right) \quad \text{and} \quad g(n^*) = \frac{n^*}{1 + n^{*2}}. \tag{4.45}$$

Roots occur for values of n^* that satisfy $f = g$.

In Figure 4.5 (a) we fix the parameter $q = 10$ and consider model behaviour as a function of the parameter r. When $r \gg 1$ there is a nonzero steady-state corresponding to $n^* \gg 1$. When $r \ll 1$ there is a nonzero steady-state corresponding to $n^* \ll 1$. In the intermediate case there can be three intersection points.

We can use the curve sketching techniques form Tutorial Sheet 1 to sketch f and g.

f is linear. There is a root at $n^* = q$. The derivative is $-r/q$. $f(0)$=r. g has a unique root at $n^* = 0$. The derivative is

$$g' = \frac{1 - n^{*2}}{(1 + n^*)^2}. \tag{4.46}$$

There is a turning point at $n^* = 1$. Here $g = 1/2$. As $n^* \to \infty$, $g \to 0$. $f'(0) = 1$.

4.4.5 Linear stability analysis

The linear stability of the model is determined by the quantity

$$H'(n) = r(1 - \frac{2n}{q}) - \frac{2n}{1 + n^2} + \frac{2n^3}{(1 + n^2)^2}. \tag{4.47}$$

Hence at the steady state $n^* = 0$

$$H'(0) = r \tag{4.48}$$

and the steady state is linearly unstable.

Given the nonzero steady states have not been calculated explicitly, we proceed using graphical analysis of stability. In Figure 4.5 (b) we plot the right-hand side of Equation 4.40 against n and examine the cases of large, small and intermediate r for a given value of q.

When r is both large and small the nonzero steady state is stable (the derivative at the roots is negative). In the case where three biologically relevant roots exist, the intermediate root is unstable.

4.4.6 Bifurcation analysis

The goal is to identify boundaries of rq parameter space where the stability changes occur and/or the number of steady states changes.

We can define points in rq parameter space where bifurcations arise by seeking values of n^* that satisfy

$$f(n^*) = g(n^*) \qquad f'(n^*) = g'(n^*). \tag{4.49}$$

The first of these equations yields

$$r(1 - \frac{n^*}{q}) = \frac{n^*}{1 + n^{*2}}, \tag{4.50}$$

and the latter yields

$$-\frac{r}{q} = \frac{1}{1 + n^{*2}} - \frac{2n^{*2}}{(1 + n^*)^2} = \frac{1 - n^{*2}}{(1 + n^{*2})^2}. \tag{4.51}$$

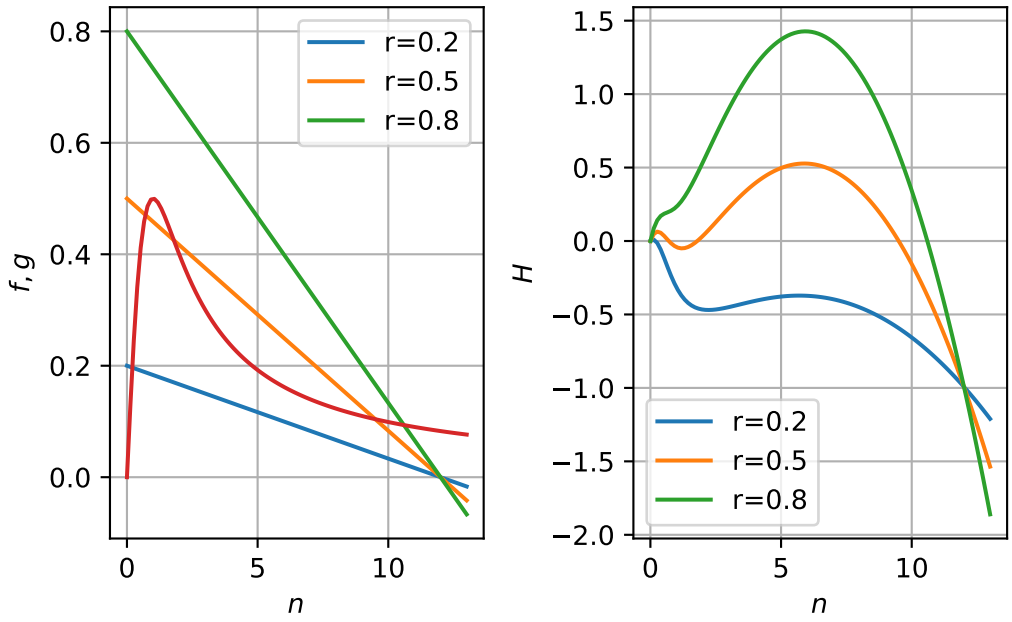


Figure 4.5: RHS of spr. budworm model

Hence

$$\frac{r}{q} = \frac{n^{*2} - 1}{(1 + n^{*2})^2}. \tag{4.52}$$

Substituting for r/q in the first equation yields

$$r - \frac{n^{*2} - 1}{(1 + n^{*2})^2} n^* = \frac{n^*}{1 + n^{*2}}, \tag{4.53}$$

which can be written in the form

$$r = \frac{2n^{*3}}{(1 + n^{*2})^2}. \tag{4.54}$$

Substituting for r in Equation 4.50 yields

$$\frac{2n^{*3}}{(1 + n^{*2})^2} = \frac{2n^{*3}}{(1 + n^{*2})^2} \frac{n^*}{q} + \frac{n^*}{1 + n^{*2}} \tag{4.55}$$

which, after some algebra, yields

$$q = \frac{2n^{*3}}{n^{*2} - 1}. \tag{4.56}$$

Hence a set of points that define bifurcations where three steady states transform to a single steady state are given in parametric form in qr parameter space by

$$\left(\frac{2n^{*3}}{n^{*2} - 1}, \frac{2n^{*3}}{(1 + n^{*2})^2} \right) \qquad n^* > 1. \tag{4.57}$$

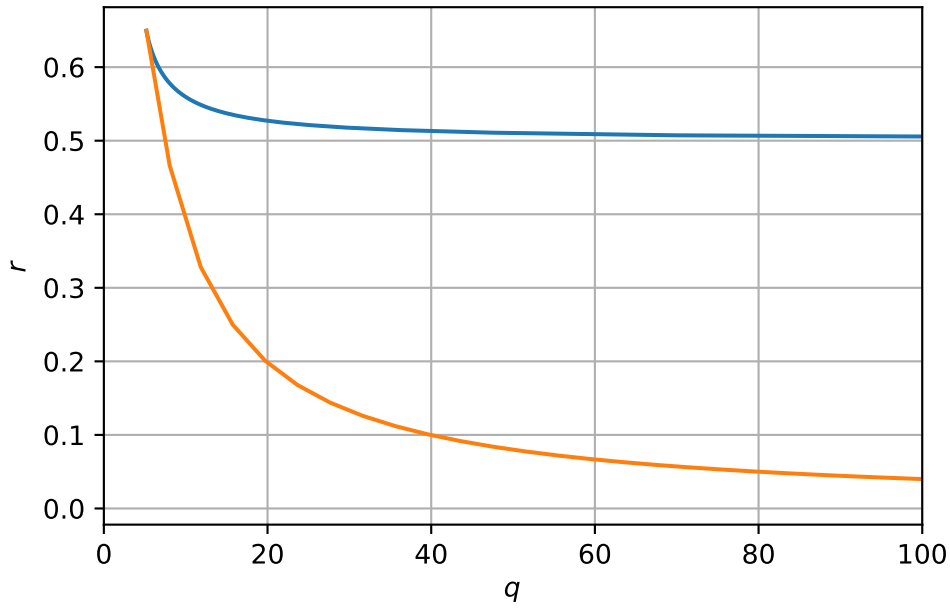


Figure 4.6: Bifurcations in the rq plane

By varying values of n^* in Figure 4.6 we plot a region of instability. Note for example that $q \to \infty$ as $n^* \to 1$ and as $n^* \to \infty$. Note also that in these limits r must take the value $1/2$ and 0, respectively.

We can show that the cusp in Figure 4.6 is given by

$$(q, r) = \left(3^{\frac{3}{2}}, \left(\frac{\sqrt{3}}{2}\right)^3\right). \tag{4.58}$$

Note that r is a decreasing function of q for $1 < n^* < \sqrt{3}$ but that r is an increasing function of n^* for $\sqrt{3} < n^* < \infty$. This can be shown by finding the turning points of r w.r.t n^*, i.e. Given that

$$r = \frac{2n^{*3}}{(1+n^{*2})^2}, \tag{4.59}$$

differentiation with respect to n^* yields

$$\frac{dr}{dn^*} = \frac{6n^{*2}}{(1+n^*)^2} - \frac{8n^{*4}}{(1+n^*)^3}. \tag{4.60}$$

The turning point satisfies

$$\frac{6n^{*2}}{(1+n^*)^2} - \frac{8n^{*4}}{(1+n^*)^3} = 0 \tag{4.61}$$

Solving for n^* yields

$$6(1 + n^{*2}) - 8n^{*2} = 0 \tag{4.62}$$

Hence

$$n^* = \sqrt{3}. \tag{4.63}$$

Thus there is a turning point that minimises r at $n^* = \sqrt{3}$.

Substitution for this value of n^* yields

$$(q, r) = \left(3^{\frac{3}{2}}, \left(\frac{\sqrt{3}}{2}\right)^3\right). \tag{4.64}$$

See Figure 4.6.

4.4.7 Hysteresis

Finally, rearranging the steady-state equation

$$r(1 - \frac{n^*}{q}) = \frac{n^*}{1 + n^{*2}},$$

we obtain

$$r = \frac{n^*}{(1 + n^{*2})(1 - \frac{n^*}{q})}. \tag{4.65}$$

Considering $n^* < q$ we compute r; plotting n^* against r yields the bifurcation curve presented in Figure 4.7.

A system exhibiting hysteresis shows a response to an increases in a control parameter that is not exactly reversed when the parameter is decreased. We can show that the spruce budworm model exhibits hysteresis by considering the argument below.

Suppose r is initially small ($r < r_1$). There is only one steady-state and any initial condition will converge towards it.

Suppose we increase the value of the parameter r. There will be a critical value of r ($r = r_1$)where a second stable steady-state arises and the model enters the bistable regime, where there are two possible stable steady-states. Given the system was originally in the first stable steady state, it will remain there.

Suppose we continue to increase r. Eventually we reach critical value of r ($r = r_2$) where the first stable steady state is lost and there is again only one stable steady-state.

Suppose we now decrease the parameter r below the threshold $r = r_2$. The system again enters the bistable regime but as the second solution is stable, it remains the solution.

Suppose we continue to decrease r until eventually $r < r_1$. We return to the case where the system has only a single stable steady state.

