Mathematical Ecology and Epidemiology

Lecture notes for Spring 2024

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Welcome

This site will contain the lecture notes and problem sheets for the Ecology and Epidemiology part of the "Mathematical Ecology, Epidemiology and Evolution" module as taught at the University of York in the Spring of 2024. The mathematics used in Mathematical Ecology and in Mathematical Epidemiology are quite similar, whereas the mathematics used in Mathematical Evolution has a different flair and that part is taught by a different lecturer, George Constable.

The Mathematical Ecology and Epidemiology part is taught in three two-week blocks, with each block consisting of 6 lectures, one problem sheet, one examples class and one small-group seminar. Between each block there will be a two-week block of Mathematical Evolution.

The notes will be created after each lecture and will continue to be periodically revised. Whenever you spot something that is not quite right, please email me at gustav.delius@york.ac.uk or submit your correction in the correction form at https://forms.gle/w17c19vWnM7wpLpz7.

1 Continuous-time population models

We are interested in modelling the time evolution of the population number $N(t)$, starting with the current population number $N(0) = N_0$. Thinking about the processes by which the population number can change, we see that we can write the rate of change in the population number as

$$\frac{dN}{dt} = \text{birth rate} - \text{death rate} + \text{immigration rate} - \text{emigration rate}. \tag{1.1}$$

The idea behind this approach is that if we understand how the rates at which these processes take place depend on the population number N, then we can find $N(t)$ by solving the above differential equation. Different assumptions about the individual rates will give us different models for N(t). We will look at some influential models now.

1.1 Exponential model

This is the simplest and oldest model, introduced by Thomas Robert Malthus in 1798. If we assume that the per-capita birth rate b and the per-capita death rate d are fixed constants, then the general differential equation Eq. 1.1 becomes the linear equation

$$\frac{dN}{dt} = bN - dN = rN, \tag{1.2}$$

where we introduced the new parameter $r = b - d$. This equation is easy to solve:

$$N(t) = N_0 \, e^{rt}. \tag{1.3}$$

If the birth rate exceeds the death rate and hence $r > 0$, the model predicts exponential growth. In the opposite case of lower birth rate than death rate the model predicts exponential decay of the population number towards extinction. Only when birth and death rates are perfectly equal can the population stay steady over time. We illustrate that in Figure 1.1.

1.2 Logistic model

Exponential population growth can not be maintained for ever. There will be a limit to the size of population that an ecosystem can maintain. When the population gets closer to this

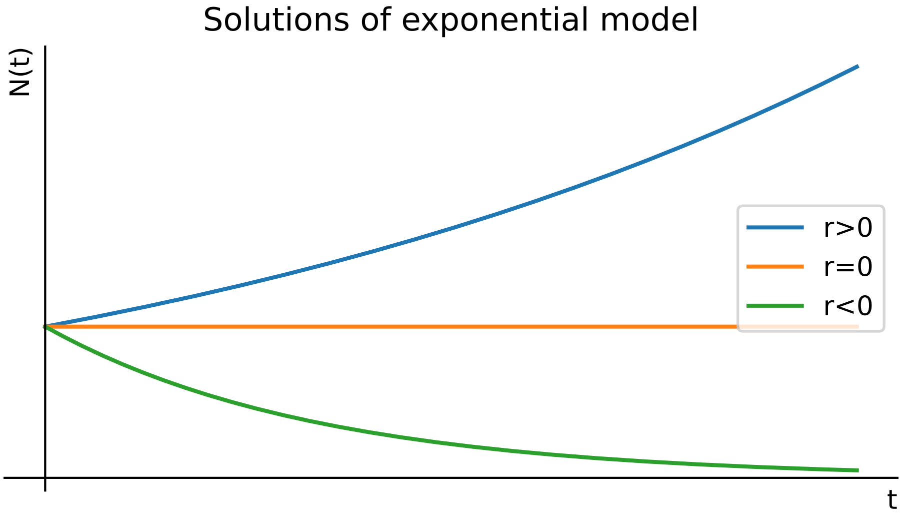

Figure 1.1: Solutions to the exponential model.

limit its growth rate will decrease, for example due to competition for limited food sources or space, or due to disease. This decrease in the growth rate is captured by the logistic equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.4}$$

where K is the carrying capacity of the environment. The extra factor of $1 - N/K$ decreases the growth rate towards zero as the population number N approaches the carrying capacity K.

In Figure 1.2 make a plot of the right-hand side of the logistic equation Eq. 1.4 to see how the growth rate depends on the population number. While that figure was created by the computer, the plot is easy to sketch by hand because the function we want to sketch is simply an upside-down parabola. The maximum of the parabola is at $N = K/2$ and the parabola crosses the N-axis at $N = 0$ and $N = K$. This means that the population growth rate is zero at $N = 0$ and $N = K$, and it is maximal at $N = K/2$.

From the plot we see that the growth rate is zero at $N = 0$ and $N = K$, and it is maximal at $N = K/2$. By realising that dN/dt is the slope of the graph of $N(t)$ we can sketch a few solutions to the logistic equation Eq. 1.4 in Figure 1.3.

The logistic equation Eq. 1.4 can be solved analytically to give

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right)e^{-rt}} = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}. \tag{1.5}$$

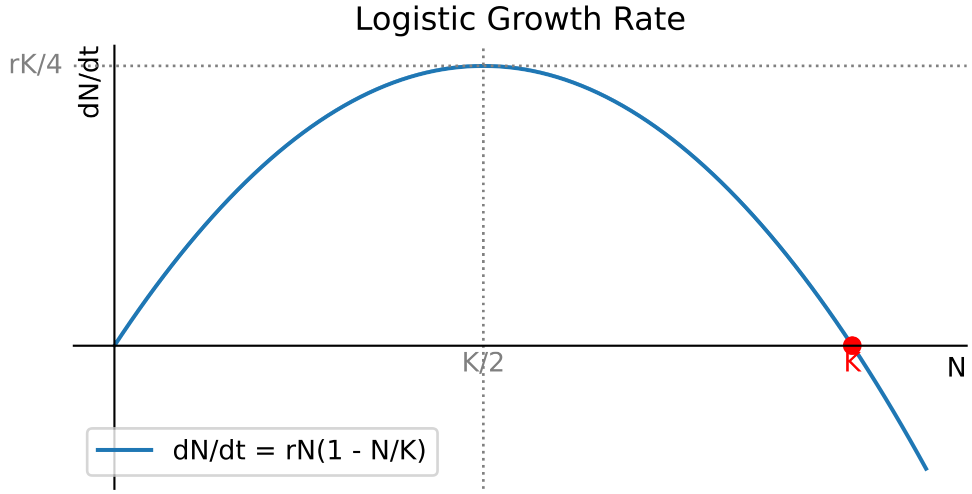

Figure 1.2: The logistic growth rate as a function of the population number.

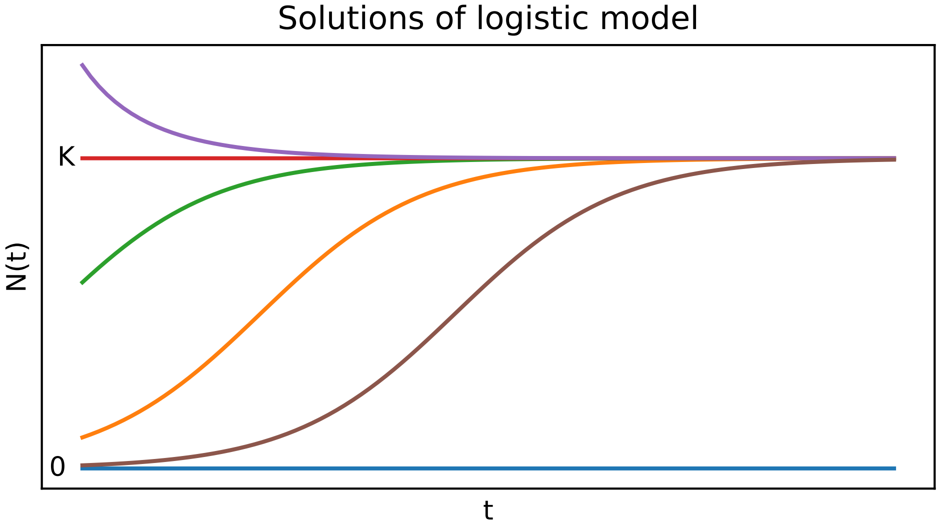

Figure 1.3: Solutions to the logistic equation.

1.3 Allee effect

Warder Clyde Allee (1885-1955) was an American ecologist who studied the effects of population density on the growth rate of a population. He found that in some cases the per-capita growth rate can increase with N. This is called the Allee effect. It can occur when the population is too small to find a mate, to find food, or to avoid predators.

Figure Figure 1.4 shows the per-capita growth rate as a function of the population number for exponential growth in black, for logistic growth in blue and two different growth rates exhibiting the Allee effect in green and red.

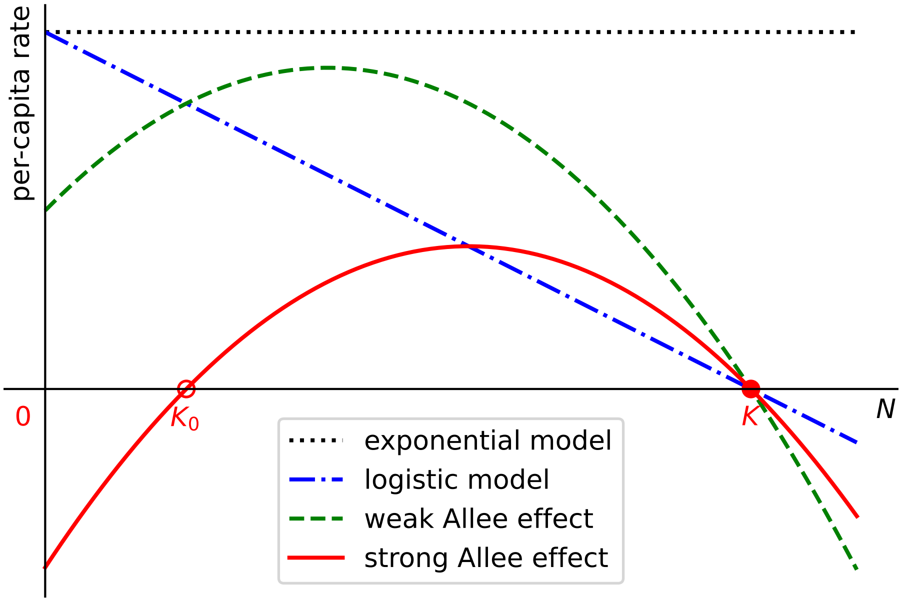

Figure 1.4: The per-capita growth rate as a function of the population number.

The green curve in Figure 1.4 shows a weak Allee effect, where the per-capita rate is small but possitive for small population sizes, then initially increases with the population size before then decreasing again as the population approaches its carrying capacity. The red curve shows a strong Allee effect, which is similar but so strong that the growth rate starts out not just small but actually negative for small N.

The simplest model for the Allee effect is the logistic equation with a modified growth rate that includes another factor that decreases the growth rate for small N:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K_0} - 1\right). \tag{1.6}$$

If $0 < K_0 < K$, this exhibits the strong Allee effect because the growth rate is negative when $N < K_0$. This means that the population will be driven towards extinction when it is below the threshold size K_0 and it will grow towards its carrying capacity when it is above K_0. This is illustrated in Figure 1.5.

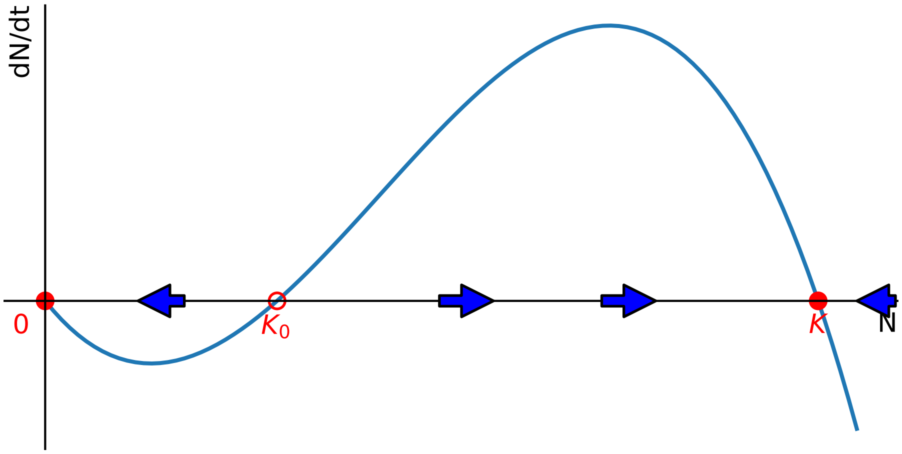

Figure 1.5: The Allee growth rate as a function of the population number.

This phenomenon is important for conservation biology because it means that small populations are particularly vulnerable to extinction. It is also important for fisheries management because it means that the population can collapse if it falls below a certain threshold size. The phenomenon is called "critical depensation". We will meet it again when we discuss harvesting later in this section.

1.4 General autonomous ODE model

The logistic model is a special case of a general autonomous ordinary differential equation (ODE) model

$$\frac{dN}{dt} = f(N), \tag{1.7}$$

where $f(N)$ is a function of N only, not t. The logistic equation Eq. 1.4 is an example of such a model with

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

If f is Lipschitz continuous, then, given $N(0) = N_0$, there exists a unique solution $N(t)$ to the initial value problem Eq. 1.7. This is a consequence of the Picard-Lindelöf theorem.

We are interested in the steady states of the model, i.e. the values N^* for which $f(N^*) = 0$. These are the values of N for which the population number does not change. To determine the stability of the steady states, we can look near N^* by writing $N(t) = N^* + n(t)$ with $n(t)$ small. Then

$$\frac{dN}{dt} = \frac{dN^*}{dt} + \frac{dn}{dt} = f(N^* + n(t)) \approx f(N^*) + f'(N^*)\, n(t).$$

We now use that $dN^*/dt = 0$ and $f(N^*) = 0$ to find

$$\frac{dn}{dt} \approx f'(N^*)\, n(t).$$

This is a linear equation for $n(t)$ with solution

$$n(t) = n(0)e^{f'(N^*)t}$$

and we can use the sign of $f'(N^*)$ to determine the stability of the steady state:

- If $f'(N^*) < 0$, then $n(t)$ will decrease towards zero, and the steady state is stable.
- If $f'(N^*) > 0$, then $n(t)$ will increase away from zero, and the steady state is unstable.

If $f'(N^*) = 0$, then we need to look at higher order terms to determine the stability.

We illustrate this in the example of the logistic model. The fixed points are $N^* = 0$ and $N^* = K$. The derivative of $f(N)$ is

$$f'(N) = r\left(1 - \frac{2N}{K}\right).$$

So we find that $f'(0) = r > 0$ and $f'(K) = -r < 0$. This means that the steady state $N^* = 0$ is unstable and the steady state $N^* = K$ is stable. This agrees with what we had already seen graphically in Figure 1.2 and Figure 1.3.

1.5 Harvesting a renewable resource

Ecologists model populations not only out of academic interest but also for practical purposes. Humans are interested in exploiting the natural resources. They want o harvest fish from the sea, to hunt deer in the forest, and to cut down trees in the jungle. They want to do this in a way that is sustainable, i.e. that does not lead to the extinction of the resource, while at the same time giving the highest yield.

My personal interest is in understanding how fish populations react to different kinds of fishing. I use coupled partial integro-differential equations for that purpose, but most fisheries management is based on simpler models and we get a good first idea by using the logistic model, which we will now modify to include harvesting.

1.5.1 Harvesting with fixed effort

We assume that in the absence of fishing the fish population number $N(t)$ is governed by the logistic equation Eq. 1.4. We also assume that the fish are harvested at a rate $EN(t)$, where E is the harvesting rate, which is determined by the effort that is put into fishing. This means that the rate of change in the fish population number is given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - EN = f(N). \tag{1.8}$$

We can rewrite this equation in the form of a logistic equation with modified parameters:

$$\frac{dN}{dt} = rN\left(\left(1 - \frac{E}{r}\right) - \frac{N}{K}\right). \tag{1.9}$$

This makes it easy to read off the fixed points $N^* = 0$ and $N^* = K\left(1 - \frac{E}{r}\right)$. The nonzero fixed point gets smaller when fishing effort E increases. This is illustrated in Figure 1.6.

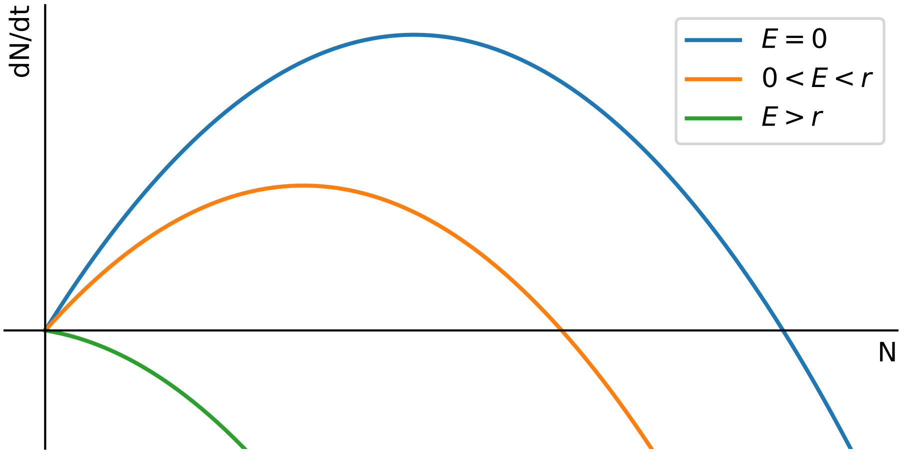

Figure 1.6: Growth rate when harvesting with fixed effort.