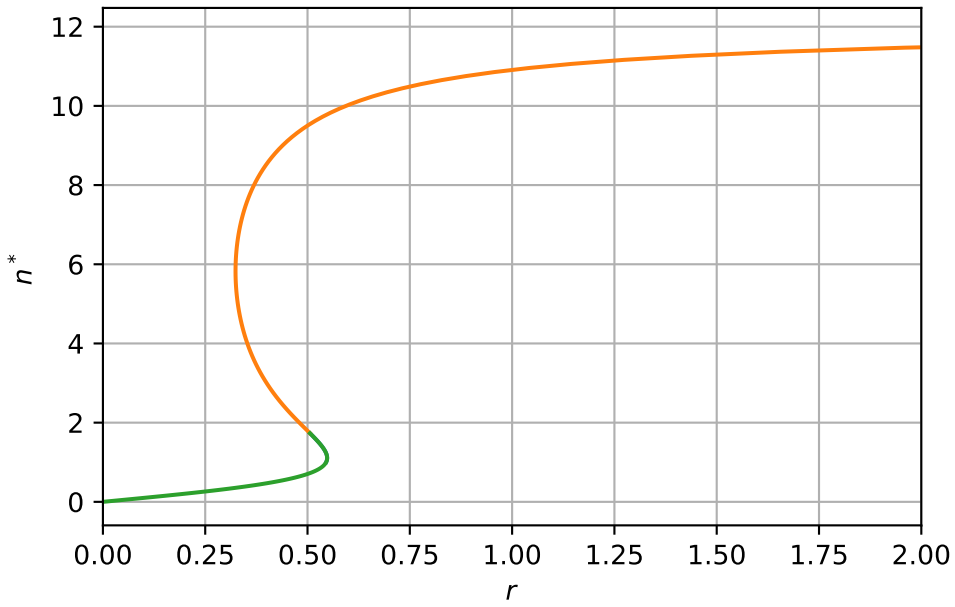


Figure 4.7: Bifurcations in the rq plane

```
<IPython.core.display.HTML object>
```

Figure 4.8: Animation demonstrating hysteresis as r increases (picks left stable critical point) and decreases (picks right stable critical point).

4.5 Harvesting

By introducing terms that represent harvesting, population models can be used to investigate management strategies for resource management. The modelling problem is to maximise the sustained yield.

Consider a model for logistic growth supplemented with a harvesting term

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - EN. \tag{4.66}$$

The term EN is the harvesting yield per unit time and the constant E represents the harvesting effort.

Steady states satisfy

$$rN^*\left(1 - \frac{N^*}{K}\right) - EN^* = 0 \tag{4.67}$$

Thus either $N^* = 0$ or

$$\left(1 - \frac{N^*}{K}\right) - E = 0 \tag{4.68}$$

Hence

$$N^* = K(1 - \frac{E}{r}). \tag{4.69}$$

Note that this is positive only if

$$E < r. \tag{4.70}$$

Thus if the harvesting rate exceeds the linear growth rate the only steady state corresponds to extinction.

The yield is,

$$Y(E) = EN^* = EK(1 - \frac{E}{r}) \tag{4.71}$$

To maximise the yields we differentiate with respect to E.

$$\frac{dY}{dE} = K - 2\frac{EK}{r}. \tag{4.72}$$

Thus the maximum yield is identified by setting

$$\frac{dY}{dE} = K - 2\frac{EK}{r} = 0. \tag{4.73}$$

THe maximum occurs at harvesting rate

$$E_c = \frac{r}{2}. \tag{4.74}$$

The maximum yield is

$$E^* = \frac{rK}{4}. \tag{4.75}$$

We identify the time scale over which stocks return to steady state by linearising about the steady state $N^* = K(1 - E/r)$, hence

$$\frac{d\hat{N}}{dt} = (E - r)\hat{N}. \tag{4.76}$$

Hence the recovery time scale is

$$T_R(E) = O(\frac{1}{r - E}). \tag{4.77}$$

As the harvesting rate approaches the linear growth rate r, not only does the steady state population tend to zero but the timescale for stocks to recover tends to infinity.

4.6 Delay differential equation models

Consider a model of the form

$$\frac{dN}{dt} = H(N(t), N(t - T)), \tag{4.78}$$

such that the right-hand side now depends on the value N not just at time t but also at some delay time $t - T$. We now need to prescribe initial conditions of the form

$$N(t) = f(t), \quad -T < t \leq 0. \tag{4.79}$$

Consider a simple case of a linear model

$$\frac{dN}{dt} = -N(t - T). \tag{4.80}$$

A steady state, N^*, is defined such that $N(t) = N(t - T) = N^*$. Hence

$$0 = -kN^*. \tag{4.81}$$

The only steady state is $N^* = 0$.

To compute the linear stability we consider solution of the linearised equation of the form

$$N(t) = e^{\lambda t}. \tag{4.82}$$

Hence

$$N(t - T) = e^{\lambda(t-T)}. \tag{4.83}$$

Substitution yields

$$\lambda e^{\lambda t} = -e^{\lambda(t-T)}. \tag{4.84}$$

Hence the eigenvalue, λ, satisfies a transcendental equation

$$\lambda = -e^{-\lambda T}. \tag{4.85}$$

This equation has no solutions for $\lambda \in \Re^+$. Hence any steady-states with real eigenvalues are linearly stable.

Now consider solutions $\lambda \in \mathbb{C}$. Let $\lambda = \mu + i\omega$. Substitution yields

$$\mu + i\omega = -e^{-\mu T}(\cos(\omega T) - i\sin(\omega T)). \tag{4.86}$$

Hence

$$\mu = -\cos(\omega T)e^{-\mu T} \tag{4.87}$$

and

$$\omega = \sin(\omega T)e^{-\mu T}. \tag{4.88}$$

For linear stability of the steady state it is required that $\mu < 0$.

If ω is a solution of Equation 4.87 and Equation 4.88 then so is $-\omega$. Hence w.l.o.g we consider the case $\omega > 0$.

Consider $\mu = 0$ in Equation 4.87. This implies

$$\omega T = \frac{\pi}{2} + 2n\pi, \quad n \in Z. \tag{4.89}$$

We consider the smallest positive root, i.e. $n = 0$, as we want to consider the smallest value of delay time, T, at which instability arises.

Note $\mu < 0$ for

$$\omega T < \frac{\pi}{2}. \tag{4.90}$$

On the stablity boundary, $\mu = 0$. Upon substitution in Equation 4.88

$$\omega = \sin(\frac{\pi}{2}) = 1. \tag{4.91}$$

Hence the steady state is linearly stable for

$$T < \frac{\pi}{2}. \tag{4.92}$$

4.7 References

5 Multi species population dynamics

In this chapter we consider models of interacitng populations.

Let $u = u(t)$ and $v = v(t)$ represent populations of two different species at continuous time t. Suppose that $u(t)$ and $v(t)$ satisfy the ordinary differential equations

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

In this section we will consider particular forms for f and g that represent different types of inter species interaction. Before considering particular examples, we develop some general techniques for analysing equations of the form Equation 5.1.

5.1 General tools

5.1.1 Steady states

(u^*, v^*) is defined to be a steady state of Equation 5.1 if

$$f(u^*, v^*) = g(u^*, v^*) = 0. \tag{5.1}$$

Hence, by definition, the time derivatives of $u(t)$ and $v(t)$ are both zero at (u^*, v^*). As was the case for single species models, steady states are obtained by solving algebraic equations.

5.1.2 Linear stability analysis

Suppose that (u^*, v^*) is a steady state of equations Equation 5.1.

We consider a change of dependent variables such that

$$u(t) = u^* + \hat{u}(t) \quad \text{and} \quad v(t) = v^* + \hat{v}(t), \tag{5.2}$$

where $\hat{u}(t)$ and $\hat{v}(t)$ are perturbations about the steady state.

Rewriting equation Equation 5.1 in the transformed variables yields

$$\begin{aligned}\frac{d\hat{u}}{dt} &= f(u^* + \hat{u}, v^* + \hat{v}),\\ \frac{d\hat{v}}{dt} &= g(u^* + \hat{u}, v^* + \hat{v}).\end{aligned}$$

Making Taylor expansions about (u^*, v^*) yields the linearised equations

$$\begin{aligned}\frac{d\hat{u}}{dt} &= \frac{\partial f}{\partial u}_{|(u^*,v^*)}\hat{u} + \frac{\partial f}{\partial v}_{|(u^*,v^*)}\hat{v} + h.o.t,\\ \frac{d\hat{v}}{dt} &= \frac{\partial g}{\partial u}_{|(u^*,v^*)}\hat{u} + \frac{\partial g}{\partial v}_{|(u^*,v^*)}\hat{v} + h.o.t.\end{aligned}$$

Upon making the assumption that the perturbations about the steady state are small, the leading order terms are linear and higher order terms are neglected. Defining

$$\mathbf{w} = \begin{pmatrix} \hat{u} \\ \hat{v} \end{pmatrix}, \tag{5.3}$$

yields the system of linear ODEs given by

$$\frac{d\mathbf{w}}{dt} = A\mathbf{w}, \tag{5.4}$$

where the matrix A, known as the Jacobian matrix, takes the form

$$A = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u^*,v^*)}. \tag{5.5}$$

The linear system arrived upon in Equation 5.4 was encountered previously in Differential Equations (MA31002). We summarise the important results here. Seeking a solution of Equation 5.4 of the form

$$\mathbf{w} = \mathbf{v}e^{\lambda t} \tag{5.6}$$

one obtains the characteristic equation

$$\lambda^2 - \lambda \mathrm{tr}(A) + \det(A) = 0, \tag{5.7}$$

which has solutions

$$\lambda = \frac{\mathrm{tr}A \pm \sqrt{\mathrm{tr}A^2 - 4\det A}}{2}. \tag{5.8}$$

Whilst a complete classification of the linear stability of a steady state can be obtained by explicitly calculating the eigenvalues, in many cases it is sufficient to deduce whether or not a steady state is stable or unstable. This can be achieved by calculating the determinant and trace of the Jacobian matrix ($\det(A)$ and $\mathrm{tr}(A)$, respectively) and referring to Figure 5.1.

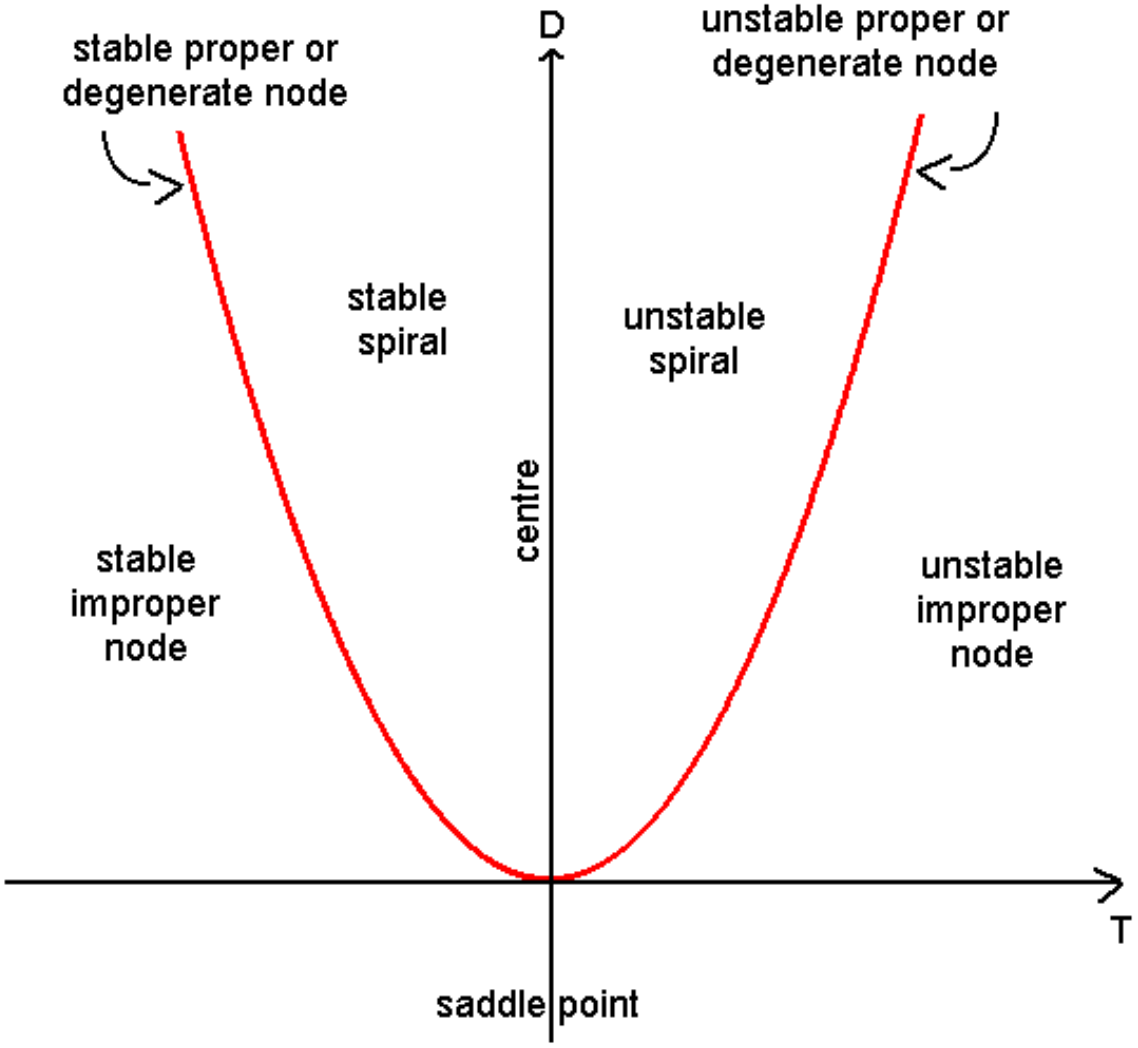


Figure 5.1: Stability in the trace detemrinant plane.

The different cases can be categorised as follows:

- $\det(A) < 0$ There is one positive and one negative real eigenvalue. Hence the steady state is a saddle which is unstable.
- $\det(A) > 0$ The steady state can be either stable or unstable, depending on $\mathrm{tr}(A)$ (and the real part of the eigenvalues).
  - If $\mathrm{tr}(A) > 0$, the steady state is unstable.
    - If $\mathrm{tr}(A)^2 > 4\det(A)$, it is an unstable node.
    - If $\mathrm{tr}(A)^2 < 4\det(A)$ it is an unstable spiral.
  - If $\mathrm{tr}(A) < 0$, the steady state is stable.
    - If $\mathrm{tr}(A)^2 > 4\det(A)$, it is an stable node.
    - If $\mathrm{tr}(A)^2 < 4\det(A)$, it is an stable spiral.

These different cases can be distinguished in the trace-determinant plane plotted in Figure 5.1.

Note that it can be shown rigorously that the linear stability of the nonlinear system is equivalent to that of the linearised system in all cases except when the steady state is a centre. In this case, nonlinear stability analysis is required to determine the stability of the nonlinear system.

The conditiondet$(A) > 0$ excludes the case that the eigenvalues are real but have opposite signs (i.e. it cannot be a saddle point).

The condition $\mathrm{tr}(A) > 0$ implies that the real part of both eigenvalues are positive (i.e. the steady state is unstable).

The condition $\mathrm{tr}(A)^2 < 4\det(A)$ implies that the eigenvalue are complex. Hence

$$\lambda_{\pm} = \mu \pm i\omega \tag{5.9}$$

and the solution of the system can be written

$$e^{\lambda t} = e^{(\mu + i\omega)t} = e^{\mu t} e^{i\omega t}. \tag{5.10}$$

Thus the magnitude of perturbation grows but it oscillates about the steady state. Hence the steady state is an unstable spiral.

5.1.3 Nullclines

Nullclines of the equations Equation 5.1 are given by the curves

$$f(u, v) = 0 \qquad \text{and} \qquad g(u, v) = 0, \tag{5.11}$$

respectively. Note that steady states arise at the intersection of nullclines.

Using the u nullclines we identify domains of the phase plane where $du/dt > 0$ and $du/dt < 0$.

Similarly, using the v nullcline we identify domains of the phase plane where $dv/dt > 0$ and $dv/dt < 0$.

The nullclines can be used to help identify confined sets and hence apply the Poincaire-Bendixson theorem.

5.1.4 Poincaire-Bendixson theorem

Suppose that the system of equations

$$\frac{du}{dt} = f(u, v), \qquad \frac{dv}{dt} = g(u, v) \tag{5.12}$$

possesses a confined set (i.e. a bounded domain in the phase plane upon which the derivative field points into the domain) that contains an unstable node or spiral. Any trajectory cannot leave the confined set, nor can it tend to the unstable steady state. The Poincaire-Bendixson theorem states that as $t \to \infty$, the trajectory will tend towards a limit cycle.

5.1.5 Dulac criterion

Suppose D is a simply connected region in the plane and that there exists a function $B(x, y)$, continuously differentiable on D, such that the expression

$$\frac{\partial}{\partial u}(Bf) + \frac{\partial}{\partial v}(Bg) \tag{5.13}$$

is not identically zero and does not change sign in D. Then there are no closed orbits in D.

5.2 The Lotka-Voltera model

Suppose that $N(t)$ and $P(t)$ represent the prey and predator population densities at time t, respectively. Consider a model of the form

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

where a, b, c and d are positive constants.

5.2.1 Nondimensionalisation

Nondimensionalising with

$$n = \frac{N}{\tilde{N}}, \quad p = \frac{P}{\tilde{P}} \text{ and } \tau = \frac{t}{\tilde{T}}, \tag{5.14}$$

yields, after changing variables,

$$\frac{dn}{d\tau} = \tilde{T}an - b\tilde{T}\tilde{P}np,$$
$$\frac{dp}{d\tau} = c\tilde{N}\tilde{T}np - d\tilde{T}p.$$

Choosing the dimensional scalings

$$\tilde{T} = 1/a, \quad \tilde{P} = a/b \quad \text{and} \quad \tilde{N} = d/c, \tag{5.15}$$

yields

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

where $\alpha = d/a$. Note that all variables and parameter are without dimensions.

5.2.2 Numerical solutions

5.2.3 Steady states

The steady-states of equation Equation 5.16 are identified by seeking solutions of

$$f(n^*, p^*) = g(n^*, p^*) = 0. \tag{5.16}$$

Hence

$$n^*(1-p^*) = 0 \qquad \alpha p^*(n^*-1). \tag{5.17}$$

The first of these equations has solutions either

$$n^* = 0 \quad \text{or} \quad p^* = 1. \tag{5.18}$$

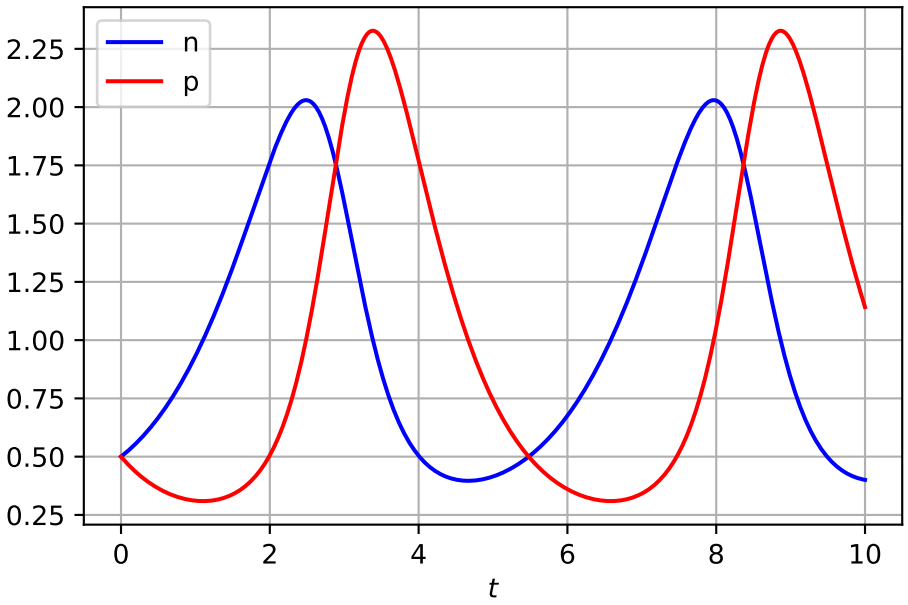


Figure 5.2: Numerical solution of Lotka-Volterra model

Substituting for $n^* = 0$ in the second equation yields $p^* = 0$. Hence one steady state is $(0, 0)$. Substituting for $p^* = 1$ in the second equation yields $n^* = 1$. Hence a second steady state is (1,1).

5.2.4 Linear stability

The linear stability of the steady states is described by the Jacobian matrix

$$A = \begin{pmatrix} \frac{\partial f}{\partial n} & \frac{\partial f}{\partial p} \\ \frac{\partial g}{\partial n} & \frac{\partial g}{\partial p} \end{pmatrix}_{(n^*,p^*)} = \begin{pmatrix} 1-p & -n \\ \alpha p & \alpha(n-1) \end{pmatrix}_{(n^*,p^*)} \tag{5.19}$$

Evaluating at (0,0) yields

$$A = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}, \tag{5.20}$$

Hence the eigenvalues of A are 1 and $-\alpha$. As $\alpha > 0$ the origin is a saddle. The eigenvectors are $[1, 0]$ and $[0, 1]$.

At (1,1)

$$A = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}, \tag{5.21}$$

and the eigenvalues are $\pm i\sqrt{\alpha}$. Therefore the steady state at (1,1) is a centre.

5.2.5 Solutions in the phase plane

See Figure 5.3 for solution trajectories plotted in the phase plane using different initial conditions. Note the expected saddle like behaviour when trajectories that are close to the origin. Furthermore, note that the different initial conditions result in distinct closed loops and that the inner-most loop, i.e. that closest to the steady-state (1,1), behaves like a centre, as expected given the linear stability analysis. However, far from the steady-state the solution trajectory deviates from the linearised model.