We are now interested in finding out at what level we should fish in order to achive the maximum sustainable yield (MSY). This is the level of fishing effort that gives the highest possible yield that can be sustained indefinitely. So we are interested in the yield at the non-zero fixed point $N^* = K\left(1 - \frac{E}{r}\right)$. The yield is the amount of fish that can be harvested per unit time, and it is given at the fixed point by

$$Y = EN^* = EK\left(1 - \frac{E}{r}\right).$$

We can find the maximum of Y by differentiating with respect to E and setting the derivative equal to zero:

$$\frac{dY}{dE} = K\left(1 - \frac{2E}{r}\right) = 0.$$

We can solve this equation for E to find the optimal fishing effort E^*:

$$E^* = \frac{r}{2}.$$

The resulting maximum sustainable yield is

$$MSY = \frac{r}{2} K \left(1 - \frac{r}{2r}\right) = \frac{rK}{4}.$$

1.5.2 Harvesting with fixed quote

Fisheries managers in the Mediterranean are aiming to control the fishing effort in order to achieve the maximum sustainable yield, and we have seen how to model that in the previous section. Fisheries in the North Sea or the North Atlantic however are instead managed by setting the total allowable catch (TAC) for the whole fleet. This is a fixed quota for the total amount of fish that can be harvested in a year. To model that policy we use the logistic equation with harvesting, but we replace the harvesting rate EN by a harvesting quota Q:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - Q. \tag{1.10}$$

This is visualised in Figure 1.7.

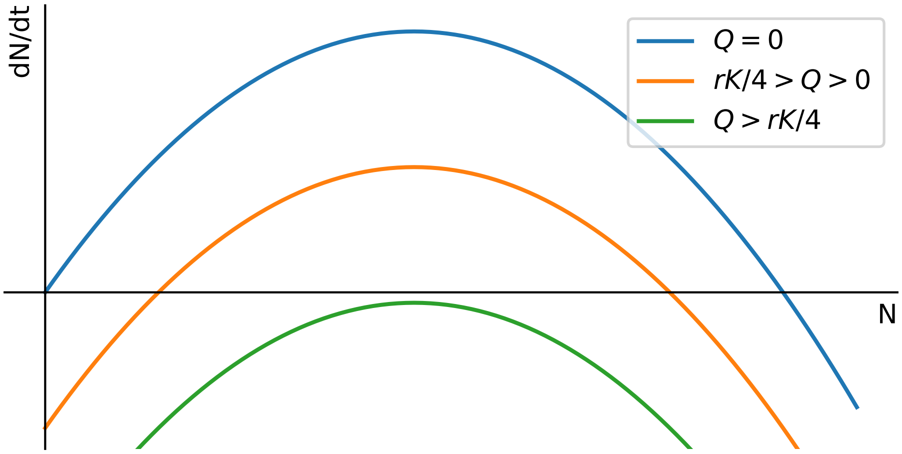

Figure 1.7: Growth rate when harvesting with fixed quota.

We see that any non-zero quota leads to critical depensation, i.e., it introduces a critical threshold below which the population will collapse. This is a well-known problem in fisheries management, and it is the reason why the TAC is set to zero for some fish stocks. As the fishing quota is increased, the critical depensation threshold moves to higher population numbers and the stable steady state moves to lower population numbers. Eventually all non-zero fixed points disappear and the population collapses.

1.6 Exercises

Exercises marked with a * are essential and are to be handed in. Exercises marked with a + are important and you are urged to complete them. Other exercises are optional but recommended.

1.6.0.1 *Sketching solutions

Exercise 1.1. Consider the population model with carrying capacity and Allee effect given by the differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K_0} - 1\right).$$

Here $r > 0$, $K > K_0 > 0$ are constants. Simply by considering the shape of the right hand side, sketch a graph with several solutions for different initial conditions. Choose two initial conditions between 0 and K_0, two initial conditions between K_0 and K and one initial condition larger than K. Note that the graph only needs to be qualitatively correct, similar to the rough sketch for the solutions of the logistic model sketched in the first lecture.

1.6.0.2 +Von Bertalanffy growth

Exercise 1.2. Assume the weight $w(t)$ of an individual fish at time t is governed by the differential equation

$$\frac{dw}{dt} = \alpha\, w^{2/3} - \beta w$$

with initial condition $w(0) = w_0$ (the weight at birth), and where α and β are positive parameters depending on the fish species.

i) Without solving the differential equation, just thinking about fixed points and their stability, determine $\lim_{t\to\infty} w(t)$.

ii) Derive the linear first order ODE for $u = w^{1/3}$ and solve it.

iii) Use the solution for u to find the solution for w.

1.6.0.3 Solving logistic equation

Exercise 1.3. By using separation of variables and partial fractions, solve the logistic equation

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

with initial condition $N(0) = N_0$.

1.6.0.4 * Harvesting with fixed effort

Exercise 1.4. Consider a population $N(t)$ that is described by the by the Gompertz model

$$\frac{dN}{dt} = \alpha N \log\frac{K}{N},$$

where α and K are positive constants. You want to harvest this population, for example by hunting or fishing, with some effort E. The rate at which you harvest individuals (which removes them from the population and hence results in an additional source of death) is proportional to the size of the population: $Y = EN$. This is called the yield. Write down the differential equation for $N(t)$ including this harvesting term. Determine the fixed points and their stability. Find the maximum sustainable yield, i.e., the maximum yield that can be sustained indefinitely.

1.6.0.5 Harvesting with fixed quota

Exercise 1.5. As in Exercise 1.4, consider a population $N(t)$ that is described by the Gompertz model. Imagine that this describes a fish population in a lake where fishing is going to be introduced, and that you are tasked with setting the quota that limits the rate at which the fishers are allowed to take fish out of the lake. The fishers demand that you set the quota to the maximum sustainable level. What is the maximum sustainable quota according to the model? Would it be wise to give in to the demand of the fishers and set the quota at this level?

1.6.0.6 Wasp model

Exercise 1.6. In a colony of the European Hornet there is a single queen that produces all the offspring. It produces two kinds of offspring: workers and reproducers. We'll denote the number of workers alive at time t by $n(t)$ and the number of reproducers by $N(t)$. The workers are responsible for collecting food. They can't breed themselves and they die in the winter. However they are necessary to allow the queen to reproduce because without the food that they are collecting the queen would have nothing to eat. So we need workers. But because they die in winter, they don't help the survival of the colony in the long run. That's where the reproducers come in. They don't do any work, but they can, if they survive the winter, breed in the next spring as new queens.

So the queen now has a strategy of how to proceed: It first of all needs to produce workers, and from time zero to time t_c it only produces workers. We assume that the birth rate is proportional to the number of workers, so that the total birth rate of workers is $rn(t)$ for some constant $r > 0$. The queen then switches to producing only reproducers from time t_c up to the start of winter at time T and we assume that the total birth rate of reproducers is $Rn(t)$ for some constant $R > 0$. We also assume that until the start of winter there are no deaths.

What is the optimal time t_c at which the queen should switch from producing workers to producing reproducers in order to achieve the largest number of producers $N(T)$ at the start of the winter and therefore to the largest number of wasps in the following year.

1.6.0.7 Wasp model with death

Exercise 1.7. In the wasp example from question 1, assume that the worker wasps die at a constant per-capita rate d but the reproducers do not die. Also assume that at time t=0 there is one worker, n(0)=1. Keep the birth rates as in Exercise 1.6. Determine the number of workers $n(t)$ for any time between t_c and T. Determine the number of reproducers at the onset of winter at time T. Derive the optimal time for the switchover time t_c.

2 Discrete-time population models

So far we have assumed that the rate of change of the population number has no explicit time dependence. However births and also deaths often happen on an annual cycle. Many fish have their spawning season in the spring, and many birds breed in the summer and annual plants produce their seed and then die in winter. In this case, the rate of change of the population number is not constant, but depends on the time of the year. We can model this by introducing a time dependence in the birth and death rates. However this will lead to equations that will be difficult to analyse. Instead we can give up on the idea of modelling the population numbers continuously through time and instead only follow how the population changes from year to year.

So we will use models of the form

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

where N_t is the population number at time t and f is some function. Time t now takes on only integer values, and the population number is only defined at these times. This is called a discrete-time model. Given the initial population number N_0, we can calculate the population number at any future time t by iterating the function f: $N_1 = f(N_0)$, $N_2 = f(N_1) = f(f(N_0)), \dots N_t = f(f(\dots f(N_0)\dots))$.

2.1 Exponential model

The simplest discrete-time model is the exponential model

$$N_{t+1} = RN_t \tag{2.2}$$

where $R > 0$ is the growth factor. This is the discrete-time version of the continuous-time exponential model. The solution to this equation is

$$N_t = N_0 R^t. \tag{2.3}$$

It is important to stress that R is not a growth *rate* but a dimensionless growth factor. Comparing the discrete-time solution to the continuous-time solution $N(t) = N_0 \exp(rt)$ we see that they agree at integer times t if we measure time in years and set

$$R = \exp(r \cdot 1 \text{ year}). \tag{2.4}$$

If you are confused by the units, remember that the exponential function is dimensionless, so the argument of the exponential function must be dimensionless. We need the extra factor of 1 year because r is a rate and has dimension 1/time.

The population number grows exponentially with time if $R > 1$ and declines exponentially if $R < 1$. To get more realistic models we again need to introduce a limited carrying capacity.

2.2 Models with limited carrying capacity

Recall how we introduced the logistic model by assuming that the per-capita birth rate declines linearly with the population number and vanishes when the population reaches its carrying capacity. This gave us the equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{2.5}$$

where r is the per-capita growth rate and K is the carrying capacity.

It turns out that there are several models which all deserve to be called the discrete-time logistic model.

2.2.1 Verhulst model

The most famous discrete-time logistic model is the Verhulst model.

$$\begin{aligned} N_{t+1} &= (R_0 + 1)N_t\left(1 - \frac{N_t}{K(R_0+1)/R_0}\right) \\ &= N_t + R_0 N_t\left(1 - \frac{N_t}{K}\right) = f(N_t). \end{aligned} \tag{2.6}$$

Again it is important to stress that R_0 is not a growth *rate* but a dimensionless growth factor.

We have written the model in two alternative forms because the first form makes the analogy with the continuous-time logistic model more obvious, while the second form makes it easier to read off the fixed point.

The fixed point is a value for which $N_{t+1} = N_t$, i.e. a value of N for which the population number does not change from year to year. Thus it is a value N^* for which $f(N^*) = N^*$. Using the second form of the model, we can see easily that the fixed points are $N^* = 0$ and $N^* = K$, so K is the carrying capacity.

A problem with the Verhulst model is that it can give rise to negative population numbers. This is not realistic, so we are motivated to modify the model to prevent this.

2.2.2 Ricker model

The Ricker model is a modification of the Verhulst model that prevents negative population numbers. It is given by

$$N_{t+1} = N_t \, e^{R_0\left(1-\frac{N_t}{K}\right)}. \tag{2.7}$$

By moving the logistic factor inside the exponential, the Ricker model prevents negative population numbers. The fixed points are still $N^* = 0$ and $N^* = K$. Ricker introduced this model to describe salmon populations.

2.2.3 Beverton-Holt model

The Beverton-Holt model is another modification of the Verhulst model which prevents negative population numbers. It is given by

$$N_{t+1} = \frac{RN_t}{1+\frac{R-1}{K}N_t}. \tag{2.8}$$

This has been a very influential model in fisheries science. On the face of it the model does not look very similar to the logistic model, but we will see the relationship when we solve the model. The Beverton-Holt model is one of the rare cases where a non-linear model can be solved exactly. The trick is to make a change of variables from N_t to $u_t = 1/N_t$. Then we have

$$u_{t+1} = \frac{1}{N_{t+1}} = \frac{1+\frac{R-1}{K}N_t}{RN_t} = \frac{u_t}{R} + \frac{R-1}{RK}. \tag{2.9}$$

This is a linear equation for u_t, and linear equations are easy to solve. The easiest way to proceed is to look at the first few terms of the sequence u_t and guess the general form of the solution. We find

$$\begin{aligned}
u_1 &= \frac{u_0}{R} + \frac{R-1}{RK}, \\
u_2 &= \frac{u_0}{R^2} + \frac{R-1}{RK}\left(1+\frac{1}{R}\right), \\
u_3 &= \frac{u_0}{R^3} + \frac{R-1}{RK}\left(1+\frac{1}{R}+\frac{1}{R^2}\right), \\
&\vdots \\
u_t &= \frac{u_0}{R^t} + \frac{R-1}{RK}\left(1+\frac{1}{R}+\frac{1}{R^2}+\ldots+\frac{1}{R^{t-1}}\right).
\end{aligned} \tag{2.10}$$

The sum in the second term is a geometric series. We know the general formula for a geometric series:

$$1 + x + x^2 + \ldots + x^{t-1} = \frac{1-x^t}{1-x}. \tag{2.11}$$

We can use this with $x = 1/R$ to sum terms in the second term. We find

$$u_t = \frac{u_0}{R^t} + \frac{R-1}{RK}\frac{1-(1/R)^t}{1-1/R}.$$

We simplify this a bit and bring everything on the same denominator.

$$u_t = \frac{u_0}{R^t} - \frac{(1/R)^t - 1}{K} = \frac{Ku_0 - 1 + R^t}{KR^t}. \tag{2.12}$$

We can now change back to $N_t = 1/u_t$ to find the solution to the Beverton-Holt model. We find

$$\begin{aligned} N_t = \frac{1}{u_t} &= \frac{KR^t}{Ku_0 - 1 + R^t} \\ &= \frac{K/u_0}{KR^{-t} - R^{-t}/u_0 + 1/u_0} \\ &= \frac{KN_0}{N_0 + (K - N_0)R^{-t}}. \end{aligned} \tag{2.13}$$

This is the solution to the Beverton-Holt model. Comparing this to the solution of the continuous-time logistic model

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)\exp(-rt)} \tag{2.14}$$

we see that they agree at integer times t if we measure time in years and set $R = \exp(r \cdot 1 \text{ year})$.

2.3 Stability and Cobwebs

We now want to study the stability of the fixed points in discrete-time models. As discussed, fixed points N^* satisfy the equation $N^* = f(N^*)$. We study the stability of the fixed points by looking at the sequence N_t for t close to the fixed point. That means we write $N(t) = N^* + n_t$ for $n_t << 1$. We then have

$$N_{t+1} = N^* + n_{t+1} = f(N_t) = f(N^* + n_t) = f(N^*) + f'(N^*)n_t + ... \tag{2.15}$$

where we have used the Taylor expansion of f around N^*. Because N^* is a fixed point, we have $f(N^*) = N^*$. Thus we find that

$$n_{t+1} \approx f'(N^*)n_t \tag{2.16}$$

where we neglected the higher order terms in the Taylor expansion. This is a linear equation for n_t that we know how to solve:

$$n_t = n_0(f'(N^*))^t. \tag{2.17}$$

So we have found that:

- If $|f'(N^*)| < 1$, then n_t will decrease with time and the fixed point is stable.
- If $|f'(N^*)| > 1$, then n_t will increase with time and the fixed point is unstable.

If $|f'(N^*)| = 1$, then we cannot say anything about the stability of the fixed point from this analysis.

In the continuous-time case we also had a graphical way to see the stability of fixed points. We will now introduce a graphical method for studying the stability of fixed points in discrete-time models, called the cobweb method.

We plot the function $f(N_t)$ and the line $N_{t+1} = N_t$. The fixed points are the intersection points of the function and the line. We then draw the graph of the sequence N_t by starting at the initial population number N_0 and iterating the function $f(N_t)$ to find N_1, then iterating the function again to find N_2, and so on. The graph of the sequence N_t is called the cobweb. The stability of the fixed points can be read off from the cobweb. If the cobweb spirals into the fixed point, as shown in Figure 2.1, then the fixed point is stable. If the cobweb spirals out of the fixed point, as shown in Figure 2.2, then the fixed point is unstable. You have to press the play button below the figures to see the cobweb diagrams in action.

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Figure 2.1: Cobweb diagram for a stable fixed point.

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Figure 2.2: Cobweb diagram for an unstable fixed point.

The oscillatory nature of the sequence N_t, hopping from one side of the fixed point to the other, that creates the cobweb pattern is due to the fact that the slope of f is negative at the fixed point. The graphical method for visualising the iterations will work also when the slope is positive at the fixed point, but it will not look like a cobweb. Figure 2.3 shows the cobweb for a stable fixed point with positive slope.

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Figure 2.3: Cobweb diagram for a fixed point with positive slope.

2.4 Discrete-time harvesting model

We will now look at an example of a discrete-time model with harvesting and apply the techniques we have learned. The model has the standard discrete-time model form $N_{t+1} =$

$f(N_t)$, where f in our example is

$$f(N) = \frac{bN^2}{1+N^2} - EN.$$

The constant $b > 2$ determines the growth rate of the population and the harvesting rate is determined by the harvesting effort E.

We start by studying the model without harvesting, so we set $E = 0$ for now. As usual, we start by looking at the steady states of the model. The fixed points are the solutions to the equation

$$N^* = \frac{b\,{N^*}^2}{1+{N^*}^2}.$$

There is the obvious solution $N^* = 0$. We can then find the non-zero solutions by dividing both sides by N^* and multiply them by $1 + {N^*}^2$ to get the equation

$$1 + {N^*}^2 = bN^*.$$

This is a quadratic equation for N^*, which we could rewrite in the more convential form

$${N^*}^2 - bN^* + 1 = 0.$$

The solutions to this equation are

$$N^*_\pm = \frac{b \pm \sqrt{b^2-4}}{2}.$$

The solutions are real if $b^2 - 4 \geq 0$, i.e. if $b \geq 2$, which we have stipulated earlier. Both solutions are positive.

We now have enough information to draw a good sketch to understand the dynamics of the model. We can draw the function $f(N)$ and the line $N_{t+1} = N_t$. It may not be immediately obvious what the sketch of $f(N) = bN^2/(1+N^2)$ looks like. We'll reason ourselves through this in steps:

- First let us consider what happens near $N = 0$. There the function is approximately $f(N) \approx bN^2$. This is a parabola that opens upwards. The function is zero at $N = 0$ and increases quadratically with N.
- Next we consider what happens as N becomes large. There the function is approximately $f(N) \approx b$. So the graph has a horizontal asymptote at $y = b$.
- We know that in between there are two fixed points. That means the graph needs to cross the diagonal line $y = N$ twice.
- Finally we observe that the function is monotonically increasing.

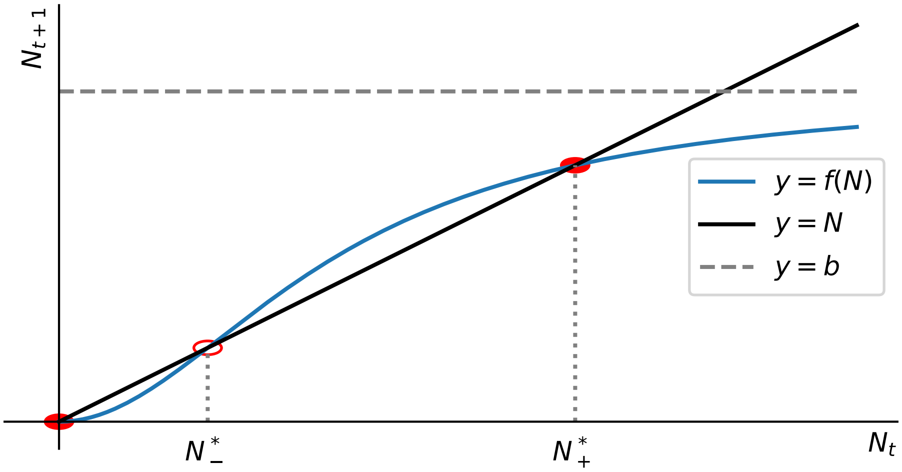

Figure 2.4: Graph of the function $f(N) = \frac{bN^2}{1+N^2}$.

If we now draw something that has all these features, we will have a sufficiently good sketch of the function for our purpose of understanding the dynamics of the model. We will necessarily end up with something that qualitatively looks like the graph in Figure 2.4.

Using our cobweb technique, or simply looking at the slope of f at the fixed points, we can easily convince ourselves that the extinction fixed point is stable, the smaller non-zero fixed point N_-^* is unstable and the larger fixed point N_+^* is stable. in Figure 2.4 we have indicated the stable fixed points by solid circles and the unstable fixed points by open circles. So when the population number is larger than N_-^* it will grow towards N_+^*, and when it is smaller than N_-^* it will go extinct. So this model exhibits a strong Allee effect with critical depensation. N_-^* is the smallest viable population size.

We can now add harvesting to the model. The extra term in the function $f(N)$ is $-EN$. This lowers the graph of $f(N)$ by an amount that grows linearly with N. This is illustrated in Figure 2.5.

We see that as the harvesting effort E increases, the two fixed points move closer together. At a critical value E_c the two fixed points merge and disappear. The population number will then go extinct for all initial population numbers.

Let us find the critical value E_c. For that we first determine the location of the fixed points in the presence of harvesting. So we solve the equation

$$N^* = \frac{b\,{N^*}^2}{1+{N^*}^2} - EN^*.$$

Again this has a solution $N^* = 0$. We can then find the non-zero solutions by dividing both

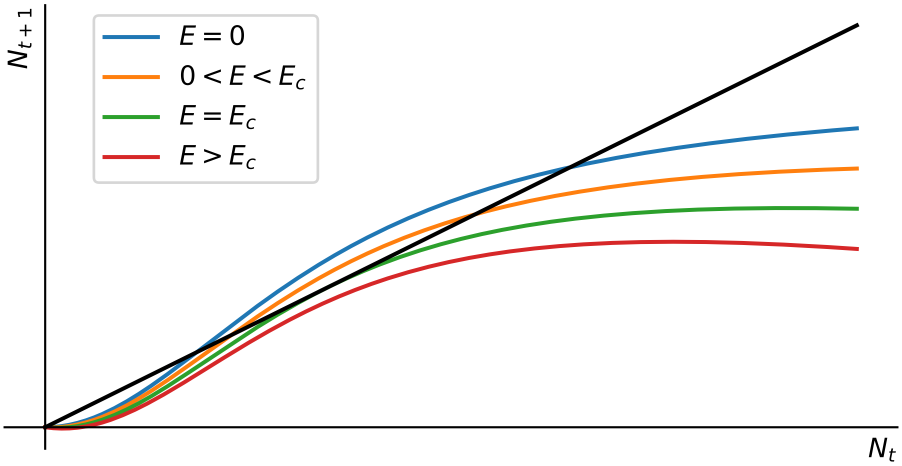

Figure 2.5: Graph of the function $f(N) = \frac{bN^2}{1+N^2} - EN$.

sides by N^* and multiply them by $1 + {N^*}^2$ to get the equation

$$(1+E){N^*}^2 - bN^* + 1 + E = 0.$$

This is solved by

$$N^*_\pm = \frac{\frac{b}{1+E} \pm \sqrt{\left(\frac{b}{1+E}\right)^2 - 4}}{2}.$$

We see that these solutions are real only if $\left(\frac{b}{1+E}\right)^2 - 4 \geq 0$, i.e., if $E < \frac{b-2}{2}$. Thus the critical effort is $E_c = \frac{b-2}{2}$. Fishing above this level will lead to extinction of the population. But even fishing just near this level is risky because the population number will be very close to the minimum viable population and a small disturbance could lead to extinction.

2.5 Bifurcations

A bifurcation is a change in the existence and/or stability of the fixed points as the parameters of the model are varied.

You have met bifurcations in continuous-time models already in your Dynamical Systems module. You have seen there that in one-dimensional systems described by a single ODE there are three different types of bifurcation: saddle-node, pitchfork, transcritical. The same types of bifurcations can occur in discrete-time models but there is also one more type: the period-doubling bifurcation.

We have already seen a bifurcation in the discrete-time harvesting model. The bifurcation was a saddle-node bifurcation, where two fixed points merge and disappear. This is also sometimes referred to as a tangent bifurcation, because at the critical value of the parameter the curve $y = f(N)$ is tangent to the line $y = N$ at the fixed point.

In the period-doubling bifurcation the stability of the fixed point changes as the parameter is varied. The fixed point changes from stable to unstable, and at the same time a stable period-2 orbit appears, where the population number oscillates between two values. The period-2 orbit is stable in the sense that if the population number is close to the orbit it will converge to the orbit. This kind of bifurcation can obviously not arise in one-dimensional continuous-time models because a continuous orbit can not move from one side of a fixed point to the other.

In the lectures we drew diagrams illustrating three of the four types of bifurcations. For a discussion of all four types in a similar fashion, you can view the following video.

2.6 Exercises

Exercises marked with a * are essential and are to be handed in. Exercises marked with a + are important and you are urged to complete them. Other exercises are optional but recommended. The exercise marked with an o will be worked through in the problems class.

2.6.0.1 + Verhulst model

Exercise 2.1. For some choices of the parameters, the Verhulst model

$$N_{t+1} = rN_t \left(1 - \frac{N_t}{K}\right) \tag{2.18}$$

can lead to negative population numbers even when initially starting with a positive population below its carrying capacity. Derive the condition on the parameters for this to happen. One good way to approach this is to think about what the cobweb diagram would have to look like for such a scenario.

2.6.0.2 * Ricker model

Exercise 2.2. Find the fixed points in the Ricker model

$$N_{t+1} = N_t\, e^{R_0\left(1 - \frac{N_t}{K}\right)}. \tag{2.19}$$

and investigate their stability. Do this both analytically and by drawing cobweb diagrams.

2.6.0.3 Beverton-Holt model

Exercise 2.3. Find the fixed points in the Beverton-Holt model

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K} N_t}. \tag{2.20}$$

and investigate their stability. Do this both analytically and by drawing cobweb diagrams.

2.6.0.4 o House finches

Exercise 2.4. *[Note: in this problem we combine a continuous time model for the dynamics within a single year with a discrete model for the dynamics from one year to the next. The subscript $t \in \mathbb{Z}$ refers to the discrete year whereas $\tau \in \mathbb{R}$ will indicate the continuous time within a single year.]*

A population of house finches resides in an isolated region in North America. In this problem you want to find out about the long-term prospects for the population.

Each year the males and females begin their search for mates at the beginning of winter with a combined population number N_t in year t, and form P_t breeding pairs by the end of this search period, the start of the breeding season.

The mate search period lasts from within-year time $\tau = 0$ to the end of the search period at within-year time $\tau = T$. Assume that there is a 1:1 sex ratio and that males $M(\tau)$ and females $F(\tau)$ locate one another randomly to make a pair at rate σ, such that the number $M(\tau)$ of males that are not in a pair at time τ satisfies

$$\frac{dM}{d\tau} = -\sigma\, M\, F$$

and similarly the number F of females that are not in a pair at time τ satisfies

$$\frac{dF}{d\tau} = -\sigma\, M\, F.$$

You are given that the number of breeding pairs that establish a nest and breed successfully is $G(P_t)P_t$, where the fraction $G(P_t)$ takes the particular form

$$G(P_t) = \frac{1}{1 + P_t/\delta},$$

where δ represents the density of available nesting sites. Each pair that reproduces successfully has a mean number c of offspring.

The probability that a bird will survive from one year to the next is s.

a) Show that the number $n(\tau) = M(\tau) + F(\tau)$ of birds *not* in a pair is governed by

$$\frac{dn}{d\tau} = -\frac{\sigma}{2} n^2, \quad n(0) = N_t.$$

b) Using the above, show that the number $n(T)$ of birds that have not found a mate at the start of the breeding season in year t is

$$n(T) = \frac{r\, N_t}{r + 2N_t}$$

where N_t is the number of birds at the start of the season in that particular year and where $r = 4/(\sigma T)$.

c) Explain why the number of pairs $P(\tau)$ is governed by

$$\frac{dP}{d\tau} = -\frac{1}{2}\frac{dn}{d\tau}, \quad P(0) = 0.$$

d) Use the above to show that the number of breeding pairs at the start of the breeding season in year t is

$$P_t := P(T) = \frac{N_t^2}{r + 2N_t}.$$

e) Show that the population N_{t+1} at the beginning of winter in year $t + 1$ is given by

$$N_{t+1} = s\, N_t + \frac{c\, N_t^2}{r + 2N_t + N_t^2/\delta}. \tag{2.21}$$

f) Find the realistic steady states of the model in Eq. 2.21 for the case that

$$\frac{c}{1-s} - 2 \geq \sqrt{\frac{4r}{\delta}}.$$

g) Draw a cobweb diagram to illustrate the stability of the steady states in the case that there are two positive steady states. Label key features of the curves.

h) What type of bifurcation occurs when there is equality in the condition in part f)?

2.6.0.5 Another model

Exercise 2.5. Consider the discrete time model

$$N_{t+1} = \frac{rN_t}{1 + (N_t/K)^b} \tag{2.22}$$

where r, b and K are positive parameters with $b > 1$. Show that the model has two steady states. Investigate the stability of the extinction steady state. Show that the non-trivial (non-zero) steady state can lose stability through a period doubling bifurcation at $b = 2r/(r-1)$, or a tangent bifurcation at $r = 1$.

3 Sex-structured population models

Up to this point we have completely ignored that there are differences between the individuals making up a population. So we ignored all structure within a population. We will now start to remedy this. In this chapter we will start with the simplest possible structure by splitting the population into males and females. Keeping track of both the abundance of males and of females separately makes sense because

- birth and death rates depend on the sex
- both a male and a female are needed to produce offspring

So in this chapter instead of just looking at a single function $N(t)$ giving the total population number, we will look at two functions $M(t)$ and $F(t)$ giving the number of males and females respectively. We again describe them by differential equations that capture that the numbers can decrease due to deaths and increase due to births.

$$\begin{aligned} \frac{dF}{dt} &= -\mu_F F + b_F\,\varphi(F,M) \\ \frac{dM}{dt} &= -\mu_M M + b_M\,\varphi(F,M). \end{aligned} \tag{3.1}$$

Here μ_F and μ_M are the death rates of females and males respectively. The rate of births now depends both on the number of females and the number of males, because both males and females are needed to produce offspring. We formulate that dependence on the number of females and the number of males as a function $\varphi(F,M)$. The functional dependence of the rate on F and M is the same for births of females and for births of males, but the extra factors b_F and b_M account for the differences between female and male birth rates.

3.1 Symmetric model

We first consider the simpler situation where birth and mortality rates are the same for males and females:

$$\mu_F = \mu_M = \mu, \quad b_F = b_M = b. \tag{3.2}$$

In this case we can get a simple ODE for the difference $F - M$ between the number of females and males:

$$\frac{d(F-M)}{dt} = -\mu(F-M). \tag{3.3}$$

This equation has the solution

$$F(t) - M(t) = (F(0) - M(0))e^{-\mu t}. \tag{3.4}$$

This means that the difference decreases exponentially over time. In particular, if we start with equal number females and males then the they will stay equal for all times.

To make further progress we need to make a concrete choice for the function $\varphi(F, M)$. We will consider the simplest possible choice

$$\varphi(F, M) = F\,M. \tag{3.5}$$

This choice is motivated by the fact that both a male and a female is needed to produce offspring. So the rate of births should increase if there are more females but also when there are more males. The simplest way to capture this is to multiply F and M.

A simple thing to note is that if $M(0) = 0$ then $M(t) = 0$ for all times. Then the number of females satisfies

$$\frac{dF}{dt} = -\mu F. \tag{3.6}$$

This has the solution

$$F(t) = F(0)e^{-\mu t}. \tag{3.7}$$

So if there are no males, the females have to die out as well.

We noted above that if initially $F(0) = M(0)$ then $F(t) = M(t)$ for all times. In that case the number of females satisfies

$$\frac{dF}{dt} = -\mu F + bF^2. \tag{3.8}$$

This is illustrated in Figure 3.1.

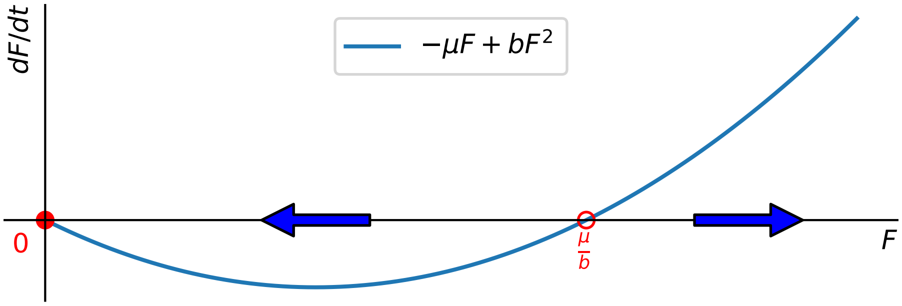

Figure 3.1: Quadratically increasing growth rate.

Note that the non-zero fixed point at $F = \mu/b$ is unstable. If $F(0) < \mu/b$ then the females and hence the males go extinct. If $F(0) > \mu/b$ then the females and hence the males grow rapidly. In fact, they grow so rapidly that the population size becomes infinite in finite time, as we can see when we solve the ODE.

We can solve Eq. 3.8 by separation of variables:

$$\int \frac{dF}{-\mu F + bF^2} = \int dt.$$

We could do the integral on the left hand side by partial fractions. But to see the problem of the population size becoming infinite in finite time it is sufficient to consider the case of $F >> 1$ where we can neglect the term $-\mu F$ in the denominator. Then we get

$$\int_{F(0)}^{F(t)} \frac{dF}{F^2} = \frac{1}{F(0)} - \frac{1}{F(t)} = \int_0^t b\, d\tilde{t} = bt.$$

and hence

$$F(t) = \frac{1}{1/F(0) - bt}. \tag{3.9}$$

So the population size becomes infinite at time $t = 1/(bF(0))$. So clearly this model is not ecologically sensible.

3.2 Female-limited reproduction

We will now consider a model where the birth rate depends only on the number of females:

$$\varphi(F, M) = F. \tag{3.10}$$

This is clearly a strong simplification but is reasonable for populations where there are always more than enough males to fertilize all females.

With this simplification, the ODE for F becomes

$$\frac{dF}{dt} = -\mu_F F + b_F F = (-\mu_F + b_F)F. \tag{3.11}$$

This has the solution

$$F(t) = F(0)e^{(-\mu_F + b_F)t}. \tag{3.12}$$

We can now use this in the equation for M:

$$\frac{dM}{dt} = -\mu_M M + b_M F = -\mu_M M + b_M F_0\, e^{(-\mu_F + b_F)t}. \tag{3.13}$$

(We have used $F(0) = F_0$ to make the equation more readable.) This is a first-order linear ODE with time-dependent inhomogeneity. We can solve it by the method of integrating factors. We first rewrite it in the form

$$\frac{dM}{dt} + \mu_M M = b_M F_0\, e^{(-\mu_F + b_F)t} \tag{3.14}$$

and then observe that the left-hand side is proportional to a total derivative:

$$\frac{dM}{dt} + \mu_M M = \frac{d}{dt}(e^{\mu_M t} M) e^{-\mu_M t} \tag{3.15}$$

Thus after multiplying both sides by $e^{\mu_M t}$ we get

$$\frac{d}{dt}(e^{\mu_M t} M) = b_M F_0 \, e^{(\mu_M - \mu_F + b_F)t}. \tag{3.16}$$

We can now integrate both sides to get

$$e^{\mu_M t} M(t) - e^{\mu_M t} M_0 = \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(\mu_M - \mu_F + b_F)t} - 1 \right). \tag{3.17}$$

This can be solved for $M(t)$:

$$M(t) = M_0 e^{-\mu_M t} + \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(-\mu_F + b_F)t} - e^{-\mu_M t} \right). \tag{3.18}$$

We have been able to fully solve this model. At this stage it is worth checking that the dependence of the solution on the parameters and on the initial conditions is reasonable.