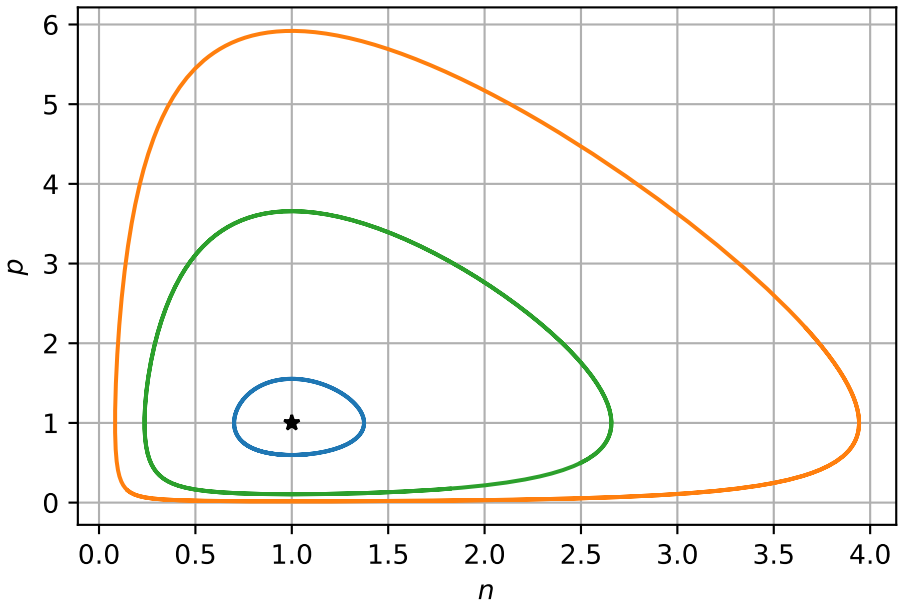


Figure 5.3: Numerical solution of Lotka-Volterra model

5.2.6 Direct integration

The Lotka-Volterra equations are a special case as they are integrable. Trajectories in the phase plane satisfy the differential equation

$$\frac{dp}{dn} = \frac{\alpha p(n-1)}{n(1-p)}, \tag{5.22}$$

Using separation of variables

$$\int \frac{1-p}{p} dp = \alpha \int \frac{n-1}{n} dn. \tag{5.23}$$

Integration yields

$$\ln p - p = \alpha(n - \ln n) + H, \tag{5.24}$$

where H is a conserved quantity that this is determined by the initial conditions. As the equations take conservative form, the Lotka-Voltera model is said to be structurally unstable, as a small perturbation to the solution at a given point in the oscillatory cycle can result in large changes elsewhere in the cycle. For example, suppose the outermost limit cycle in Figure 5.3 is perturbed by a small amount at the point (1,0.1) onto its nearest limit cycle. Later in the cycle these two trajectories deviate by a large amount.

5.3 Competition

In models of competition, two or more species compete for the same resource or in some way inhibit each other's growth. Letting $N_1(t)$ and $N_2(t)$ represent the population density of two species, we consider the ODEs

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

where r_1, r_2, K_1 and K_2 are positive constants. As before, the $r's$ are linear growth rates and the K's are carrying capacities. The parameters b_{12} and b_{21} measure the competitive effect of N_2 on N_1 and N_1 on N_2, respectively.

5.3.1 Nondimensionalisation

After nondimensionalising using the change of variables

$$n_1 = \frac{N_1}{K_1} \quad n_2 = \frac{N_2}{K_2} \quad \tau = \frac{t}{\frac{1}{r_1}}, \tag{5.25}$$

we obtain the equations

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

where

$$\rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}. \tag{5.26}$$

5.3.2 Steady states

The steady states of Equation 5.26 are identified in the usual manner, i.e. by seeking $({n_1}^*, {n_2}^*)$ such that

$$f({n_1}^*, {n_2}^*) = g({n_1}^*, {n_2}^*) = 0. \tag{5.27}$$

The steady state equations are

$${n_1}^*\left(1 - {n_1}^* - a_{12}{n_2}^*\right) = 0 \qquad {n_2}^*\left(1 - {n_2}^* - a_{21}{n_1}^*\right) = 0. \tag{5.28}$$

The first equation has solution

$$n_1^* = 0 \tag{5.29}$$

or

$$\left(1 - {n_1}^* - a_{12}{n_2}^*\right) \implies n_2 = \frac{1}{a_{12}}(1 - n_1^*). \tag{5.30}$$

Consider $n_1^* = 0$. Substitution in the second equation yields

$${n_2}^*\left(1 - {n_2}^*\right) = 0. \tag{5.31}$$

Hence either $n_2^* = 0$ or $n_2^* = 1$. Hence two steady states are $(0, 0)$ and $(0, 1)$.

Now consider $n_2^* = \frac{1}{a_{12}}(1 - n_1^*)$ with $n_1^* \neq 0$.

Substitution in the second steady state equation yields

$$\frac{1}{a_{12}}(1-n_1^*)\left(1-\frac{1}{a_{12}}(1-n_1^*)-a_{21}{n_1}^*\right) \tag{5.32}$$

Hence either $n_1^* = 1$ or

$$\left(1-\frac{1}{a_{12}}(1-n_1^*)-a_{21}{n_1}^*\right)=0 \implies n_1^* = \frac{1-a_{12}}{1-a_{12}a_{21}}. \tag{5.33}$$

In the case where $n_1^* = 1$, we find that $n_2^* = 0$. Hence the steady state is (1,0).

In the case where

$$n_1^* = \frac{1-a_{12}}{1-a_{12}a_{21}} \tag{5.34}$$

we find that

$$n_2^* = \frac{1-a_{21}}{1-a_{12}a_{21}} \tag{5.35}$$

Hence the steady state is

$$\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right). \tag{5.36}$$

5.3.3 Nullclines

The nullclines for Equation 5.26 are straight lines given by

$$n_1 = 0 \qquad n_2 = \frac{1-n_1}{a_{12}}, \tag{5.37}$$

and

$$n_2 = 0 \qquad n_2 = 1-a_{21}n_1. \tag{5.38}$$

Note that the steady states $(0,0)$, $(1,0)$ and $(0,1)$ are always biologically relevant (i.e. independently of the parameter values for a_{12} and a_{21}).

However, the coexistence steady state is only biologically relevant if the nullclines intersect in the positive quadrant and this occurs only in certain regions of the model's parameter space.

In the cases where $a_{12}, a_{21} < 1$ and $a_{12}, a_{21} > 1$ there is a coexistence steady state (i.e. the nullclines intersect in the positive quadrant).

However, if $a_{21} < 1$ and $a_{12} > 1$ or $a_{12} < 1$ and $a_{21} > 1$ there is not a biologically relevant, coexistence steady state (i.e. the nullclines do not intersect in the positive quadrant).

Hence there are are four qualitatively different types of solution to consider.

5.3.4 Linear stability

The linear stability of the different steady states is determined by calculating the Jacobian matrix

$$A = \begin{pmatrix} \frac{\partial f}{\partial n_1} & \frac{\partial f}{\partial n_2} \\ \frac{\partial g}{\partial n_1} & \frac{\partial g}{\partial n_2} \end{pmatrix}_{(n_1{}^*, n_2{}^*)} = \begin{pmatrix} 1 - 2n_1 - a_{12}n_2 & -a_{12}n_1 \\ -\rho a_{21} n_2 & \rho(1 - 2n_2 - a_{21}n_1) \end{pmatrix}_{(n_1{}^*, n_2{}^*)}. \quad (5.39)$$

At (0,0)

$$A = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix}. \quad (5.40)$$

Hence the eigenvalues of the Jacobian are 1 and ρ. As $\rho > 0$, the origin is therefore an unstable node (there are two real positive eigenvalues).

At (1,0)

$$A = \begin{pmatrix} -1 & -a_{12} \\ 0 & \rho(1 - a_{21}) \end{pmatrix}. \quad (5.41)$$

The trace and determinant are given by

$$\det A = \rho(a_{21} - 1) \quad \text{and} \quad \mathrm{tr}A = -1 + \rho(1 - a_{21}). \quad (5.42)$$

Hence if $a_{21} < 1$, $\det A < 0$ and (1,0) is a saddle point and thus unstable (see Figure 5.1).

If $a_{21} > 1$, $\det A > 0$ and $\mathrm{tr}A < 0$. Hence (1,0) is a stable node.

Hence the parameter a_{21}, which describes how strongly Population 1 inhibits the growth rate of Population 2, determines whether or not the steady state representing extinction of Population 2 but not Population 1 is stable or not.

At (0,1)

$$A = \begin{pmatrix} 1 - a_{12} & 0 \\ -\rho a_{21} & -\rho \end{pmatrix}. \quad (5.43)$$

In this case if $a_{12} < 1$, $\det A < 0$ and (0,1) is a saddle point. If $a_{12} > 1$, $\det A > 0$ and $\mathrm{tr}A < 0$ and (0,1) is a stable node. Hence the parameter a_{12}, which describes how strongly Population 2 inhibits the growth rate of Population 1, determines whether or not the steady state representing extinction of Population 1 but not Population 2 is stable or not.

At the coexistence steady state, recall the steady state is

$$\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right). \tag{5.44}$$

Note that this steady state is only biologically relevant in the cases $a_{21} < 1, a_{12} < 1$ or $a_{21} > 1, a_{12} > 1$. Evaluating the Jacobian yields

$$A = \frac{1}{1-a_{12}a_{21}} \begin{pmatrix} a_{12}-1 & -a_{12}(1-a_{12}) \\ -\rho a_{21}(1-a_{21}) & \rho(a_{21}-1) \end{pmatrix}. \tag{5.45}$$

The determinant and trace of the Jacobian are given by

$$\begin{aligned} \det A &= \rho\left((a_{12}-1)(a_{21}-1) - a_{12}a_{21}(1-a_{12})(1-a_{21})\right)\frac{1}{(1-a_{12}a_{21})^2}, \\ &= \rho\frac{(a_{12}-1)(a_{21}-1)}{(1-a_{12}a_{21})}, \end{aligned}$$

and

$$\mathrm{tr}A = \left(a_{12}-1+\rho(a_{21}-1)\right)\frac{1}{1-a_{12}a_{21}}, \tag{5.46}$$

respectively.

Let's firstly consider the case where $a_{21} < 1$ and $a_{21} < 1$. This implies that $a_{21} - 1 < 0$ and $a_{12} - 1 < 0$, hence evaluating the signs of the different products yields

$$\det A = \rho(-)(-)(+) > 0 \tag{5.47}$$

and

$$\mathrm{tr}A = \rho(-) + (-) < 0. \tag{5.48}$$

Therefore the coexistence steady state is a stable node or spiral.

In the case where $a_{21} > 1$ and $a_{12} > 1$

$$\det A = \rho(+)(+)(-) < 0. \tag{5.49}$$

Hence the coexistence steady state is a saddle.

5.3.5 Phase portrait

See Figure 5.5 for phase portraits of three of the four cases that we have considered. It is expected that you can sketch phase portraits. Key details to consider are the steady states and their linear stability. You should also sketch the nullclines and depict the sign of the derivatives in the phase plane on either side of the nullclines. You should also sketch one or more sample trajectories.

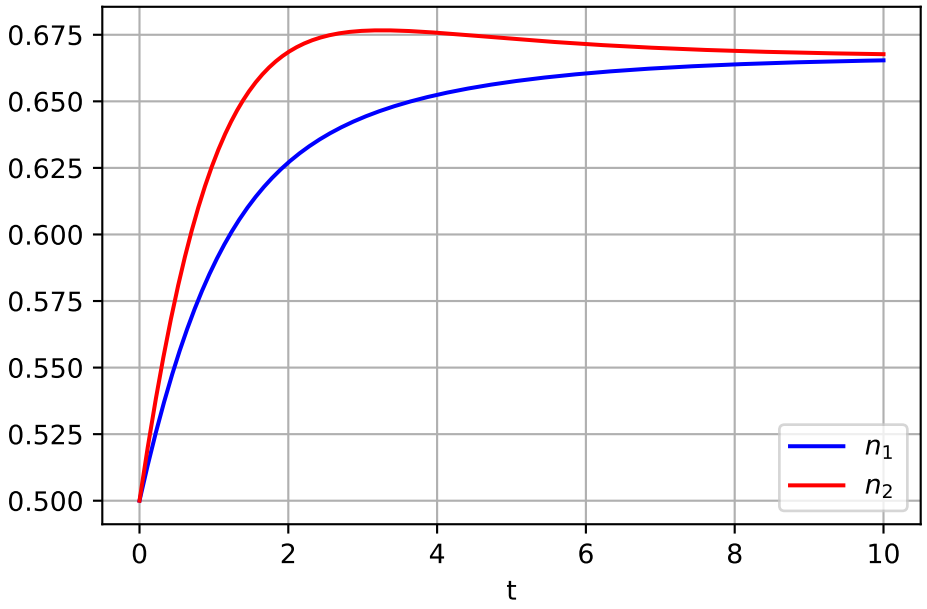


Figure 5.4: Numerical solutions of competition model

5.3.6 Insight

The model therefore has four qualitatively different behaviours that are described as follows: Consider the case where $a_{21} > 1$. This represents the case of Population 1 strongly competing with Population 2.

- If $a_{12} > 1$, Population 2 also strongly competes with Population 1. In this case, there are four biologically relevant steady states, two of which are stable (1,0) and (0,1). The coexistence steady state is a saddle and thus unstable. The model is bistable and the initial conditions determine whether solutions end up at (1,0) or (0,1) (see Figure 5.5). The biological interpretation of this solution is that one species will always win and completely outcompete the other. Even if the two populations are equal ($K_1 = K_2$ and $a_{21} = a_{12} > 1$), one species will always win and the other will become extinct.

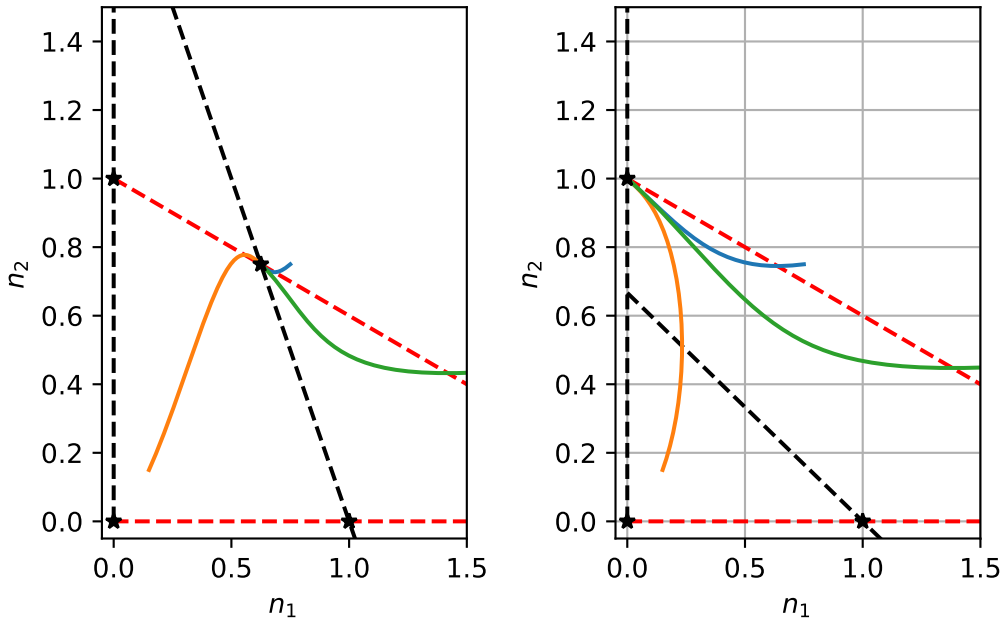


Figure 5.5: Numerical solution of the competition model

- If $a_{12} < 1$, Population 2 weakly competes with Population 1. There is no coexistence steady state and the only stable steady state is (1,0). Hence Population 1 always wins and Population 2 always becomes extinct.

Now consider the case where $a_{21} < 1$. This represents the case of Population 1 weakly competing with Population 2.

- If $a_{12} > 1$, Population 2 strongly competes with Population 1. There is nonexistence steady state and the only stable steady state is (0,1). Hence Population 2 always wins and Population 1 always becomes extinct.
- If $a_{12} < 1$, Population 2 also weakly competes with Population 1. The coexistence steady state is stable and the steady states (1,0) and (0,1) are unstable.

5.4 Symbiosis/Mutualism

When the interactions between two species results in mutually benefit, it is known as mutualism or symbiosis. To study this behaviour, we consider a model of the form

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

Note the only difference with the competition model is that the sign of the interaction term has changed. Hence we will not work through all the details as the analysis is the same as before.

5.4.1 Nondimensionalisation

Using the same nondimensionalisation as the competition model, we obtain the nondimensional equations

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

5.4.2 Steady states

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

$$({n_1}^*, {n_2}^*) = \left(\frac{1 + a_{12}}{1 - a_{12}a_{21}}, \frac{1 + a_{21}}{1 - a_{12}a_{21}}\right). \tag{5.50}$$

The coexistence steady state is biological relevant if $a_{12}a_{21} < 1$

5.4.3 Nullclines

The n_1 nullclines satisfy

$$n_1 = 0, \quad n_2 = \frac{1}{a_{12}}(n_1 - 1). \tag{5.51}$$

The n_2 nullclines satisfy

$$n_2 = 0, \quad n_2 = 1 + a_{21}n_1. \tag{5.52}$$

Note that both nullclines have a positive slope.

5.4.4 Linear stability

Using a similar analysis to the competition model, it can be shown that the steady states (0,0), (1,0) and (0,1) are unstable. When $a_{12}a_{21} < 1$ there is a stable coexistence steady state. See Figure 5.6.

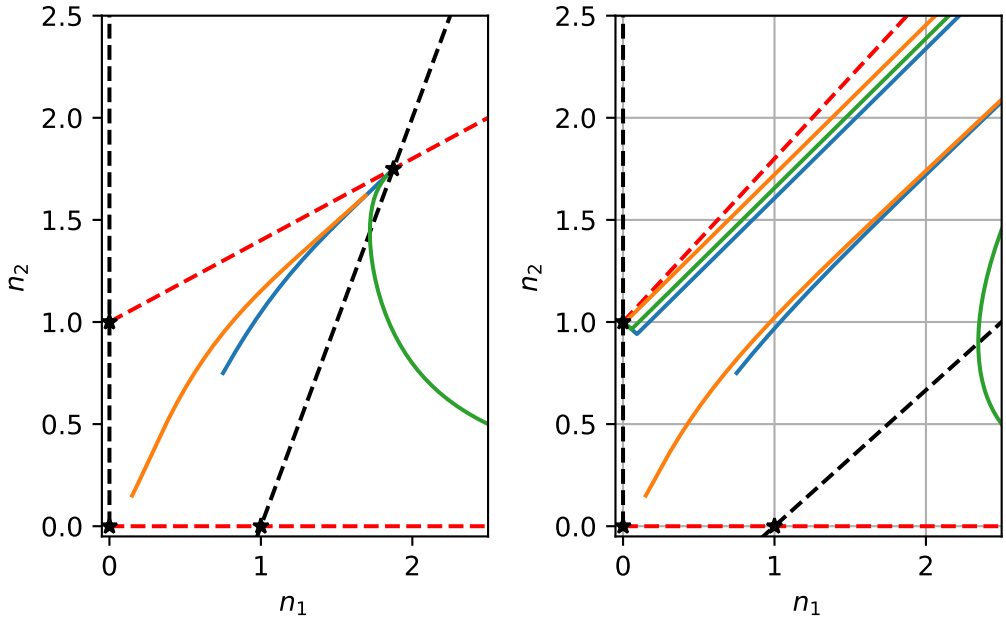


Figure 5.6: Numerical solution of the symbiosis model

5.4.5 Insight

The important parameter in the model is the product $a_{12}a_{21}$. This quantifies the total amount of cooperativity in the model. All steady states that involve the extinction of a species are unstable. In the case where if $a_{12}a_{21} < 1$ there is a stable steady state. Note that steady states of both variables are higher than they would be in the absence of the other species. In the $a_{12}a_{21} > 1$ there is no coexistence steady state and both populations grow in an unbounded manner.

6 Biochemical kinetics

Biochemical kinetics concern the concentration of chemical substances in biological systems. In this section we neglect spatial variation in concentrations, effectively assuming chemical reactions occur in environments that are "well-mixed".

6.1 The law of mass action

We denote the i^{th} chemical species using the notation C_i. The concentration of molecule type C_i is denoted $[C_i]$ and represents the number of molecules of C_i per unit volume.

Suppose $C_1, ..C_M$ undergo the reaction

$$\lambda_1 C_1 + \lambda_2 C_2 + ... + \lambda_m C_M \underset{k_b}{\overset{k_f}{\rightleftharpoons}} \gamma_1 C_1 + \gamma_2 C_2 + ...\gamma_M C_M. \tag{6.1}$$

the law of mass action states that the forward reaction proceeds at rate

$$k_f [C_1]_1^{\lambda} [C_2]_2^{\lambda} .. [C_M]_M^{\lambda} \tag{6.2}$$

whilst the backward reaction proceeds at rate

$$k_b [C_1]_1^{\gamma} [C_2]_2^{\gamma} .. [C_M]_M^{\gamma} \tag{6.3}$$

where k_f and k_b are dimensional rate constants.

> **Example**
>
> Suppose A and B react to produce C. Hence
>
> $$A + B \overset{k}{\rightarrow} C. \tag{6.4}$$
>
> The law of mass action states that the rate of the reaction is
>
> $$k[A][B]. \tag{6.5}$$

Using the reaction rates, we write down ordinary differential equations that describe how concentrations of a given molecule will change in time. Hence

$$\frac{d[C]}{dt} = k[A][B]. \tag{6.6}$$

Example

Consider the reversible reaction

$$A + B \underset{k_-}{\overset{k_+}{\rightleftharpoons}} C. \tag{6.7}$$

Define dependent variables, identify reaction rates and derive ordinary differential equations that describe how concentrations evolved in time.
The dependent variables are:

$$[A](t), \quad [B](t), \quad [C](t). \tag{6.8}$$

Applying the law of mass action yields the reaction rates:

$$k_+[A][B] \quad \text{and} \quad k_-[C]. \tag{6.9}$$

The ODEs are

$$\begin{aligned}
\frac{d[A]}{dt} &= -k_+[A][B] + k_-[C], \\
\frac{d[B]}{dt} &= -k_+[A][B] + k_-[C], \\
\frac{d[C]}{dt} &= k_+[A][B] - k_-[C].
\end{aligned}$$

For a given set of initial conditions,

$$[A](t=0) = [A]_0, \quad [B](t=0) = [B]_0, \quad [C](t=0) = [C]_0, \tag{6.10}$$

the ODEs can be solved and hence the concentrations of the different molecules described as time evolves.