Next let us take a look at the sex ratio as $t \to \infty$. We find

$$\begin{aligned} s = \lim_{t\to\infty} \frac{M(t)}{F(t)} &= \lim_{t\to\infty} \frac{M_0 e^{-\mu_M t} + \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(-\mu_F + b_F)t} - e^{-\mu_M t} \right)}{F_0 e^{(-\mu_F + b_F)t}} \\ &= \frac{b_M}{b_F - \mu_F + \mu_M}. \end{aligned} \tag{3.19}$$

Just for fun let us check what this model would predict for the sex ratio in the population of the US, using data about births and deaths from 1992.

$$\begin{aligned} \mu_F &= 807/100,000/\text{year}, \quad & \mu_M &= 902/100,000/\text{year}, \\ b_F &= 1480/100,000/\text{year}, \quad & b_M &= 1550/100,000/\text{year}. \end{aligned} \tag{3.20}$$

Substituting these values into Eq. 3.19 we get $s \approx 0.9841$. The actual ratio in the US in 1992 was 0.953. Of course this is not to be taken seriously. To start with, human populations are not solely female-limited. But there are many other criticisms that can be made of this model when applied to human populations.

3.3 Harmonic mean model

We will now consider a model where the birth rate depends on both the number of males and the number of females. We choose to set $\varphi(F, M)$ to a weighted average of F and M:

$$\varphi(F, M) = D\,M + (1 - D)F \tag{3.21}$$

with some suitably chosen weighting factor D. We want to keep the feature that when there is an overabundance of males, then the birth rate is limited mostly by the number of females and vice versa. So we choose $D = M/(F+M)$, which is the relative abundance of males. This makes $1 - D = F/(F + M)$, which is the relative abundance of females. This gives

$$\varphi(F, M) = \frac{M}{F+M}F + \frac{F}{F+M}M = \frac{2FM}{F+M}. \tag{3.22}$$

We can now use this in the ODEs for F and M:

$$\begin{aligned} \frac{dF}{dt} &= -\mu_F F + b_F \frac{2FM}{F+M}, \\ \frac{dM}{dt} &= -\mu_M M + b_M \frac{2FM}{F+M}. \end{aligned} \tag{3.23}$$

We will not try to solve this coupled system of nonlinear ODEs. Instead we will directly look at the long-term sex ratio. We can derive an ODE for the sex ration M/F:

$$\frac{d}{dt}\frac{M}{F} = \frac{\frac{dM}{dt}F - M\frac{dF}{dt}}{F^2}. \tag{3.24}$$

Because we are only interested in the long-term behavior we look at the fixed point of this equation, hence we set the left-hand side to zero. We then get

$$\frac{dM}{dt}F - M\frac{dF}{dt} = 0. \tag{3.25}$$

We can now use the ODEs for F and M to get

$$\frac{dM}{dt}F - M\frac{dF}{dt} = \left(-\mu_M M + b_M \frac{2FM}{F+M}\right) F - M\left(-\mu_F F + b_F \frac{2FM}{F+M}\right) = 0. \tag{3.26}$$

We multiply by $F + M$ and divide by FM to get

$$-\mu_M(F + M) + 2b_M F + \mu_F(F + M) - 2b_F M = 0. \tag{3.27}$$

Collecting terms proportional to F and M we get

$$(-\mu_M + 2b_M + \mu_F)F = (\mu_M - \mu_F + 2b_F)M. \tag{3.28}$$

We can now solve this equation for the asymptotic sex ratio

$$s = \lim_{t\to\infty} \frac{M(t)}{F(t)} = \frac{\mu_M - \mu_F + 2b_F}{-\mu_M + 2b_M + \mu_F}. \tag{3.29}$$

Even though the sex ratio approaches a fixed point as $t \to \infty$, the population numbers themselves do not. Once the sex ratio has settled to the value s, we have $M = sF$ and we can use this to get a single ODE for F:

$$\begin{aligned} \frac{dF}{dt} &= -\mu_F F + b_F \frac{2MF}{F+M} \\ &= -\mu_F F + \frac{2s}{s+1} b_F F. \end{aligned} \tag{3.30}$$

This is a linear equation and has the solution

$$F(t) = F_0 e^{(-\mu_F + \frac{2s}{s+1} b_F)t}. \tag{3.31}$$

Similarly we obtain

$$M(t) = M_0 e^{(-\mu_M + \frac{2}{s+1} b_M)t}. \tag{3.32}$$

So we have an exponential growth model for both F and M, but the exponent has a modified birth rate that takes the sex ratio into account.

To arrive at more realistic models we should introduce a carrying capacity into the model.

3.4 Exercises

3.4.0.1 * Geometric mean sex-structured model

Exercise 3.1. Consider the sex-structured population model

$$\frac{dF}{dt} = -\mu_F F + b_F \phi(F, M), \quad \frac{dM}{dt} = -\mu_M M + b_M \phi(F, M),$$

where $F(t)$ denotes the number of females and $M(t)$ the number of males and μ_F, μ_M, b_F, b_M are positive constants. Make the choice

$$\phi(F, N) = \sqrt{FM}.$$

Determine the asymptotic sex ratio

$$s = \lim_{t\to\infty} \frac{M(t)}{F(t)}?$$

What is the numerical value of s when $\mu_F = 2, \mu_M = 1, b_F = 1/2, b_M = 3/2$ per year?

3.4.0.2 Dominance structure

Exercise 3.2. We consider a population of primates and split this into three components:

M: dominant (alpha) males,

F: dominant (alpha) females,

Q: subordinate males or females.

Only alpha males and alpha females mate to reproduce offspring. The subordinate individuals are prevented from mating. The alpha females are too engaged with looking after their young to gather food and instead rely on the food gathered by the subordinate individuals. We propose to model this with the equations

$$\begin{aligned}\frac{dF}{dt} &= b_F F - \frac{\mu_F F}{Q} F,\\ \frac{dM}{dt} &= b_M F - \mu_M M,\\ \frac{dQ}{dt} &= b_Q F - \mu_Q Q,\end{aligned}$$

where $b_F > \mu_F, b_M > \mu_M$ and $b_Q > \mu_Q$ are all positive constants.

(a) One of the terms incorporates a ratio of different components. Describe what this might be intended to model.

(b) Derive an ODE for the ratio F/Q. Either by recognising the ODE for F/Q as equivalent to one for which the solution was given in the lecture notes, or by integrating the ODE, give the solution for F/Q as a function of time, with initial condition $F(0) = F_0, Q(0) = Q_0$.

(c) By using your solution from the previous part or by other means, show that as $t \to \infty$ the ratio between alpha females and subordinate individuals goes to

$$\frac{b_F + \mu_Q}{b_Q + \mu_F}.$$

(d) Derive an expression for the long-term alpha female to alpha male ratio $R = \lim_{t\to\infty} F/M$ in terms of the model parameters and show that it is positive.

(e) Describe a limitation of the birth terms in the model and suggest improved expressions.

4 Age-structured population model

4.1 Continuous time model

In the previous chapter we structured the population by a discrete variable, the sex of the individuals. This gave rise to a system of coupled ODEs, one ODE for each class of individuals. In this section we will structure the population by a continuous variable, the age of the individuals. This will give rise to a partial differential equation (PDE) for the age-dependent population density. We will solve this PDE and study the long-term behaviour of the population and its age distribution.

So instead of describing the population just by the total number of individuals $N(t)$, we will describe it by the density $n(t, a)$ of individuals at age a. The total number $N(t)$ of individuals in the population is then given by the integral of $n(t, a)$ over all ages. More generally, the total number of individuals in the population that are between age a_1 and a_2 is given by the integral of $n(t, a)$ over the interval $[a_1, a_2]$. You are familiar with the concept of density from probability theory, where continuous random variables are described by a probability density rather than a probability. You may also be familiar with the concept from physics, where the density of a material describes how the mass is distributed over space. Here, the density $n(t, a)$ describes how the individuals are distributed over ages.

To derive the PDE for the age-structured population density, we consider how the density changes over an infinitesimal time interval δt due to deaths:

$$n(t + \delta t, a + \delta t) = n(t, a) - \mu(a) n(t, a) \delta t. \tag{4.1}$$

Note how we had to take into account that over the time interval δt the age of the individuals has increased by δt. We now Taylor-expand the left-hand side around t and a:

$$n(t + \delta t, a + \delta t) = n(t, a) + \frac{\partial n}{\partial t} \delta t + \frac{\partial n}{\partial a} \delta t + \mathcal{O}(\delta t^2). \tag{4.2}$$

Cancelling the $n(t, a)$ terms on both sides and dividing by δt gives us the PDE for the age-structured population density:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a) n. \tag{4.3}$$

This equation captures the effect of individuals aging and dying, but it does not capture how they are born. Individuals are born with age 0. These offspring can be produced by parents of any ages, but with an age-dependent rate $b(a)$. This gives

$$n(t,0) = \int_0^\infty b(a) n(t,a)\, da. \tag{4.4}$$

This is a boundary condition for the PDE. It says that the density of individuals at age 0 is given by the total number of offspring produced by the individuals of all ages.

We will now solve the PDE for the age-structured population density by the method of separation of variables. We will make the Ansatz $n(t,a) = f(t)r(a)$. You have seen this trick for finding solutions of linear, homogeneous PDEs in other modules, like Waves and Fluids for example. Substituting this Ansatz into the PDE gives

$$f'(t)r(a) + f(t)r'(a) = -\mu(a) f(t) r(a). \tag{4.5}$$

Dividing by $f(t)r(a)$ gives

$$\frac{f'(t)}{f(t)} + \frac{r'(a)}{r(a)} = -\mu(a). \tag{4.6}$$

We now collect all terms that depend on t on the left-hand side and all terms that depend on a on the right-hand side:

$$\frac{f'(t)}{f(t)} = -\frac{r'(a)}{r(a)} - \mu(a). \tag{4.7}$$

Because the left-hand side is independent of a and the right-hand side is independent of t, both sides must be equal to a constant. We introduce the separation constant γ and write

$$\frac{f'(t)}{f(t)} = \gamma, \quad \frac{r'(a)}{r(a)} = -\gamma - \mu(a). \tag{4.8}$$

These are now linear ODEs and hence easy to solve. The first ODE has the solution

$$f(t) = f(0) e^{\gamma t} \tag{4.9}$$

and the second ODE has the solution

$$r(a) = r(0) \exp\left(-\int_0^a \mu(a')\, da' - \gamma a\right). \tag{4.10}$$

So altogether we have the population density

$$n(t,a) = n(0,0) e^{\gamma t} \exp\left(-\int_0^a \mu(a')\, da' - \gamma a\right), \tag{4.11}$$

where $n(0,0) = f(0)r(0)$ is the initial density of individuals at age 0.

So far we don't yet know the value of the separation constant γ. This will be determined by the boundary condition. If we substitute the solution Eq. 4.11 into the boundary condition Eq. 4.4, we get

$$n(0,0)e^{\gamma t} = \int_0^\infty b(a)n(0,0)e^{\gamma t}\exp\left(-\int_0^a \mu(a')\,da' - \gamma a\right)\,da. \tag{4.12}$$

We can cancel the common factor $n(0,0)e^{\gamma t}$ on both sides to get the condition

$$1 = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(a')\,da' - \gamma a\right)\,da = \phi(\gamma). \tag{4.13}$$

We have introduced the shorthand notation $\phi(\gamma)$ for the integral on the right-hand side. The condition Eq. 4.12 is a transcendental equation for γ. We cannot solve it analytically for γ. But we observe that ϕ is a monotonically decreasing function of γ. This observation alone allows us to make a statement about the sign of γ. According to Eq. 4.9 the sign of γ determines whether the total population grows expnentially or goes extinct.

If γ is positive, then the monotonicity of ϕ tells us that $\phi(0) > \phi(\gamma) = 1$ and vice versa. Conversely, if γ is negative, then $\phi(0) < \phi(\gamma) = 1$ and vice versa. So to determine the sign of γ we only have to look at the value of

$$\phi(0) = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(a')\,da'\right)\,da. \tag{4.14}$$

- If $\phi(0) > 1$, then $\gamma > 0$ and the population grows exponentially.
- If $\phi(0) < 1$, then $\gamma < 0$ and the population goes extinct.

This result actually has a very intuitive explanation. The factor

$$\exp\left(-\int_0^a \mu(a')\,da'\right) =: l(a) \tag{4.15}$$

is the probability that an individual survives up to age a. Therefore $\phi(0)$ is the expected number of offspring produced by an individual during its lifetime. If this number is greater than 1, then the population grows exponentially. If it is less than 1, then the population goes extinct.

4.2 Discrete time model

In the continuous-time age-structured population model discussed in the previous section we had assumed that births take place continuously through time. If however reproduction is an annual event, taking place in a short breeding season for example, then it is more natural to model the population in discrete time. We will now derive the discrete-time version of the age-structured population model and then study the long-term behaviour of the population and its age distribution.

4.2.1 Model description

Both time and age will be discrete variables. We will take them to be integers counting years. We will describe the population by the numbers $N_{a,t}$ of individuals of age a at time t. The total number N_t of individuals in the population at time t is then given by the sum of $N_{a,t}$ over all ages.

The parameters of our model will be the probabilities S_a of surviving from age $a-1$ to age a and the number of offspring b_a produced by an individual when they reach age a. Because the number of individuals at age a at time $t+1$ is the number of individuals that a year earlier were at age $a-1$ and have survived to age a, we have

$$N_{a,t+1} = S_a N_{a-1,t}. \tag{4.16}$$

When individuals reach age a, they each produce b_a offspring. The total number of offspring produced at time t is therefore given by

$$N_{0,t} = \sum_{a=1}^{\infty} b_a N_{a,t}. \tag{4.17}$$

This is a boundary condition for the discrete-time model. It says that the number of individuals at age 0 at time t is given by the total number of offspring produced by the individuals of all ages at time t. This is the discrete-time analogue of the boundary condition Eq. 4.4 for the continuous-time model.

Note that in Eq. 4.17 both sides of the equation are at time t. That is because reproduction is taken to happen instantaneously at time t. It is conventional to use Eq. 4.16 to rewrite the boundary condition Eq. 4.17 as an equation for $N_{0,t+1}$:

$$N_{0,t+1} = \sum_{a=1}^{\infty} b_a N_{a,t+1} = \sum_{a=1}^{\infty} b_a S_a N_{a-1,t} = \sum_{a=1}^{\infty} F_{a-1} N_{a-1,t}, \tag{4.18}$$

where we have introduced the fecundity $F_a := b_{a+1} S_{a+1}$.

Eq. 4.16 and Eq. 4.18 are the equations for the discrete-time age-structured population model. They are a system of coupled difference equations, one equation for each age class. We would like to solve them to determine the numbers $N_{a,t}$ of individuals at each age at each time. Notice that Eq. 4.16 looks very simple and we could use it to determine $N_{a,t}$ for $a = 1, 2, 3, \ldots$ in terms of $N_{0,t}$,

$$\begin{aligned} N_{a,t} &= S_a N_{a-1,t} = S_a S_{a-1} N_{a-2,t} = \cdots \\ &= S_a S_{a-1} \cdots S_1 N_{0,t} = l_a N_{0,t}, \end{aligned} \tag{4.19}$$

where we used that the product $S_a S_{a-1} \cdots S_1$ is the probability of surviving from age 0 to age a, which we denote by l_a. However Eq. 4.18 spoils the game because it tells us that we won't know $N_{0,t}$ until we know $N_{a,t}$ for all ages a. This is a typical feature of age-structured population models. The number of individuals at age 0 at time t depends on the number of individuals at all other ages at time t. Solving both Eq. 4.16 and Eq. 4.18 together is a non-trivial task.

4.2.2 Stable age distribution

In analogy to the continuous-time model, we will now look for a solution of the form

$$N_{a,t} = \lambda^t r(a) \tag{4.20}$$

This is a solution in which the age distribution $r(a)$ remains stable from one year to the next, but the total population grows or shrinks by a factor λ each year. This means in particular that for this solution $N_{a,t+1} = \lambda N_{a,t}$ for all ages a. For $a = 1$ this gives

$$N_{1,t+1} = \lambda N_{1,t} = S_1 N_{0,t} \tag{4.21}$$

and hence

$$N_{1,t} = \frac{S_1}{\lambda} N_{0,t}. \tag{4.22}$$

Similarly we can express $N_{2,t}$ in terms of $N_{0,t}$:

$$N_{2,t} = \frac{S_2}{\lambda} N_{1,t} = \frac{S_1 S_2}{\lambda^2} N_{0,t}. \tag{4.23}$$

We can continue this process to express $N_{a,t}$ in terms of $N_{0,t}$:

$$N_{a,t} = \frac{S_1 S_2 \cdots S_a}{\lambda^a} N_{0,t} = \frac{l_a}{\lambda^a} N_{0,t}. \tag{4.24}$$

Finally, for the newborns we have

$$N_{0,t+1} = \lambda N_{0,t} = \sum_{a=1}^{M} F_{a-1} N_{a-1,t} = \sum_{a=1}^{M} F_{a-1} \frac{l_{a-1}}{\lambda^{a-1}} N_{0,t}. \tag{4.25}$$

Dividing the equation by $\lambda N_{0,t}$ gives

$$1 = \sum_{a=1}^{M} F_{a-1} \frac{l_{a-1}}{\lambda^a}. \tag{4.26}$$

Using that $F_{a-1} = b_a S_a$ and $S_a l_{a-1} = l_a$ we can rewrite this equation as

$$1 = \sum_{a=1}^{M} b_a \, l_a \, \lambda^{-a} =: \psi(\lambda). \tag{4.27}$$

This is the Euler-Lotka equation for the stable age distribution. Compare it to the corresponding equation for the continuous-time model Eq. 4.13 with $e^\gamma = \lambda$. The only difference is that the continuous-time model has an integral over age, while the discrete-time model has a sum over age.