6.1.1 Example

The previous example have had stochiometric constants all set to unity (i.e. all reactions involved a molecules of one species interaction with one from another). Consider the reaction in which one molecule of species A with m of species B giving rise to n molecules of species B

and p molecules of species C, i.e.

$$A + mB \xrightarrow{k_1} nB + pC. \tag{6.11}$$

The law of mass action says that the rate of the forward reaction is

$$k_1[A][B]^m. \tag{6.12}$$

The governing ODEs are

$$\begin{aligned}
\frac{d[A]}{dt} &= -k_1[A][B]^m, \\
\frac{d[B]}{dt} &= (n-m)k_1[A][B]^m, \\
\frac{d[C]}{dt} &= pk_1[A][B]^m.
\end{aligned}$$

Example

Consider the reversible reaction

$$A + A \underset{k_-}{\overset{k_+}{\rightleftharpoons}} B. \tag{6.13}$$

Define dependent variables, identify reaction rates and derive ordinary differential equations that describe how concentrations evolved in time.
The reaction rates are

$$k_+[A]^2 \tag{6.14}$$

and

$$k_-[B]. \tag{6.15}$$

The ODEs are

$$\begin{aligned}
\frac{d[A]}{dt} &= -2k_+[A]^2 + 2k_-[B], \\
\frac{d[B]}{dt} &= k_+[A]^2 - k_-[B],
\end{aligned}$$

6.2 Enzyme kinetics

Biochemical reactions are often regulated by enzymes (substances that convert a substrate into another substrate). Consider a chemical reaction in which substrate, S, reacts with an enzyme, E, to form a complex, C. Suppose the complex can either undergo the reverse reaction or go on to form a product, P, with the release of the enzyme, i.e.

$$S + E \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C \xrightarrow{k_2} P + E. \tag{6.16}$$

6.2.1 Deriving the model equations

For notational convenience we let lower case letter denote concentrations, i.e.

$$s(t) = [S](t), \quad c(t) = [C](t), e(t) = [E](t), p(t) = [P](t). \tag{6.17}$$

Applying the law of mass action the above enzyme kinetic scheme can be described by the system of ODES

$$\begin{aligned}
\frac{ds}{dt} &= -k_1 se + k_{-1} c, \\
\frac{de}{dt} &= -k_1 se + k_{-1} c + k_2 c, \\
\frac{dc}{dt} &= k_1 se - k_{-1} c - k_2 c, \\
\frac{dp}{dt} &= k_2 c.
\end{aligned}$$

We consider initial conditions such that at $t = 0$ the reaction has not yet started, i.e. there is no product or complex formed

$$s(0) = s_0, \quad e(0) = e_0, \quad c(0) = 0, \quad p(0) = 0, \tag{6.18}$$

where s_0 and e_0 represent the initial concentrations of substrate and enzyme, respectively.

6.2.2 Numerical solutions

In Figure 6.1 we plot numerical solutions of Equation 6.18. For this solution we have chosen initial conditions such that

$$\frac{e_0}{s_0} \ll 1. \tag{6.19}$$

Note that c and e evolve rapidly in time close to the initial data whilst those of s and p do not.

6.2.3 Reducing the dimensions of the model

Whilst there are four dependent variables in the problem ($s(t)$, $c(t)$, $e(t)$ and $p(t)$), the description of the problem can be simplified by noting that the variable $p(t)$ does not couple back to the other variables, i.e. if we can solve the system for $s(t)$, $e(t)$ and $c(t)$ then $c(t)$ can be expressed as a function of time and

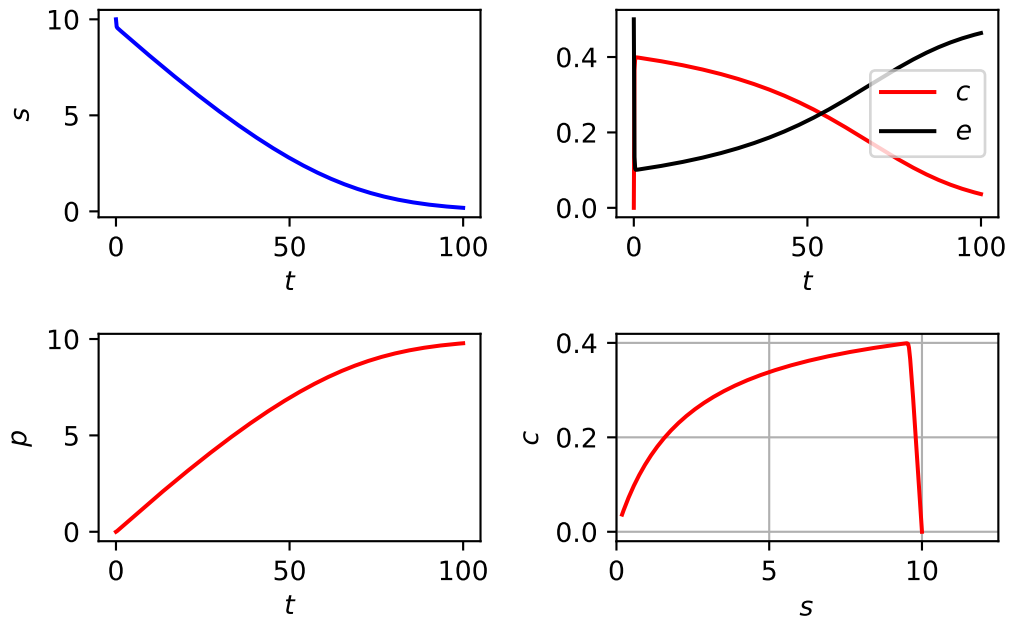


Figure 6.1: Numerical solutions of the Michaelis Menten model

$$p(t) = k_2 \int c(t)dt + C_1. \tag{6.20}$$

Furthermore, there is a conserved quantity in the system. Note that

$$\frac{de}{dt} + \frac{dc}{dt} = 0, \tag{6.21}$$

which reflects the fact that enzyme exists either in free form or bound to the product. Integrating yields

$$c(t) + e(t) = C_2. \tag{6.22}$$

Evaluating at $t = 0$,

$$e_0 = C_2. \tag{6.23}$$

Hence

$$c(t) + e(t) = e_0 \tag{6.24}$$

and the variable $e(t)$ can be replaced by

$$e(t) = e_0 - c(t) \tag{6.25}$$

Given

$$e(t) = e_0 - c(t), \tag{6.26}$$

substitute in

$$\frac{ds}{dt} = -k_1 se + k_{-1}c,$$
$$\frac{dc}{dt} = k_1 se - k_{-1}c - k_2 c,$$

Hence

$$\frac{ds}{dt} = -k_1 s(e_0 - c) + k_{-1}c,$$
$$\frac{dc}{dt} = k_1 s(e_0 - c) - (k_{-1} + k_2)c,$$

6.2.4 The quasi-steady state approximation (QSSA)

A usual approach to these equations is to assume that the timescale of complex dynamics is very fast compared to that of substrate dynamics.

To make the QSSA we assume that one of the variables (in this case c), is in equilibrium

$$dc/dt \sim 0. \tag{6.27}$$

In which case the second equation yields

$$c = \frac{e_0 s(t)}{s(t) + K_m}, \tag{6.28}$$

where

$$K_m = \frac{k_{-1} + k_2}{k_1}, \tag{6.29}$$

is known as the Michaelis constant.

Now consider

$$\frac{ds}{dt} = -k_1 s(e_0 - c) + k_{-1}c,$$

By QSSA

$$-k_1 s(e_0 - c) + k_{-1} c = -k_2 c = -k_2 \frac{e_0 s(t)}{s(t) + K_m}, \tag{6.30}$$

Hence

$$\frac{ds}{dt} = -k_2 \frac{e_0 s(t)}{s(t) + K_m},$$

Note this could be achieved by direct substitution for $c(t)$.

6.2.5 Enzyme kinetics: the Michaelis-Menten quasi-steady state approximation (QSSA)

6.2.5.1 Nondimensionalisation

Nondimensionalisation using

$$\tau = k_1 e_0 t, \quad u = \frac{s}{s_0}, \quad v = \frac{c}{e_0}, \tag{6.31}$$

yields the ODEs

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

where

$$\lambda = \frac{k_2}{k_1 s_0}, \quad K = \frac{k_{-1} + k_2}{k_1 s_0}, \quad \epsilon = \frac{e_0}{s_0}. \tag{6.32}$$

6.2.5.2 Asymptotic expansions: the outer solution

We consider the (often realised) case where the amount of enzyme in the system is small compared with the amount of substrate, i.e.

$$\epsilon \ll 1. \tag{6.33}$$

The presence of the small parameter ϵ allows us to use perturbation theory to calculate approximate solutions to Equation 6.32. However, the problem is singular owing to the $\epsilon dv/dt$ term.

We propose an outer solution of the form

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

Substituting the expansions in Equation 6.32 yields

$$\frac{du_0}{d\tau} + \epsilon\frac{du_1}{d\tau} + \epsilon^2\frac{du_2}{d\tau} + ... = -(u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + ...) +$$
$$(u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + ... + K - \lambda)(v_0(\tau) + \epsilon v_1(\tau) + \epsilon^2 v_2(\tau) + ...).$$

Gathering terms as coefficients of the different powers of ϵ yields

$$\frac{du_0}{d\tau} + \epsilon\frac{du_1}{d\tau} + ... = -u_0(\tau) + (u_0(\tau) + K - \lambda)v_0 + \epsilon(-u_1(\tau) + u_1 v_0 + v_1 u_0 + v_1(K - \lambda)) + O(\epsilon^2),$$

where terms of order ϵ^2 have been neglected.

Considering the v equation yields

$$\epsilon(\frac{dv_0}{d\tau} + \epsilon\frac{dv_1}{d\tau} + \epsilon^2\frac{dv_2}{d\tau} + ..) = u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + ...$$
$$-(u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + ... + K)(v_0(\tau) + \epsilon v_1(\tau) + \epsilon^2 v_2(\tau) + ...).$$

Gathering terms as coefficients of the different powers of ϵ yields

$$\epsilon\frac{dv_0}{d\tau} + \epsilon^2\frac{dv_1}{d\tau} + ... = u_0(\tau) - u_0(\tau)v_0(\tau) - v_0 K$$
$$+\epsilon(u_1(\tau) - u_0 v_1 - u_1 v_0 - K v_1) + O(\epsilon^2).$$

At $O(1)$

$$\frac{du_0}{d\tau} = -u_0 + (u_0 + K - \lambda)v_0$$
$$0 = u_0 - u_0 v_0 - v_0 K.$$

Solving the algebraic equation yields

$$v_0 = \frac{u_0}{u_0 + K}, \tag{6.34}$$

and substituting in the u_0 equation yields

$$\frac{du_0}{d\tau} = -u_0 + (u_0 + K - \lambda)\frac{u_0}{u_0 + K} = -\frac{\lambda u_0}{u_0 + K}. \tag{6.35}$$

Integrating yields

$$u_0 + K \ln u_0 = -\lambda\tau + A, \tag{6.36}$$

where A is an integration constant.