By the same argument as in the continuous case we can see that if the expected number of offspring produced by an individual during its lifetime, $\sum_{a=1}^{M} b_a \, l_a = \psi(1)$, is greater than 1 then the population grows exponentially. If it is less than 1, then the population goes extinct.

We will now determine the stable age distribution for a specific example.

Example 4.1. For the spotted owl the age-dependent reproduction numbers are

$$b_a = \begin{cases} 0 & \text{if } a < 2, \\ b & \text{if } a \geq 2 \end{cases} \tag{4.28}$$

for some constant b. The age-dependent survival probabilities are

$$S_a = \begin{cases} 1 & \text{if } a = 1, \\ l & \text{if } a = 2, \\ p & \text{if } a > 2 \end{cases} \tag{4.29}$$

for some constants l and p. Those values of the survival probabilities from year to year lead to the following values of the survival probabilities from birth to age a:

$$l_a = \begin{cases} 1 & \text{if } a = 1, \\ l\,p^{a-2} & \text{if } a \geq 2. \end{cases} \tag{4.30}$$

Substituting these values into the expression for $\psi(\lambda)$ in Eq. 4.44 gives

$$\begin{aligned} \psi(\lambda) &= bl\sum_{a=2}^{\infty} p^{a-2}\lambda^{-a} = lb\lambda^{-2}\sum_{n=0}^{\infty}\frac{p}{\lambda} \\ &= lb\lambda^{-2}\frac{1}{1-\frac{p}{\lambda}} = \frac{lb}{\lambda(\lambda-p)}, \end{aligned} \tag{4.31}$$

where we made use of the formula for a geometric series, valid if $|p/\lambda| < 1$ [1]. In particular, the expected number of offspring produced by an individual in their lifetime is

$$\psi(1) = lb/(1-p).$$

If this is greater than 1, then the population grows exponentially. If it is less than 1, then the population goes extinct.

In this case the Euler-Lotka equation $\psi(\lambda) = 1$ becomes the quadratic equation for λ:

$$\psi(\lambda) = \frac{lb}{\lambda(\lambda-p)} = 1 \quad \Leftrightarrow \quad \lambda^2 - \lambda p - lb = 0. \tag{4.32}$$

The solutions are

$$\lambda_{\pm} = \frac{p \pm \sqrt{p^2 + 4lb}}{2}. \tag{4.33}$$

We are interested in the positive solution λ_+. Substituting this value for λ back into Eq. 4.42 and Eq. 4.20 we see that we have found the solution

$$N_{a,t} = \left(\frac{p + \sqrt{p^2 + 4lb}}{2}\right)^{t-a} l_a N_{0,0} \tag{4.34}$$

for any choice of $N_{0,0}$.

---

[1] If $\lambda \geq p$, then $\psi(\lambda)$ diverges and does not satisfy the Euler-Lotka equation $\psi(\lambda) = 1$.

4.2.3 Leslie matrix

In the case where there is a maximal age m beyond which there is no reproduction, either because $b_a = 0$ for $a > m$ or because there are not older individuals because $S_{m+1} = 0$, we can then collect the equations for $N_{a,t+1}$ for $a = 0, 1, 2, \dots, m-1$ (Eq. 4.16 and Eq. 4.18) into a matrix equation:

$$\begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{m-1} \end{pmatrix}_{t+1} = \begin{pmatrix} F_0 & F_1 & \cdots & F_{m-2} & F_{m-1} \\ S_1 & 0 & \cdots & 0 & 0 \\ 0 & S_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & S_{m-1} & 0 \end{pmatrix} \begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{m-1} \end{pmatrix}_t . \tag{4.35}$$

Note that we did not need to include the equation for $N_{m,t+1}$ in the matrix equation because $N_{m,t+1}$ is not needed to calculate the reproduction. Once the matrix equation Eq. 4.35 is solved, we can determine $N_{m,t+1}$ separately from Eq. 4.16 if we are interested, and similarly for all older age classes that do not reproduce, if any.

The matrix on the right-hand side of Eq. 4.35 is a so-called Leslie matrix. Let us denote it by L. The equation Eq. 4.35 is a matrix equation of the form

$$\mathbf{N}_{t+1} = L\,\mathbf{N}_t, \tag{4.36}$$

where $\mathbf{N}_t$ is the column vector of the numbers $N_{a,t}$ and L is the Leslie matrix.

We now have the task of solving the homogeneous linear difference equation Eq. 4.36 with constant coefficients (the Leslie matrix L does not depend on time). You know from earlier modules that when confronted with a homogeneous linear *differential* equation with constant coefficients you can solve it with an exponential Ansatz. The same works for linear difference equations. We make the Ansatz

$$\mathbf{N}_t = \lambda^t \mathbf{v} \tag{4.37}$$

and substitute it into Eq. 4.36. This gives

$$\lambda^{t+1}\mathbf{v} = L\lambda^t\mathbf{v}. \tag{4.38}$$

Dividing by λ^t gives

$$\lambda\mathbf{v} = L\mathbf{v}. \tag{4.39}$$

This means that our Ansatz works if we choose λ to be an eigenvalue of the Leslie matrix L and $\mathbf{v}$ to be the corresponding eigenvector.

In the case where all eigenvalues of the Leslie matrix are distinct[2], the general solution is the linear combination of the solutions for each eigenvalue.

$$\mathbf{N}_t = c_1\lambda_1^t\mathbf{v}_1 + c_2\lambda_2^t\mathbf{v}_2 + \cdots + c_m\lambda_m^t\mathbf{v}_m, \tag{4.40}$$

where $\lambda_1, \lambda_2, \dots, \lambda_m$ are the eigenvalues of the Leslie matrix and $\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_m$ are the corresponding eigenvectors. The constants $c_1, c_2, \dots, c_m$ are determined by the initial conditions.

Example 4.2. Consider a population with the reproduction numbers b_a and the survival probabilities S_a given in the following table:

a	b_a	S_a	F_a
0	0	—	0
1	0	1	1/2
2	1	1/2	1
3	2	1/2	0
4	0	1/2	0

The final column in that table is calculated from the previous ones using $F_a := b_{a+1}S_{a+1}$. In this example the maximum age m beyond which there is no reproduction is $m = 3$. Hence the corresponding Leslie matrix is a 3×3 matrix. It is given by

$$L = \begin{pmatrix} F_0 & F_1 & F_2 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{pmatrix} = \begin{pmatrix} 0 & 1/2 & 1 \\ 1 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix}. \tag{4.41}$$

Assume that the at time $t = 0$ we only have 10 individuals all of age 0, i.e.,

$$\mathbf{N}_0 = \begin{pmatrix} 10 \\ 0 \\ 0 \end{pmatrix}. \tag{4.42}$$

We can then calculate the numbers at the following times $t = 1, 2, 3, \dots$ by repeated multiplication by the Leslie matrix L:

$$\mathbf{N}_1 = L\mathbf{N}_0 = \begin{pmatrix} 0 & 1/2 & 1 \\ 1 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix} \begin{pmatrix} 10 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 10 \\ 0 \end{pmatrix},$$

---

[2] In the case where there are repeated eigenvalues, the general solution is just a bit more complicated. Luckily in ecology, we are rarely interested in that case, because the probability that a real ecosystem is exactly so that this special case arises is zero.

$$\mathbf{N}_2 = L\mathbf{N}_1 = \begin{pmatrix} 5 \\ 0 \\ 5 \end{pmatrix}, \quad \mathbf{N}_3 = L\mathbf{N}_2 = \begin{pmatrix} 5 \\ 5 \\ 0 \end{pmatrix}, \cdots .$$

Continuing like this (using a computer) we observe that the population converges to a stable age distribution.

$$\lim_{t\to\infty} \mathbf{N}_t = \begin{pmatrix} 4 \\ 4 \\ 2 \end{pmatrix}. \tag{4.43}$$

To understand this phenomenon we look for the eigenvalues and eigenvectors of the Leslie matrix. The eigenvalues are the solutions of the characteristic equation

$$\begin{aligned} 0 = \det(L - \lambda I) = \begin{vmatrix} -\lambda & 1/2 & 1 \\ 1 & -\lambda & 0 \\ 0 & 1/2 & -\lambda \end{vmatrix} = -\lambda^3 + \frac{1}{2}\lambda + \frac{1}{2} \\ = (1-\lambda)\left(\lambda^2 + \lambda + \frac{1}{2}\right) \end{aligned} \tag{4.44}$$

We can read off that the solutions are

$$\lambda_) = 1, \quad \lambda_\pm = -\frac{1}{2} \pm \frac{1}{2}i. \tag{4.45}$$

Because the magnitude of the eigenvalues $\lambda_\pm$ is less than 1, we have that $\lim_{t\to\infty} \lambda_\pm^t = 0$. This means that the stable age distribution is given by the eigenvector corresponding to the eigenvalue $\lambda_0 = 1$:

$$\lim_{t\to\infty} \mathbf{N}_t = \lim_{t\to\infty} \left(c_0\lambda_0^t\mathbf{v}_0 + c_+\lambda_+^t\mathbf{v}_+ + c_-\lambda_-^t\mathbf{v}_-\right) = c_0\mathbf{v}_0.$$

In general, if the Leslie matrix has a unique dominatn eigenvalue λ_0 with a corresponding eigenvector $\mathbf{v}_0$, then

$$\lim_{t\to\infty} \frac{\mathbf{N}_t}{\lambda_0^t} = c_0\mathbf{v}_0,$$

where c_0 is a constant that depends on the initial conditions. This means that the population converges to a stable age distribution. The stable age distribution is given by the eigenvector corresponding to the dominant eigenvalue of the Leslie matrix.

Luckily, there is a theorem about the eigenvalues and eigenvectors of non-negative matrices that we can use to determine whether a Leslie matrix has a unique dominant eigenvalue. We start by associating the Leslie matrix with a directed graph. The graph has m vertices and a directed edge from vertex i to vertex j if and only if the Leslie matrix has a non-zero entry in column i and row j. The graph is called the Leslie graph. We call the Leslie matrix irreducible if its Leslie graph is strongly connected, which means that there is a directed path between any two nodes. We call the Leslie matrix primitive if the greatest common divisor of the lengths of all circuits in the Leslie graph is 1. The following theorem is then true:

Theorem 4.1. *If the Leslie matrix is irreducible and primitive, then it has a unique dominant eigenvalue that is real and positive. The corresponding right eigenvector is real and strictly positive.*

This is a special case of the Perron-Frobenius theorem, which is a general theorem about non-negative matrices, and is used extensively in the theory of Markov chains. The above theorem is exactly what we need, because it tells us when the Leslie matrix has a unique dominant eigenvalue and a corresponding eigenvector that gives the stable age distribution.

4.3 Exercises

4.3.1 Continuous time

4.3.1.1 * Age-independent rates

Exercise 4.1. In the continuous-time age-structured population model consider the case where $b(a) = b$ and $\mu(a) = \mu$ are both constant. Repeat all steps of the analysis but simplifying the expressions at each step by using the constant values for birth and death rates.

1. Solve the partial differential equation of the age-structured model by making the Ansatz $n(t, a) = f(t)r(a)$ and introducing the separation constant γ.
2. Use the boundary condition at $a = 0$ to determine the value of γ.
3. Give the condition under which the population goes extinct and compare it to the condition in the exponential model from chapter 1.

4.3.1.2 o Harvestings an age-structured population

Exercise 4.2. Consider an age-structured fish population in which all individuals above the maturity age a_m are reproducing, at a fixed rate, so that

$$b(a) = \begin{cases} 0 & \text{if } a < a_m, \\ b & \text{if } a \geq a_m. \end{cases} \tag{4.46}$$

All fish at all ages experience a natural death rate μ_0. In addition, fish above the maturity size are harvested at a constant rate μ_F, so that

$$\mu(a) = \begin{cases} \mu_0 & \text{if } a < a_m, \\ \mu_0 + \mu_F & \text{if } a \geq a_m. \end{cases} \tag{4.47}$$

By calculating the expected number of offspring per individual, determine the limit on the harvesting rate μ_F that allows the population to be sustainable.

4.3.1.3 Seasonal mortality

Exercise 4.3. Consider an age-structured population model in which, in addition to an age-dependent mortality, there is also a seasonal mortality. The population is described by a function $n(t,a)$ giving the density of individuals of age a at time t which satisfies the equations

$$\partial_t n(t,a) + \partial_a n(t,a) = -(\mu(a) + m(t))\, n(t,a), \tag{4.48}$$

$$n(t,0) = \int_0^\infty b(a) n(t,a) da. \tag{4.49}$$

The birth rate $b(a)$ and the mortality rates $\mu(a)$ and $m(t)$ are all positive.

(a) By substituting the ansatz $n(t,a) = p(t)r(a)$ into equation Eq. 4.48 and separating variables with a separation constant γ, derive solutions for $p(t)$ and $r(a)$ and hence for $n(t,a)$, involving γ.

(b) By substituting your solution from part (a) into equation Eq. 4.49, derive an equation for γ. Write this in the form $\phi(\gamma) = 1$ for some function ϕ. Show that this ϕ is a monotonic function.

(c) Assume that the seasonal mortality rate $m(t)$ is periodic with period 1 and denote by F the averaged seasonal mortality. By considering the population at the end of each season, show that the population will go extinct if $\gamma < F$.

(d) Explain how you can use a property of the function ϕ to eliminate γ from the condition for extinction. Thus finally give the condition for extinction in terms of $b(a), \mu(a)$ and F.

4.3.2 Discrete time

4.3.2.1 * Fibonacci population

Exercise 4.4. Consider a population in which individuals on average produce one offspring when they turn 1 year old and another offspring when they turn 2 years old. After that they die. Assume that there is no mortality before they turn 2 year old.

1. Formulate the above information in terms of values for the reproduction numbers b_a and the survival probabilities S_a.
2. Write down the Leslie matrix for this population.

3. Assume that at $t = 0$ we start with 1 individual of age 0. By hand, calculate the numbers of individuals at each age at time $t = 1, 2, 3, 4$ and 5.
4. Using the Leslie matrix, calculate the stable age distribution and the long-term growth factor (the factor by which the total population changes from one year to the next).

4.3.2.2 Semelparous population

Exercise 4.5. Consider a population in which individuals die after having given birth for the first time at age 3. The life history parameters are given by the following table:

a	b_a	S_a
1	0	1
2	0	1/2
3	6	1/3

1. Calculate the Leslie matrix for this population.
2. Assume that at $t = 0$ we start with 10 individual, all of age 0. Use the Leslie matrix to calculate the numbers of individuals of ages $0, 1, 2$ at times $t = 1, 2, 3$. What will happen in the long run? Will the population evolve towards a stable age distribution?
3. Draw the graph associated with the Leslie matrix and determine whether the Leslie matrix is irreducible and primitive.

4.3.2.3 Eastern Screech Owl

Exercise 4.6. This exercise is most suitable for you if you are willing to use a computer to find eigenvalues and eigenvectors of matrices.

The Eastern Screech Owl is a small owl that is found in the eastern United States and Canada. It is a cavity-nesting bird, which means that it nests in holes in trees. It is able to adapt to diverse habitats, including wooded residential neighbourhoods and parks in suburban areas. In suburban areas, these owls find a variety of nesting opportunities, such as tree cavities, nest boxes, and even abandoned buildings, which may be less available in intensively farmed rural areas or dense forests. Additionally, the suburban settings can offer a rich supply of prey, including insects, small mammals, and other small creatures, partly due to the lower prevalence of large predators.

Below is a life table collected for two different habitats, suburban and rural, in Texas.

Age	Suburban		Rural	
a	l_a	b_a	l_a	b_a
0	1.00	0.0	1.00	0.0
1	0.49	0.8	0.30	0.8
2	0.18	1.3	0.11	1.1
3	0.10	1.5	0.06	1.6
4	0.06	1.6	0.04	1.0
5	0.04	1.3	0.02	1.0
6	0.03	1.3		
7	0.02	1.3		
8	0.02	1.3		
9	0.01	1.3		
10	0.01	1.3		

For each of the two populations do the following:

1. Calculate the reproductive number, i.e., the expected number of offspring produced by a single individual during its lifetime.
2. Calculate the Leslie matrix. Note that the table gives the survival probabilities l_a from birth to age a instead of the yearly survival probabilities S_a. The yearly survival probabilities can be calculated from the life table by $S_a = l_a/l_{a-1}$.
3. Use the Leslie matrix to calculate the stable age distribution and the long-term growth factor (the factor by which the total population changes from one year to the next).
4. Calculate the average age in the stable age distribution as well as the average age of parents of newborns.

5 Interacting populations

Ecological systems are complex networks of interactions involving multiple species, which can be categorized into different trophic levels based on their roles in the ecosystem. Understanding these interactions is crucial for studying ecosystem dynamics, population control, and biodiversity. While the study of multiple interacting species can become quite intricate, analyzing the interactions between two species offers a more manageable framework while still providing significant insights into the dynamics of ecological relationships. This chapter focuses on two-species interactions, offering a foundational understanding that can be applied or extended to more complex scenarios.