When posing a solution as an expansion, a necessary question to ask is when the expansion is a valid? On the outer scale we have shown that

$$v_0 = \frac{u_0}{u_0 + K}. \tag{6.37}$$

Note that the expression

$$v_0 = \frac{u_0}{u_0 + K} \tag{6.38}$$

does not satisfy the initial condition $v(0) = 0$. As $u_0(0) = 1$, we find that at $\tau = 0$

$$v_0 = \frac{1}{1 + K} \neq 0. \tag{6.39}$$

Hence the proposed expansion is not valid at least near $\tau = 0$.

6.2.5.3 Asymptotic expansions: the inner solution

This issue can be rectified by proposing a different scaling for time and recalculating a series solution in the new coordinate system.

We proceed by making the change of variable

$$\sigma = \frac{\tau}{\epsilon}. \tag{6.40}$$

Note that $\sigma = 1$ corresponds to $\tau = \epsilon$. Hence the proposed rescaling of time will give rise to what is called the inner solution to the problem (close to $t = 0$).

To distinguish inner and outer solutions we relabel dependent variables such that

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

Note that

$$\frac{d}{d\tau} = \frac{1}{\epsilon}\frac{d}{d\sigma}. \tag{6.41}$$

Hence upon changing variables

$$\frac{1}{\epsilon}\frac{dU}{d\sigma} = -\epsilon U + \epsilon(U + K - \lambda)V,$$
$$\frac{1}{\epsilon}\,\epsilon\frac{dV}{d\sigma} = U - (U + K)V.$$

Upon tidying

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

We seek series solutions to Equation 6.42 of the form

$$U(\sigma;\epsilon) = U_0(\sigma) + \epsilon U_1(\sigma) + \epsilon^2 U_2(\sigma) + ... = \sum_{n=0}^{\infty} U_n(\sigma)\epsilon^n,$$
$$V(\sigma;\epsilon) = V_0(\sigma) + \epsilon V_1(\sigma) + \epsilon^2 V_2(\sigma) + ... = \sum_{n=0}^{\infty} V_n(\sigma)\epsilon^n.$$

Substitution yields

$$\begin{aligned}\frac{dU_0}{d\sigma} + \epsilon\frac{dU_1}{d\sigma} + ... &= \epsilon\left(U_0 + \epsilon U_1 + ... + (U_0 + \epsilon U_1 + + K - \lambda)(V_0 + \epsilon V_1 + ...)\right)\\ \frac{dV_0}{d\sigma} + \epsilon\frac{dV_1}{d\sigma} + ... &= (U_0 + \epsilon U_1 + ...) - (U_0 + \epsilon U_1 + ... + K)(V_0 + \epsilon V_1 + ...).\end{aligned} \tag{6.42}$$

Hence at leading order

$$\frac{dU_0}{d\sigma} = 0$$
$$\frac{dV_0}{d\sigma} = U_0 - (U_0 + K)V_0.$$

Given the initial condition $U(0) = 1$ we obtain that the inner solution is

$$U(\sigma) = 1. \tag{6.43}$$

Substituting in the second equation gives

$$\frac{dV_0}{d\sigma} = 1 - (1+K)V_0. \tag{6.44}$$

Given $V_0(0) = 0$ we obtain

$$V_0 = \frac{1 - e^{-(1+K)\sigma}}{1+K}. \tag{6.45}$$

6.2.5.4 Asymptotic expansions: matching the inner and outer solutions

Inner and outer solutions are matched by taking limits

$$\lim_{\tau\to 0}(u_0(\tau), v_0(\tau)) = \lim_{\sigma\to\infty}(U_0(\sigma), V_0(\sigma)). \tag{6.46}$$

Note that

$$\lim_{\sigma\to\infty} V_0(\sigma) = \lim_{\sigma\to\infty} \frac{1 - e^{-(1+K)\sigma}}{1+K} = \frac{1}{1+K}, \tag{6.47}$$

and

$$\lim_{\tau\to 0}(v_0(\tau)) = \lim_{\tau\to 0} \frac{u_0}{u_0 + K} = \frac{1}{1+K}. \tag{6.48}$$

Hence the v variables are already matching in the appropriate limit.

Similarly

$$\lim_{\sigma\to\infty} U_0(\sigma) = 1, \tag{6.49}$$

hence we require that

$$\lim_{\tau\to 0} u_0(\tau) = 1. \tag{6.50}$$

Hence for

$$(u_0 + K\ln u_0 = -\lambda\tau + A) \tag{6.51}$$

to hold as $\tau \to 0$ implies $A = 1$.

6.3 The Brusselator

The Brusselator is an abstract model that can be used to demonstrate oscillations in (bio)-chemical systems. Consider a chemical reaction where five chemical species, A, B, D, X and Y, react according to the scheme

$$\begin{aligned} A &\xrightarrow{k_1} X, \\ B + X &\xrightarrow{k_2} Y + D, \\ 2X + Y &\xrightarrow{k_3} 3X, \\ X &\xrightarrow{k_4} E. \end{aligned}$$

Assuming that the concentration of A and B ($[A]$ and $[B]$, respectively) are in vast excess (i.e. the amount that A and B get depleted by the reactions is negligible compared with the total amount of A and B present), their concentration are treated as constants. Furthermore, as D and E are products but not reactants (they only appear on the right-hand side of reactions) we do not concern ourselves with their dynamics.

6.3.1 Deriving model equations

To make the steps leading to ODEs obvious, it is useful to rewrite the reaction scheme in the form

$$\begin{aligned} A &\xrightarrow{k_1} X, \\ B + X &\xrightarrow{k_2} Y + D, \\ X + X + Y &\xrightarrow{k_3} X + X + X, \\ X &\xrightarrow{k_4} E. \end{aligned}$$

Applying the law of mass action yields that the four reactions occur at rates:

- $k_1[A]$,
- $k_2[B][X]$,
- $k_3[X]^2[Y]$,
- $k_4[X]$.

The total time derivative of $[X]$ is obtained by visiting each X in the reaction scheme once and adding the corresponding reaction rate to the right-hand side of the ODE, i.e.

$$\frac{d[X]}{dt} = \overbrace{k_1[A]}^{R1-lhs} - \overbrace{k_2[B][X]}^{R2-lhs} - \overbrace{k_3[X]^2[Y]}^{R3-lhs} - \overbrace{k_3[X]^2[Y]}^{R3-lhs} + \overbrace{k_3[X]^2[Y]}^{R3-rhs} + \overbrace{k_3[X]^2[Y]}^{R3-rhs} + \overbrace{k_3[X]^2[Y]}^{R3-rhs} - \overbrace{k_4[X]}^{R4-lhs},$$
$$= k_1[A] - k_2[B][X] + k_3[X]^2[Y] - k_4[X].$$

Similarly for species Y we obtain that the total rate of change in time is

$$\frac{d[Y]}{dt} = k_2[B][X] - k_3[X]^2[Y]. \tag{6.52}$$

6.3.2 Nondimensionalisation

Upon making the change of variables

$$x = \sqrt{\frac{k_3}{k_4}}[X], \qquad y = \sqrt{\frac{k_3}{k_4}}[Y], \quad \text{and} \quad \tau = k_4 t, \tag{6.53}$$

yields

$$\begin{aligned} \frac{dx}{d\tau} &= a - bx + x^2 y - x = f(x,y), \\ \frac{dy}{d\tau} &= bx - x^2 y = g(x,y), \end{aligned} \tag{6.54}$$

where

$$a = [A]\frac{k_1}{k_4}\sqrt{\frac{k_3}{k_4}} \quad \text{and} \quad b = [B]\frac{k_2}{k_4}. \tag{6.55}$$

6.3.3 Steady states analysis

Seeking steady states (x^*, y^*) of equations Equation 6.54 such that

$$f(x^*, y^*) = g(x^*, y^*) = 0 \tag{6.56}$$

yields

$$(x^*, y^*) = (a, \frac{b}{a}). \tag{6.57}$$

6.3.4 Linear stability analysis

The Jacobian matrix is

$$A = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} = \begin{pmatrix} -b + 2xy - 1 & x^2 \\ b - 2xy & -x^2 \end{pmatrix}. \tag{6.58}$$

Evaluating the Jacobian at $(a, b/a)$ yields

$$A = \begin{pmatrix} b - 1 & a^2 \\ -b & -a^2 \end{pmatrix}. \tag{6.59}$$

The determinant of the Jacobian is

$$\det A = -(b-1)a^2 + a^2 b = a^2 > 0, \tag{6.60}$$

Hence $(a, b/a)$ is not a saddle. The trace of the Jacobian is

$$\mathrm{tr} A = b - 1 - a^2. \tag{6.61}$$

Hence if $b > 1 + a^2$ the trace is positive and, referring to Figure 5.1, the steady state is linearly unstable. Otherwise, the steady state is linearly stable.

In Figure 6.2 we numerically solve Equation 6.54 in the case of oscillatory solutions. Note that when the steady state is unstable, the numerical solution indicates that the system has limit cycle solutions. A valid question to ask is whether one can prove that this is the case.

6.3.5 Applying the Poincaire-Bendixson theorem

Recall that the Poincaire-Bendixson theorem can be used to prove the existence of limit cycle solutions in a case where a bounding set encloses a single unstable steady state. Hence given the case of the Brusselator with $b > a^2 + 1$, the identification of a bounding set will allow application of the Poincaire-Bendixson theorem and hence prove the existence of limit cycle solutions.