Mathematical Framework for Two-Species Interactions

To model the interactions between two species, we employ a system of two autonomous coupled ordinary differential equations (ODEs). These equations describe the rate of change of the population sizes over time, capturing the essence of their interaction. The general form of these equations is given by:

$$\frac{dX}{dt} = f(X, Y), \qquad \frac{dY}{dt} = g(X, Y). \tag{5.1}$$

where X and Y represent the population sizes of the two species, and $f(X, Y)$ and $g(X, Y)$ are functions that describe how the populations influence each other. These functions are crafted based on the nature of the interaction between the species, reflecting the underlying biological processes.

Types of Two-Species Interactions

The dynamics of two interacting species are generally categorized into three primary types, each with its unique characteristics and implications for the populations involved:

- **Predator-Prey Interactions:** In this type of interaction, one species (the predator) feeds on the other (the prey). The population growth of the predator increases with increased availability of the prey, while the prey population is negatively affected by the presence of the predator. Mathematically, this interaction often leads to oscillatory dynamics, exemplified by the classic Lotka-Volterra model.
- **Competition:** When two species compete for the same resources, their growth rates are adversely affected by their interaction. This situation is characterized by negative impacts on both species' growth rates, potentially leading to the exclusion of one species or to a stable coexistence, depending on the specific conditions and competition coefficients.

- **Mutualism:** This positive interaction benefits both species, leading to an increase in their growth rates. The mutualistic relationship is such that each species provides some benefit to the other, which could be in the form of nutrients, shelter, or any other factor that enhances growth or survival.

While this chapter focuses on these primary interaction types, it's important to recognize the spectrum of interactions in nature, including parasitism, amensalism, and others. Moreover, the real-world ecological systems often exhibit a mix of these interactions, adding layers of complexity. By starting with the analysis of two-species systems, we lay the groundwork for understanding more intricate interactions and the overall dynamics of ecosystems.

5.1 Lotka-Volterra Model

The Lotka-Volterra model, developed independently by Alfred Lotka in 1925 and Vito Volterra in 1926, serves as a foundational mathematical model for understanding the dynamic interplay between a prey population (denoted by N) and a predator population (denoted by P).

Model Formulation

The model assumes that the prey population, in the absence of predators, grows exponentially with a per capita growth rate $a > 0$. However, the prey die due to being eaten by predators, and we assume that the per-capita mortality rate grows in proportion to the abundance of predators, with some proportionality constant $b \geq 0$. This leads to the equation

$$\frac{dN}{dt} = N(a - bP). \tag{5.2}$$

Conversely, the predators benefit from the abundance of prey and we encode that by giving them a per-capita growth cN, where $c \geq 0$. We assume that the per capita mortality rate is a constant d. This yields the following equation for the predator dynamics:

$$\frac{dP}{dt} = P(cN - d). \tag{5.3}$$

The two plots in Figure 5.1 generated from the Lotka-Volterra model provide a visual representation of the dynamics between a predator and prey population over time. The phase plane plot illustrates the cyclic nature of the interaction between the prey (N) and predator (P) populations, depicting a closed trajectory that indicates the continuous oscillation of both populations in relation to each other: as the prey population increases, it provides more food for the predators, which then also increase in number. However, as the predator population grows, it puts more pressure on the prey, leading to a decline in the prey population, which eventually causes the predator population to decrease due to lack of food.

The plot at the bottom shows the prey and predator populations over time. It highlights the periodic rises and falls of each population, showing how the increase in the prey population precedes the increase in the predator population, followed by a subsequent decline in the prey and then the predator population. The time series plot complements the phase plane by showing how the dynamics unfold over time.

Non-dimensionalization of the Model

Non-dimensionalization is a crucial step to reduce the complexity of the model by decreasing the number of parameters, thereby simplifying the analysis. By introducing the non-dimensional variables $u = \frac{cN}{d}$, $v = \frac{bP}{a}$, and the non-dimensional time $\tau = at$, along with the parameter $\alpha = \frac{d}{a}$, we can transform the Lotka-Volterra equations into a more tractable form:

$$\frac{du}{d\tau} = u(1-v), \quad \frac{dv}{d\tau} = \alpha v(u-1). \tag{5.4}$$

Phase plane paths

To determine the phase plane paths we consider v as a function of u which satisfies the equation

$$\frac{dv}{du} = \frac{\frac{dv}{d\tau}}{\frac{du}{d\tau}} = \frac{\alpha v(u-1)}{u(1-v)}. \tag{5.5}$$

We rewrite this by separating the variable and integrate:

$$\int \frac{1-v}{v} dv = \alpha \int \frac{u-1}{u} du. \tag{5.6}$$

This gives

$$\log v - v = \alpha(u - \log u) + \text{constant}. \tag{5.7}$$

So even though u and v are changing with time, this particular combination stays constant. This is a conserved quantity. Let us suggestively call the constant of the motion H for Hamiltonian and write it in terms of new variables $p = \log u$ and $q = \log v$:

$$H(q,p) = v - \log v + \alpha(u - \log u) = e^q - q + \alpha(e^p - p). \tag{5.8}$$

Hamilton's equations

$$\dot{q} = \frac{dH}{dp}, \quad \dot{p} = -\frac{dH}{dq} \tag{5.9}$$

then reproduce our equations of motion.

This formulation underscores the conservative nature of the model, where the energy-like quantity H is conserved, leading to neutrally stable periodic orbits. This Hamiltonian nature is a rather special feature of the Lotka-Volterra model. Any slight modification of the model will destroy the conserved quantity and the periodic orbits. Thus we should not expect to see such perfect periodic predator-prey cycles in nature. We will discuss more realistic predator-prey models later.

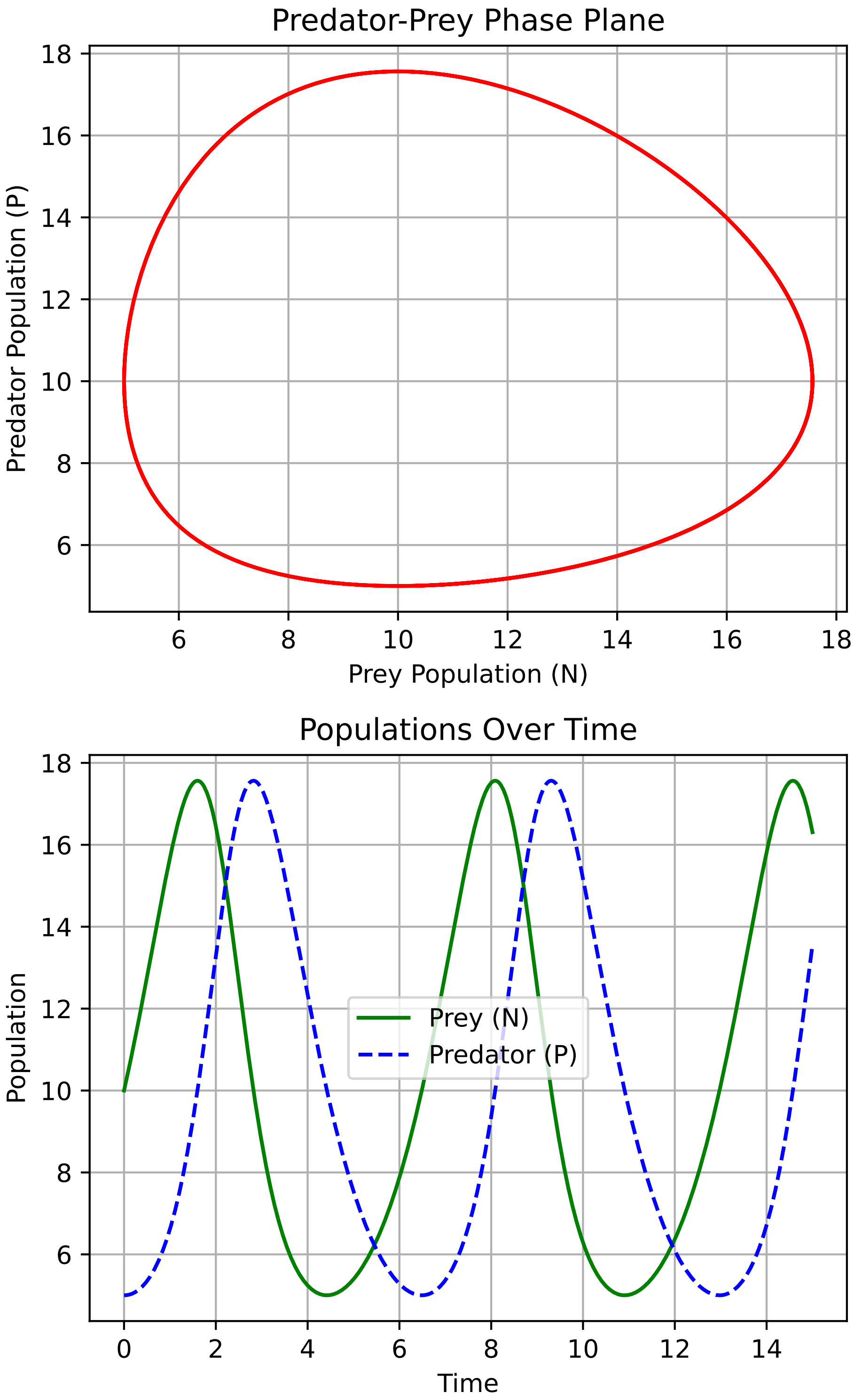

Figure 5.1: Solutions to the Lotka-Volterra model with parameters $a = 1.0$, $b = 0.1$, $c = 0.1$, and $d = 1.0$ and initial conditions $N_0 = 10$ and $P_0 = 5$.

5.2 Linear Stability Analysis

Before we study more realistic models, we revisit the concept of linear stability analysis, an essential tool in understanding the dynamics near the fixed points of systems described by autonomous coupled ordinary differential equations (ODEs) of the form

$$\frac{dX}{dt} = f(X,Y), \quad \frac{dY}{dt} = g(X,Y). \tag{5.10}$$

Let us denote the fixed points (stable states) of the system as (x^*, y^*). They satisfy $f(x^*, y^*) = 0$ and $g(x^*, y^*) = 0$.

Linearization around the Fixed Points

To analyze the stability of these fixed points, we introduce small perturbations x and y around them, setting $X = x^* + x$ and $Y = y^* + y$. By applying a Taylor expansion and retaining only the linear terms, we obtain a linearized system:

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \mathbf{A}(x^*, y^*)\begin{pmatrix} x \\ y \end{pmatrix}, \tag{5.11}$$

where the Jacobian matrix $\mathbf{A}$ is defined as:

$$\mathbf{A} = \begin{pmatrix} f_X & f_Y \\ g_X & g_Y \end{pmatrix}_{(x^*, y^*)}. \tag{5.12}$$

Eigenvalue Analysis for Stability

The solution to the linearized system takes the form $(x, y) = \mathbf{v}e^{\lambda t}$, where $\mathbf{v}$ is an eigenvector of $\mathbf{A}$, and λ is the corresponding eigenvalue. By setting the determinant of $\mathbf{A} - \lambda\mathbf{I}$ to zero, we obtain the characteristic equation:

$$\det(\mathbf{A} - \lambda\mathbf{I}) = \begin{vmatrix} f_X - \lambda & f_Y \\ g_X & g_Y - \lambda \end{vmatrix}_{(x^*, y^*)} = 0, \tag{5.13}$$

which leads to the eigenvalues:

$$\lambda = \frac{\mathrm{Tr}\mathbf{A} \pm \sqrt{(\mathrm{Tr}\mathbf{A})^2 - 4\det\mathbf{A}}}{2}. \tag{5.14}$$

The stability of the fixed point is determined by the sign of the real parts of the eigenvalues:

- If both eigenvalues have negative real parts, the fixed point is stable (attracting).
- If both eigenvalues have positive real parts, the fixed point is unstable (repelling).

- If the eigenvalues have real parts of opposite signs, the fixed point is a saddle point, which is unstable.
- For a complex conjugate pair of eigenvalues, if the real part is positive, the system exhibits an unstable spiral; if the real part is negative, the system exhibits a stable spiral.

This analysis is pivotal for understanding how small deviations from equilibrium evolve over time, providing insights into the system's long-term behavior near the fixed points. For instance, in the context of the predator-prey dynamics, such analysis helps elucidate under what conditions the populations will return to equilibrium after a disturbance or potentially diverge away from it.

We can reformulate the stability conditions of a fixed point in terms of the determinant and trace of the Jacobian matrix. We need to recall how these two characteristics of the Jacobian relate to the eigenvalues. For a 2x2 matrix A with eigenvalues λ_1 and λ_2, the trace $\mathrm{Tr}(A)$ is the sum of the eigenvalues, and the determinant $\mathrm{Det}(A)$ is the product of the eigenvalues:

- $\mathrm{Tr}(A) = \lambda_1 + \lambda_2$
- $\mathrm{Det}(A) = \lambda_1 \lambda_2$

Using these relationships, we can express the conditions for the stability of fixed points as follows:

1. **Stable (Attracting) Fixed Point:** If both eigenvalues have negative real parts, their sum (the trace) is negative, and their product (the determinant) is positive because the product of two negative numbers is positive. Therefore, for stability, $\mathrm{Tr}(A) < 0$ and $\mathrm{Det}(A) > 0$. Additionally, to ensure that both eigenvalues are real and negative, we require that $\mathrm{Tr}(A)^2 - 4\mathrm{Det}(A) \geq 0$ to avoid complex eigenvalues.

2. **Unstable (Repelling) Fixed Point:** If both eigenvalues have positive real parts, the trace is positive, and the determinant is positive (the product of two positive numbers is positive). Thus, for instability, $\mathrm{Tr}(A) > 0$ and $\mathrm{Det}(A) > 0$.

3. **Saddle Point (Unstable):** If the eigenvalues have real parts of opposite signs, the determinant (the product of the eigenvalues) is negative. So, for a saddle point, $\mathrm{Det}(A) < 0$, regardless of the trace.

4. **Spiral Points:** For a complex conjugate pair of eigenvalues, the determinant will be positive (since the product of complex conjugates is positive), but the stability depends on the sign of the real part of the eigenvalues, which is represented by the trace. Here, we also need to ensure that $\mathrm{Tr}(A)^2 - 4\mathrm{Det}(A) < 0$ to confirm that the eigenvalues are complex.

    - **Unstable Spiral:** If the real part is positive, $\mathrm{Tr}(A) > 0$ and $\mathrm{Det}(A) > 0$.
    - **Stable Spiral:** If the real part is negative, $\mathrm{Tr}(A) < 0$ and $\mathrm{Det}(A) > 0$.

These conditions provide a concise way to determine the stability of fixed points using only the determinant and trace of the Jacobian matrix, without explicitly computing the eigenvalues.

Example 5.1 (Linear Stability Analysis of the Lotka-Volterra Model)**.** To explore the stability of steady states in the Lotka-Volterra model, we analyze the system near its fixed points using the Jacobian matrix $\mathbf{A}$. For the non-dimensionalized Lotka-Volterra system, the Jacobian matrix is given by

$$\mathbf{A} = \begin{pmatrix} 1-v & -u \\ \alpha v & \alpha(u-1) \end{pmatrix}. \tag{5.15}$$

Steady State at $(u, v) = (0, 0)$

For the fixed point $(u, v) = (0, 0)$, we substitute these values into the Jacobian matrix and find the eigenvalues:

$$\mathbf{A} = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}. \tag{5.16}$$

The eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = -\alpha$, indicating that this fixed point is a saddle point due to the eigenvalues having opposite signs. This configuration is inherently unstable as trajectories near the point will diverge away along the direction associated with the positive eigenvalue.

Steady State at $(u, v) = (1, 1)$

At the fixed point $(u, v) = (1, 1)$, the Jacobian matrix becomes:

$$\mathbf{A} = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}. \tag{5.17}$$

The characteristic equation for the eigenvalues λ is $\lambda^2 + \alpha = 0$, leading to complex eigenvalues $\lambda = \pm i\sqrt{\alpha}$. The real part of these eigenvalues is zero, indicating that this fixed point is a center. Trajectories around this point are closed loops, implying that the system exhibits neutrally stable periodic behavior around the $(1, 1)$ steady state.

The period T of the oscillations can be determined from the imaginary part of the eigenvalues, which is $\sqrt{\alpha}$, so the period $T = \frac{2\pi}{\sqrt{\alpha}}$.

5.3 More Realistic Predator-Prey Models

While the basic Lotka-Volterra model provides a fundamental understanding of predator-prey interactions, more nuanced models incorporate additional biological realism. These models may account for factors like limited resources, satiation, prey switching, predator avoidance, and many others.

5.3.1 Generalized Predator-Prey Model

The generalized model introduces a function $F(N, P)$ representing the prey population's per-capita growth and a function $G(N, P)$ for the predator's per-capita growth rate, so that the dynamics are:

$$\frac{dN}{dt} = NF(N, P), \quad \frac{dP}{dt} = PG(N, P). \tag{5.18}$$

The prey might exhibit logistic growth in the absence of predators. To model this we could choose

$$F(N, P) = r\left(1 - \frac{N}{K}\right) - R(N)P, \tag{5.19}$$

where r is the intrinsic growth rate, K is the carrying capacity, and $R(N)$ models how the predation rate of a predator changes with the prey population size. $NR(N)$ is the rate at which each individual predator consumes prey. The dependence of this rate on the prey population size N is often referred to as "functional response" in the ecological literature. Holling introduced three types of functional responses, which are widely used in predator-prey models:

5.3.1.1 Holling Type functional responses

1. **Type I** $NR(N) = bN$, which corresponds to the standard Lotka-Volterra model. This simplification lacks realism as it assumes an unlimited predator appetite regardless of prey population size.
2. **Type II** $NR(N) = \frac{AN}{N+B}$, with A and B being positive constants. In this model, the rate approaches a saturation level A for large N, reflecting a limit to the predator's consumption rate. This model is more realistic as it accounts for the predator's limited appetite, which might be because there is a minimum handling time, the time the predator needs to consume a prey item.
3. **Type III** $NR(N) = \frac{AN^2}{N^2+B^2}$. This response includes a saturation effect like the previous example but also models that if the prey is rare the predator may not be able to find it. This model is more complex and captures the idea that predators may switch to alternative prey when the primary prey is scarce. It may also encode a learning effect, where the predator's efficiency in capturing prey increases with experience so that initially the predator's consumption rate increases with prey density.