We begin by defining the nullclines of the system. The x nullcline is given by

$$y = \frac{1 + b}{x} - \frac{a}{x^2}. \tag{6.62}$$

The y nullclines are given by

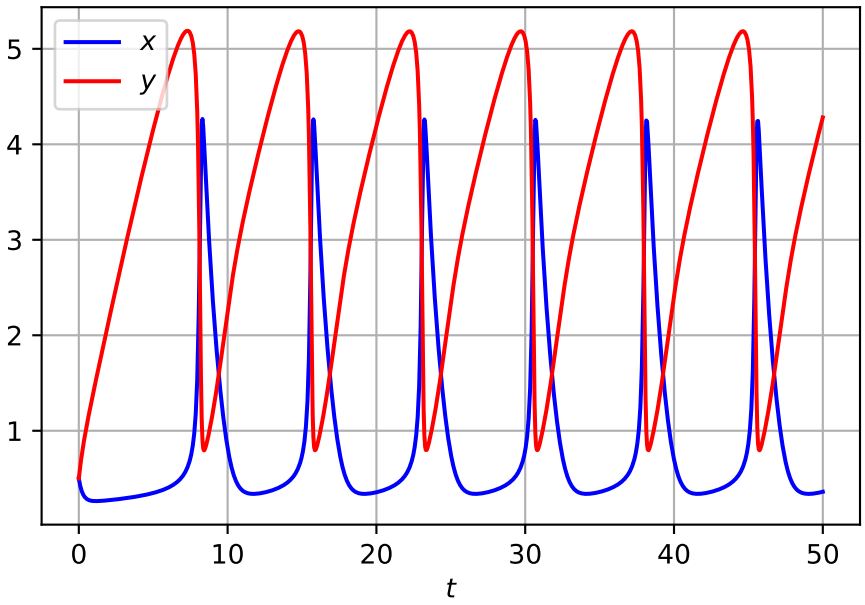


Figure 6.2: Numerical solutions of the Brusselator model

$$y = \frac{b}{x} \quad \text{and} \quad x = 0. \tag{6.63}$$

In the positive quadrant, this nullcline has a single root at $a/(1+b)$, tends to 0 as $x \to \infty$ and has a maximum at $x = 2a/(1+b)$.

In Figure 6.3 we plot the the oscillatory solution together with the nullclines. Note that the nullclines separate the phase plane into regions of constant sign. Note that the x nullcline separates the phase plane into regions where $dx/dt > 0$ and $dx/dt < 0$. Similarly, the y nullcline separates the phase plane into regions where $dy/dt > 0$ and $dy/dt < 0$.

Note that signs for dx/dt can be determined by considering behaviour of the function f as one moves away from the nullcline where, by definition, $f = 0$. Consider some point that sits on the x nullcline. While keeping the x value fixed, increase y so the point moves vertically in the phase plane. This implies that f has increased because the only term to change is $x^2 y$. Hence f increases upon increasing y and therefore dx/dt is positive for all points above the x nullcline. Alternatively, note that in the Jacobian matrix we have calculated that $\partial f/\partial y$ is positive.

6.3.5.1 A confined set

To define a confined set, we construct the closed loop ABCDEA in phase space (see Figure 6.4) where the points A, B, C, D and E are defined as follows. Let the points A and B be two

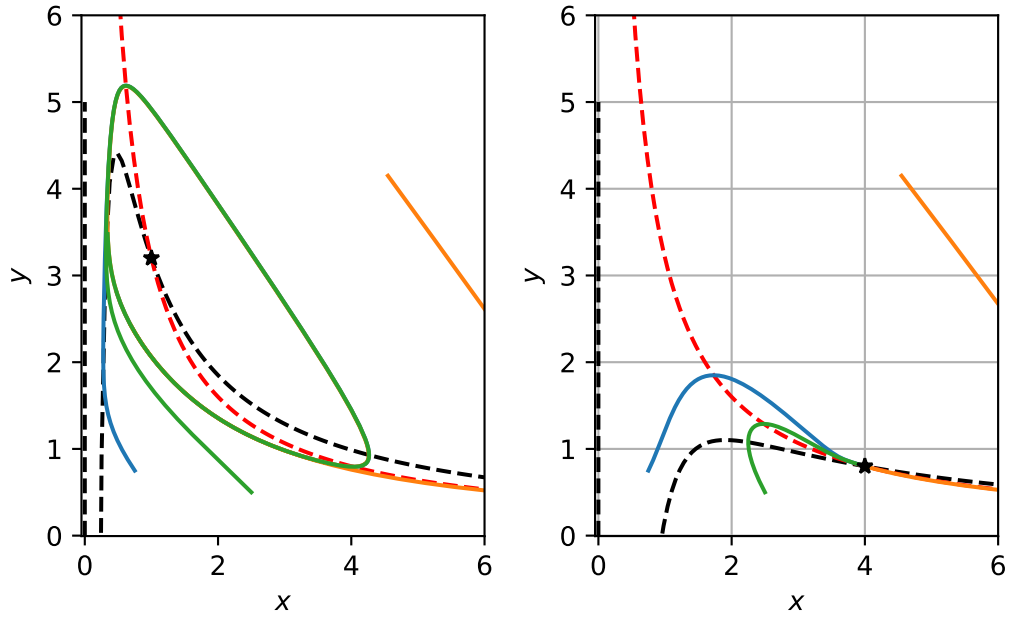


Figure 6.3: Numerical solution of the Brusselator.

points on the x axis with coordinates

$$(\delta, 0) \tag{6.64}$$

and

$$\left(\frac{a}{1+b}, 0\right). \tag{6.65}$$

respectively. We choose $\delta > a$. The outward normal to the line segment AB is $\mathbf{n} = [0, -1]$. To show that the trajectories point inwards along AB, we compute

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = -\frac{dy}{dt}. \tag{6.66}$$

As the line segment AB sits below the y nullcline, $dy/dt > 0$ in this region. Hence

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = -\frac{dy}{dt} < 0. \tag{6.67}$$

Hence trajectories point inwards on the line segment AB.

Let C represent the point

$$\left(\frac{a}{1+b}, b\frac{1+b}{a}\right). \tag{6.68}$$

The normal vector to the line segment BC is $\mathbf{n} = [-1, 0]$. As BC lies to the left of the x nullcline, in a region where $dx/dt > 0$, then

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = -\frac{dx}{dt} < 0. \tag{6.69}$$

Hence trajectories point inwards on the line segment BC.

Consider the line segment CD where D has coordinates

$$\left(k, b\frac{1+b}{a}\right), \tag{6.70}$$

with $k > a$

The normal to this line segment is [0,1]. As CD lies in a region of the phase plane where $dy/dt < 0$,

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = \frac{dy}{dt} < 0. \tag{6.71}$$

Hence trajectories point inwards on the line segment CD.

Let E be a point that sits on the x nullcline at some position

$$\left(\delta, \frac{\delta(1+b) - a}{\delta^2}\right), \tag{6.72}$$

such that DE is a straight line with outwardly pointing normal vector $[1, 1]$. Along DE

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = a - bx + x^2y - x + bx - x^2y = a - x < 0 \tag{6.73}$$

for $x > a$. As $k > a$, $x > a$ for all points on DE, hence trajectories point inwards on DE.

Finally, consider the line segment EA which has normal vector $\mathbf{n} = [1, 0]$. As $dx/dt < 0$ along EA

$$\mathbf{n}.\left[\frac{dx}{dt}, \frac{dy}{dt}\right] = \frac{dx}{dt} < 0. \tag{6.74}$$

Hence at all points on the closed loop ABCDEA trajectories point inwards (see Figure 6.4). Hence ABDCEA is a confined set and the Poincaire-Bendixson theorem states that the system exhibits limit cycle solutions when the steady state is unstable. This is precisely the behaviour that we see numerically in Figure Figure 6.3.

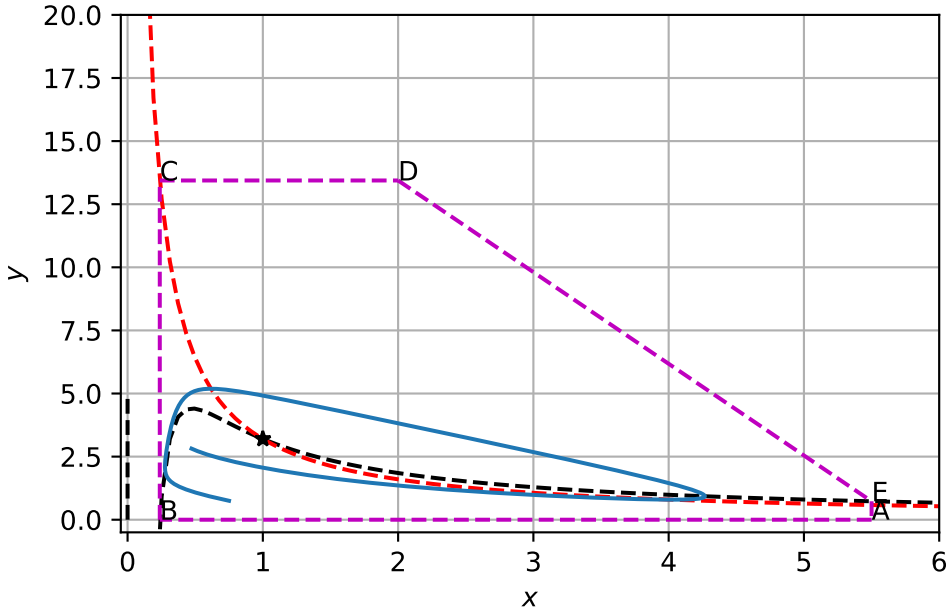


Figure 6.4: Numerical solution of the Brusselator.

Part III

Appendices

7 Python

7.1 Symbolic calculations

Symbolic calculations ahve been performed using the Python library Sympy.

This library comes with tutorials.

You are encouraged to familiarise yourself with the syntax by working through some of the tutorial examples provided at the links above.

Many of the calculations that we do throughout the course involve solving systems of algebraic equations

7.2 Numerical solution of difference equations

Difference equations have been solved using a for loop. Routinse have been written to solve either single or coupled system of difference equaitons.

7.3 Numerical integration of ODEs

Throughout the notes systems of ODEs have been integrated using the Scipy function odeint.

7.4 Plotting

Line graphs are plotted using the Python library Matplotlib.

8 Curve sketching

8.1

In the module we will be required to graph of nonlinear function.

Consider a nonlinear function

$$f(x;p), \quad x \in \mathfrak{R}. \tag{8.1}$$

where p is a constant.

For example,

$$f(x) = rx(1-x), \quad x \in \mathfrak{R}.$$

Our goal is usually to sketch f in qualitatively distinct cases. For example: the graph of f when $r = 1$ is *qualitatively* equivelent to the graph of f when $r = 2$. However, when $r = -1$ it is qualitatively distinct.

The challenge is to firstly identify qualitatively distinct cases. Then sketch f for each of these cases.

T0 identify qualitatively distinct cases we test the properties of f as follows:

1. Identify the *biologically relevant* roots of f. We define x^* such that

   $$f(x^*;p) = 0.$$

   Biologically relevant solutions require $x^* \geq 0$.

   Does the number of biologically relevant solutions depend on the parameter p?

2. Identify the turning points of f.
   Differentiate f with respect to x. Identify turning points, x_c, such that

   $$\left.\frac{df}{dx}\right|_{x=x_c} = 0.$$

   Are there any turning points? Are they biologically relevant? Does the number of biologically relevant solutions depend on the parameter p?

3. Identify limiting behaviour as $x \to \infty$. Compute the limit

$$\lim_{x \to \infty} f(x; p) = 0.$$

4.

Britton, Nicholas F, and NF Britton. 2003. *Essential Mathematical Biology*. Vol. 453. Springer.

Edelstein-Keshet, Leah. 2005. *Mathematical Models in Biology*. SIAM.

Ludwig, Donald, Dixon D Jones, Crawford S Holling, et al. 1978. "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest." *Journal of Animal Ecology* 47 (1): 315–32.

Murray, J. D. 2002. *Mathematical Biology i: An Introduction*. Springer.