5.3.2 Example

Consider a model where the prey growth rate follows logistic dynamics in the absence of prey and predation mortality is described by a Holling type II function encoding satiation effects. The predator's growth rate goes down as the prey population decreases. The model equations are:

$$\frac{dN}{dt} = N\left[r\left(1-\frac{N}{K}\right)-\frac{A}{N+B}P\right], \quad \frac{dP}{dt} = Ps\left(1-\frac{hP}{N}\right), \tag{5.20}$$

where r, K, A, B, s, and h are positive constants.

Nondimensionalization

To reduce the complexity, we nondimensionalize the system with $\tau = tr$, $u = \frac{N}{K}$, $v = \frac{hP}{K}$, $a = \frac{A}{hr}$, $b = \frac{B}{K}$, and $c = \frac{s}{r}$, leading to:

$$\frac{du}{d\tau} = u(1-u) - a\frac{uv}{u+b}, \quad \frac{dv}{d\tau} = cv\left(1-\frac{v}{u}\right). \tag{5.21}$$

Stability Analysis of Steady States

The steady states (u^*, v^*) include $(1, 0)$ and a coexistence steady state (u_+^*, u_+^*), where

$$u_+^* = \frac{1-a-b+\sqrt{(1-a-b)^2+4b}}{2}. \tag{5.22}$$

The community matrix $\mathbf{A}(u, v)$ at these points helps determine their stability. For the fixed point $(1, 0)$, where the prey population is at carrying capacity and there are no predators, we have find

$$\mathbf{A}(1,0) = \begin{pmatrix} -1 & -\frac{a}{1+b} \\ 0 & c \end{pmatrix}. \tag{5.23}$$

The eigenvalues -1 and c have opposite sign, indicating that the fixed point is a saddle point.

At the coexistence fixed point (u_+^*, u_+^*) the Jacobian is more complex and we will skip the analysis here.

5.4 Competition Models

In ecological systems, species often compete for limited resources, such as food or territory. This competition influences their growth rates and can determine their survival and dominance within an ecosystem. The Lotka-Volterra competition model provides a framework to study these dynamics, extending the principles of logistic growth to account for interspecies interactions.

5.4.1 Lotka-Volterra Competition Dynamics

The model is formulated as follows for two competing species N_1 and N_2:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + b_{12} N_2}{K_1}\right), \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2 + b_{21} N_1}{K_2}\right), \end{aligned} \tag{5.24}$$

where r_i is the intrinsic growth rate and K_i is the carrying capacity of species i. The coefficients b_{ij} represent the competitive effect of species j on species i, effectively reducing the carrying capacity for species i due to the presence of species j.

5.4.2 Nondimensionalization of the Model

To simplify the analysis, we nondimensionalize the system using:

$$u_i = \frac{N_i}{K_i}, \quad a_{ij} = \frac{b_{ij} K_j}{K_i}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \tag{5.25}$$

leading to:

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12} u_2), \qquad \frac{du_2}{d\tau} = \rho u_2 (1 - u_2 - a_{21} u_1). \tag{5.26}$$

5.4.3 Analysis of Steady States

The system has four potential steady states: $(0,0)$, $(0,1)$, $(1,0)$, and a coexistence steady state $\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)$.

To determine the stability of these points, we evaluate the Jacobian matrix $\mathbf{A}(u_1, u_2)$ at each steady state and analyze its eigenvalues:

1. **At** $(0,0)$**:** The eigenvalues are 1 and ρ, indicating an unstable node as both are positive.
2. **At** $(1,0)$**:** The eigenvalues are -1 and $\rho(1 - a_{21})$. This point is a saddle if $a_{21} < 1$ and a stable node if $a_{21} > 1$.
3. **At** $(0,1)$**:** By symmetry, this point behaves like $(1,0)$ with roles reversed between species.
4. **Coexistence point** $\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)$**:** The stability is determined by the sign of the trace and the determinant of $\mathbf{A}$. The system's behavior at this point depends on the specific values of a_{12} and a_{21}, indicating potential scenarios where both species can coexist or one outcompetes the other.

5.4.4 Nullclines and Phase Portraits

Nullclines, where the growth rate of one of the species are zero, are a very useful aid when drawing phase plane diagrams, also known as phase portraits. The nullclines for the Lotka-Volterra competition model are:

- u_1 nullclines: $du_1/d\tau = 0$ when $u_1 = 0$ or $u_2 = \frac{1-u_1}{a_{12}}$.
- u_2 nullclines: $du_2/d\tau = 0$ when $u_2 = 0$ or $u_2 = 1 - a_{21}u_1$.

Along the u_1 nullclines the flow is purely vertical and along the u_2 nullclines the flow is purely horizontal. The intersection of the nullclines gives the steady states of the system. We can now draw the phase portrait to visualize the dynamics of the system. Very rough sketches are enough to understand the dynamics.

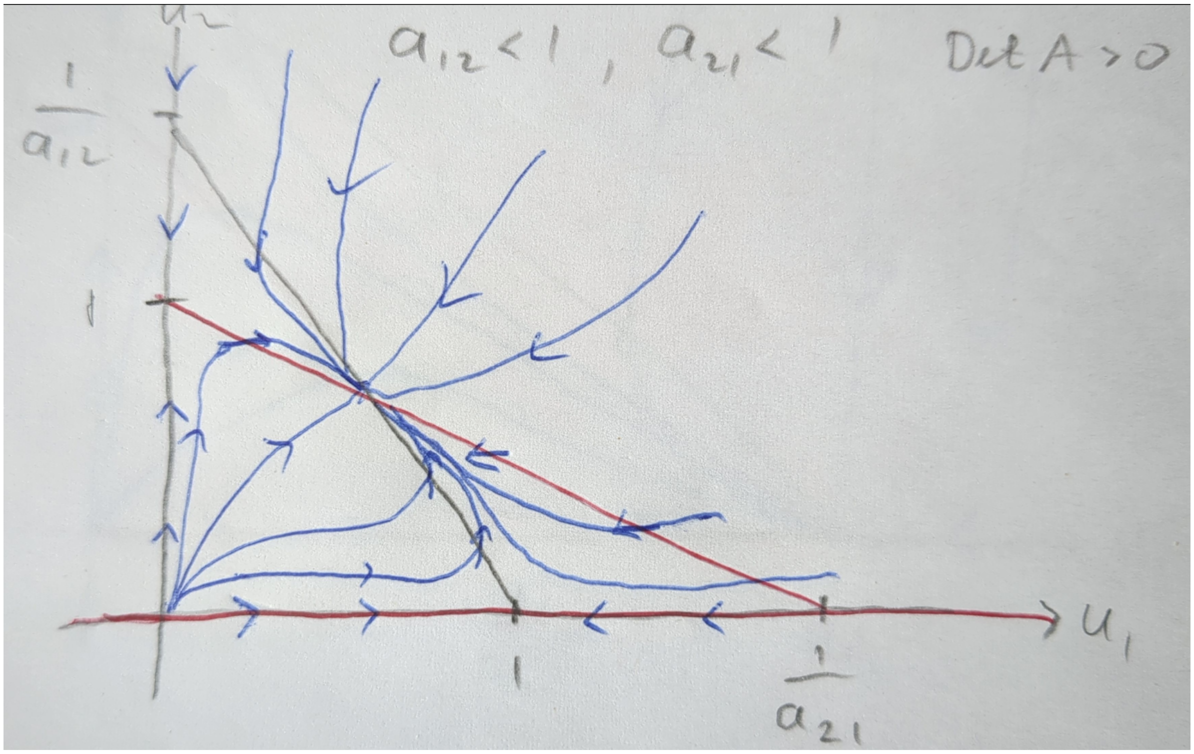

Figure 5.2: Phase portrait of competition model when $a_{12} < 1$ and $a_{21} < 1$.

Figure 5.2 shows the phase portrait of the competition model when $a_{12} < 1$ and $a_{21} < 1$. The nullclines are shown in grey and red, the flow lines in blue, with the arrows indicating the direction of the flow. The system exhibits a stable coexistence steady state, where both species persist in the ecosystem.

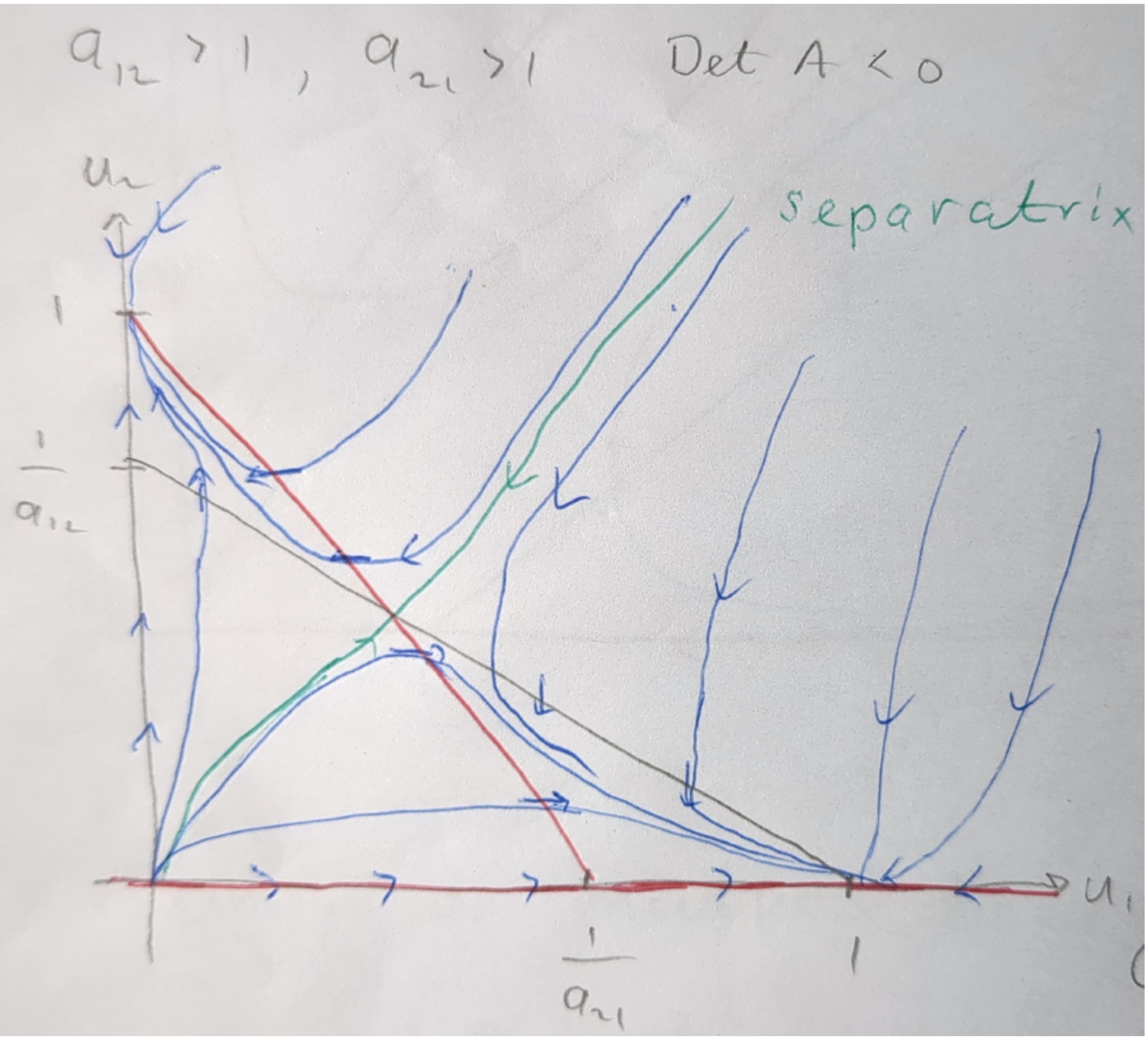

Figure 5.3: Phase portrait of competition model when $a_{12} > 1$ and $a_{21} > 1$.

Figure 5.3 illustrates the phase portrait of the competition model when $a_{12} > 1$ and $a_{21} > 1$. In this scenario, the coexistence steady state is a saddle, leading to the exclusion of one species. Which species dominates depends on the initial conditions. If the initial condition is below the separatrix, species 1 will dominate, and if it is above, species 2 will dominate.

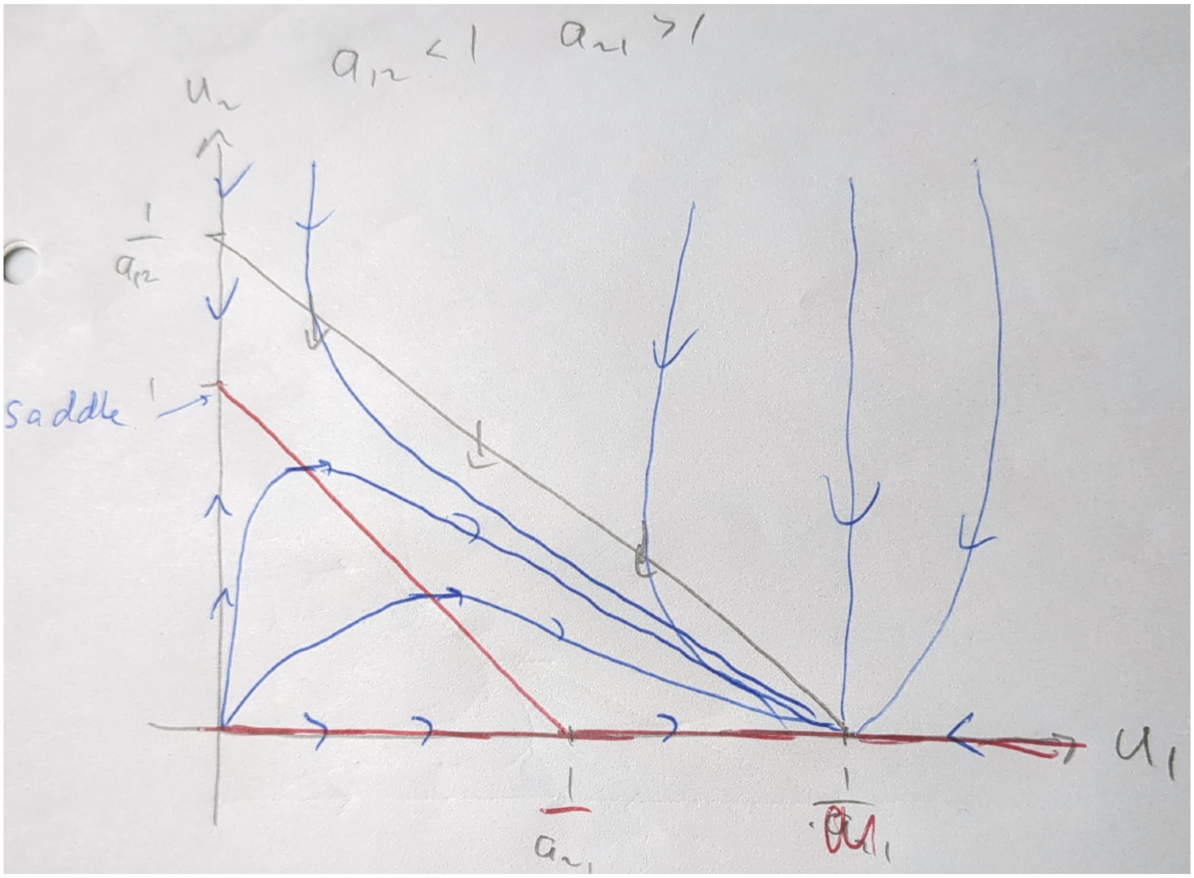

Figure 5.4: Phase portrait of competition model when $a_{12} < 1$ and $a_{21} > 1$.

Figure 5.4 depicts the phase portrait of the competition model when $a_{12} < 1$ and $a_{21} > 1$. In this case, the coexistence steady state has disappeared (it has moved into a region with negative population numbers that is not ecologically relevant). Irrespective of initial conditions, the system will evolve towards the state where only species 1 exists. Species 2 is driven to extinction.

We are not drawing the case $a_{12} > 1$ and $a_{21} < 1$ as it is similar to the case $a_{12} < 1$ and $a_{21} > 1$ just with the role of species 1 and 2 reversed. In this case species 2 will dominate and species 1 will go extinct.

5.4.5 Competitive Exclusion Principle

The competitive exclusion principle, proposed by Gause in the 1930s, states that two species competing for the same resources cannot coexist indefinitely, with one species eventually outcompeting the other.

In the model we studied the two species shared resources but each also had its own resources, hence we observed a weaker form of the competitive exclusion principle. The coexistence steady state was stable when the competition was weak enough, allowing both species to persist in the ecosystem. This highlights the delicate balance between competition and coexistence in ecological systems, where the strength of interspecies interactions plays a crucial role in determining the long-term dynamics of species populations.

5.5 Mutualism Models

In ecological systems, mutualism refers to interactions where all participating species benefit, leading to increased growth rates. An example is the relationship between plants and their seed dispersers, such as insects, where both parties gain advantages from their association.

5.5.1 Example

This model incorporates logistic growth, akin to the competition model, but with a twist to account for the mutualistic interaction:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}\right], \qquad \frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_2}\right], \tag{5.27}$$

where r_i, K_i, and b_{ij} are all positive constants, with b_{ij} representing the mutualistic benefit to species i from species j. Notice that we simply changed the sign of the competition terms in the competition model to turn them into mutualistic terms

5.5.2 Nondimensionalization of the Model

Using nondimensional variables $u_i = N_i/K_i$, $a_{ij} = b_{ij}K_j/K_i$, $\tau = r_1 t$, and $\rho = r_2/r_1$, the equations transform to:

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2), \qquad \frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1). \tag{5.28}$$

This is as in the competition model but with the signs in front of a_{12} and a_{21} reversed.

5.5.3 Steady States and Stability

The system has the steady states $(0,0)$, $(0,1)$, $(1,0)$, and $\left(\frac{1+a_{12}}{\delta}, \frac{1+a_{21}}{\delta}\right)$, where $\delta = 1 - a_{12}a_{21}$. The coexistence steady state is ecologically relevant only if $\delta > 0$.

- **At** $(0,0)$**:** The eigenvalues are 1 and ρ, indicating an unstable node.
- **At** $(0,1)$ **and** $(1,0)$**:** These points are saddles, with eigenvalues showing a mix of positive and negative signs.
- **At the mutualistic steady state:** The trace and determinant of the community matrix $\mathbf{A}$ suggest that this point is stable if $\delta > 0$.

5.5.4 Nullclines and Phase Portraits

The equations for the nullclines for this model are similar to those in the competition model, but now with positive slope rather than negative slope.

- u_1 nullclines: $du_1/d\tau = 0$ when $u_1 = 0$ or $u_2 = \frac{u_1 - 1}{a_{12}}$.
- u_2 nullclines: $du_2/d\tau = 0$ when $u_2 = 0$ or $u_2 = 1 + a_{21}u_1$.

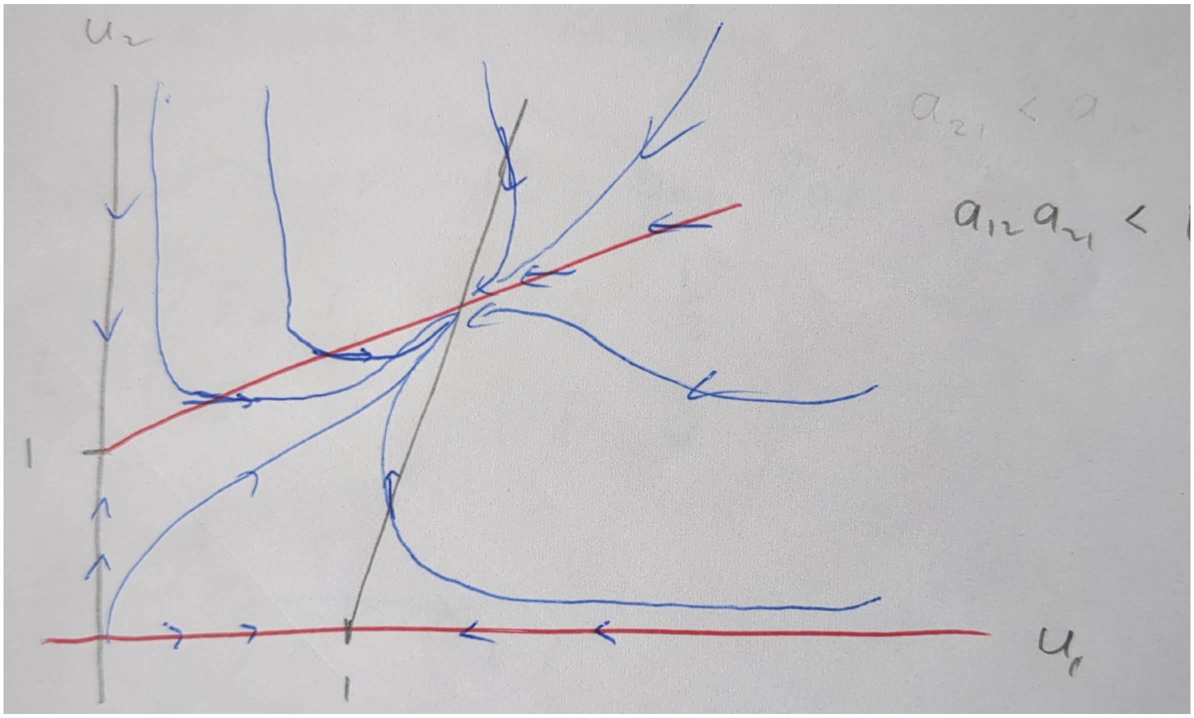

Figure 5.5: Phase portrait of mutualistic model when $a_{12}a_{21} < 1$.

Figure 5.5 illustrates the phase portrait of the mutualism model when $a_{12}a_{21} < 1$. The nullclines are shown in grey and red, with the flow lines in blue. The system exhibits a stable coexistence steady state, where both species benefit from the mutualistic interaction.

5.5.5 Limitations and Unbounded Growth

A cautionary note is that if the mutualistic coefficients $a_{12}a_{21}$ are too large, leading to $\delta < 0$, the model predicts unbounded growth, which is unrealistic. This phenomenon, known as May's "orgy of mutual benefaction," highlights the need for constraints in mutualism models to avoid predicting ecological impossibilities.

Through this mutualism model, we gain insights into how species interactions can foster increased growth and stability, contrasting with competitive dynamics. It underscores the diversity of ecological interactions and their varying implications for species survival and community structure.

5.6 Exercises

5.6.0.1 Two-species model 1

Exercise 5.1.

Consider a model for the interaction of two species with populations N_1 and N_2

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \tag{5.29}$$

$$\frac{N_2}{dt} = r_2 N_2 \left(1 - b_{21}\frac{N_1}{K_2}\right), \tag{5.30}$$

where all the parameters are positive.

a) What type of interaction exists between N_1 and N_2?

b) Non-dimensionalize the system by introducing $u = N_1/K_1$ and $v = N_2/K_2$ as well as a non-dimensional time variable. What are the resulting non-dimensional parameters? Give the equations of motion for u and v in terms of these parameters.

c) Determine the steady states in the non-dimensionalised system. Investigate their stability. At what values of the parameters do bifurcations take place?

d) Determine the nullclines and use these to make rough phase-plane sketches (You will need two sketches).

e) Describe under what ecological circumstances N_2 becomes extinct.
   Do the same for N_1. Show that the principle of competitive exclusion holds irrespective of the size of the parameters.

5.6.0.2 Two-species model 2

Exercise 5.2.

A model for the interaction between two species with populations N_1 and N_2 is determined to be

$$\begin{aligned} \frac{dN_1}{dt} &= rN_1\left(1-\frac{N_1}{K}\right) - aN_1N_2\left(1-\exp(-bN_1)\right), \\ \frac{dN_2}{dt} &= -dN_2 + cN_2\left(1-\exp(-bN_1)\right), \end{aligned} \tag{5.31}$$

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

a) Introducing the dimensionless variables and parameters

$$u = \frac{N_1}{K}, \quad v = \frac{aN_2}{r}, \quad \tau = rt, \quad \beta = bK, \tag{5.32}$$

   show that

$$\begin{aligned} \frac{du}{d\tau} &= u(1-u) - uv\left(1-e^{-\beta u}\right), \\ \frac{dv}{d\tau} &= -\delta v + \alpha v\left(1-e^{-\beta u}\right), \end{aligned} \tag{5.33}$$

   giving the positive constants α and δ in terms of c, d and r.

b) Describe the relevance of each term and, hence, determine the type of interaction between the two populations.

c) Show that the non-negative fixed points are given by $(u^*, v^*) = (0,0), (1,0)$ and $(u_1, (1-u_1)\alpha/\delta)$, where $u_1 = -\ln(1-\delta/\alpha)/\beta$, and that the steady state where u^* and v^* are both non-zero can only exist if $\alpha > \delta$ and $\beta > \beta_c = -\ln(1-\delta/\alpha)$.

d) Show that the community matrix, A, is given by

$$A = \begin{pmatrix} 1-2u-v(1-e^{-\beta u})-\beta uve^{-\beta u} & -u\left(1-e^{-\beta u}\right) \\ \alpha v\beta e^{-\beta u} & -\delta+\alpha(1-e^{-\beta u}) \end{pmatrix}. \tag{5.34}$$

e) Assuming henceforth that $\delta/\alpha < 1$, determine the linear stability of each of the fixed points.

f) Sketch the (u, v) phase portrait to indicate the stability of each steady state for the two cases $\beta > \beta_c$ and $0 < \beta < \beta_c$ (remember $\alpha > \delta$).

5.6.0.3 Predator-prey model with Allee effect

Exercise 5.3.

Consider the predator-prey model with Allee effect in the prey:

$$\begin{aligned} \frac{dN}{dT} &= rN\left(\frac{N}{K_0} - 1\right)\left(1 - \frac{N}{K}\right) - cNP, \\ \frac{dP}{dT} &= bNP - mP, \end{aligned} \tag{5.35}$$

where $N(T)$ is the number of prey and $P(T)$ is the number of predators at time T, and r, K, c, b, m are positive constants with $0 < K_0 < K$. The populations $N(T), P(T)$ are non-negative quantities.

(a) Provide brief biological interpretations for r, K, K_0, c, b, m for the above predator-prey model. What is the biological role of K_0 in the modified prey growth rate?

(b) Introduce the dimensionless variables $\frac{N}{K} = x$, $\frac{cP}{r} = y, rT = t$ and show that the above system can be reduced to

$$\begin{aligned} \frac{dx}{dt} &= x\left(\frac{x}{y} - 1\right)(1 - x) - y = x[g(x) - y], \\ \frac{dy}{dt} &= \beta(x - \alpha y). \end{aligned} \tag{5.36}$$

How are the new dimensionless constants α, β expressed in terms of the original parameters?

(c) For the dimensionless system:

  i) Calculate the nullclines, clearly stating any conditions for their existence.

  ii) Use your answer from (i) to sketch nullclines, depicting their intersections and the vector field direction along each isocline in the phase plane.

  iii) Find the fixed points.

(d) For the non-trivial fixed point, where both predators and preys may coexist:

  i) Calculate the Jacobian at this point in terms of the function $g(x), g'(x)$, where $'$ denotes derivative in respect with x.

ii) Evaluate the characteristic equation and study the stability of this fixed point as the parameter   varies within the range $< \; < 1$, classifying the non-trivial fixed point accordingly (i.e. node, spiral, centre or saddle point).

iii) Calculate the critical point where the Hopf bifurcation occurs and give an estimate for the period of oscillation.

6 Epidemics

> "As a matter of fact, all epidemiology, concerned as it is with the variation of disease from time to time or from place to place, must be considered mathematically, however many variables are implicated, if it is to be considered scientifically at all."
> – Sir Ronald Ross

Mathematical epidemiology applies mathematical modelling and statistical analysis to understand the spread of infectious diseases within populations. This is an important topic for several reasons:

1. *Control and prevention of diseases*: Mathematical models can be used to predict the spread of infectious diseases, estimate the effectiveness of control measures, and inform public health policy. By studying mathematical epidemiology, researchers and public health officials can develop strategies to prevent and control the spread of diseases, which can save lives and reduce healthcare costs.
2. *Improved disease surveillance*: Mathematical models can also be used to estimate disease incidence, prevalence, and mortality rates, which can help to improve disease surveillance systems. By accurately tracking disease outbreaks, public health officials can respond quickly to control and prevent further spread of the disease.
3. *Understanding disease transmission dynamics*: Mathematical models can provide insight into the transmission dynamics of infectious diseases, such as how they spread within populations, how they interact with different populations, and how they evolve over time. This understanding is critical for developing effective disease control measures and for predicting the potential impact of emerging diseases.
4. *Development of vaccines and treatments*: Mathematical modelling can aid in the development of new vaccines and treatments for infectious diseases. By understanding the transmission dynamics and the immune response to diseases, researchers can develop more effective vaccines and treatments that can prevent or reduce the severity of infections.

Before we get started, let us explain some terms used to describe different levels of disease prevalence and spread:

1. *Epidemic*: An epidemic refers to the sudden increase in the number of cases of a disease above what is normally expected in a given population and geographic area. The outbreak is usually limited to a specific community or region and can be caused by a new or re-emerging infectious agent. The epidemic may last for several weeks or months before it is brought under control.
2. *Pandemic*: A pandemic is an epidemic that has spread over a larger geographic area, often spanning multiple countries or continents. A pandemic is usually caused by a new strain of an existing virus or by a completely new virus that can spread quickly and easily from person to person. Pandemics can have a significant impact on public health and can cause widespread illness and death.
3. *Endemic*: An endemic disease is one that is regularly found in a population or geographic area at a consistent and predictable rate. Endemic diseases may cause illness and death but are typically well-controlled by routine public health measures, such as vaccination and surveillance. For example, malaria is endemic in many parts of the world, and measures such as mosquito control and antimalarial medications are used to prevent and treat the disease.

6.1 SIR model

The SIR model is a very idealised mathematical model that is commonly used to describe the spread of infectious diseases in a population. The acronym SIR stands for Susceptible, Infected, and Recovered, which are the three main compartments of the model.

The SIR model was first introduced in 1927 by Kermack and McKendrick in their landmark paper “A Contribution to the Mathematical Theory of Epidemics”. The model was developed in response to the major epidemics of the early 20th century, such as the Spanish flu pandemic of 1918-1919, which highlighted the need for a quantitative understanding of the spread of infectious diseases.

The SIR model was one of the first mathematical models to be developed for the study of infectious disease dynamics, and it remains one of the most widely used and influential models in the field of mathematical epidemiology. The model has been used to study a wide range of infectious diseases, including measles, tuberculosis, HIV/AIDS, and COVID-19, and has been extended and adapted to address new challenges and incorporate new data sources.

The SIR model and its variants have played a key role in informing public health policy and practice, by providing insights into the impact of different intervention strategies, such as vaccination, quarantine, and social distancing. The model has also helped to guide the design of clinical trials and the development of new drugs and vaccines, and has contributed to our understanding of the fundamental principles of infectious disease transmission.

6.1.1 Three-compartment model

In the SIR model, individuals in a population are divided into three groups: those who are susceptible to the disease (S), those who are infected with the disease (I), and those who have recovered from the disease and are now immune (R). The model assumes that individuals can move between these compartments over time as the disease spreads through the population.

The R component is also sometimes referred to as the "Removed" component in case where it also contains individuals that have been removed from being affected by the illness by other causes. For example in the case of a fatal disease they might have died.

The SIR model is based on a set of ordinary differential equations, which describe the rate of change of each compartment over time. The equations are

$$\begin{aligned} \frac{dS}{dt} &= -\beta IS/N, \\ \frac{dI}{dt} &= \beta IS/N - \gamma I, \\ \frac{dR}{dt} &= \gamma I, \end{aligned} \tag{6.1}$$

where:

- S is the number of susceptible individuals in the population
- I is the number of infected individuals in the population
- R is the number of recovered (and immune) individuals in the population
- $N = S + I + R$ is the total population size
- β is the transmission rate of the disease, which describes how easily the disease is transmitted from an infected individual to a susceptible individual
- γ is the recovery rate of the disease, which describes how quickly infected individuals recover and become immune to the disease

The first equation describes the rate of change of the susceptible compartment over time. It states that the number of susceptible individuals decreases over time as they become infected with the disease at a rate proportional to the proportion I/N of infected individuals and the transmission rate β. The minus sign indicates that the number of susceptible individuals is decreasing over time.

The second equation describes the rate of change of the infected compartment over time. It states that the number of infected individuals increases over time at the same rate at which the susceptibles become infected, and decreases over time as infected individuals recover at a rate γ.

The third equation describes the rate of change of the recovered compartment over time. It states that the number of recovered individuals increases over time as infected individuals recover and become immune at the recovery rate γ.

We can represent the SIR model graphically by a directed graph with one node for each component and directed edges between the nodes to represent the flow of individuals between the compartments. This is illustrated in Figure 6.2. We have labeled the edges by the per-capita rates.

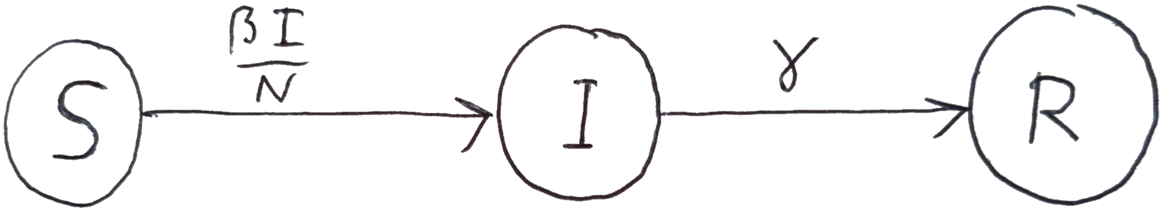

Figure 6.1: Graphical representation of the SIR model.

6.1.2 Assumptions made by SIR model

Like all models, the SIR model makes a number of simplifying assumptions to make the calculations tractable and the results interpretable. It is important to note that therefore an SIR model will not capture all of the nuances of disease transmission in a real population. The assumptions made by the SIR model include:

1. Fixed population: The SIR model assumes that the total population size $N = S + I + R$ is fixed and does not change over time. We can see that by observing that
$$\frac{dN}{dt} = \frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} = 0. \tag{6.2}$$
So there is no population dynamics such as birth or natural death (death from the illness itself can be included by viewing the R component as the "removed" component) or immigration or emigration. Neglecting population dynamics is fine if the spread of the disease happens much faster than the population dynamics.
2. Well-mixed population: The SIR model assumes that the population is well-mixed, meaning that all individuals have the same probability of coming into contact with one another, regardless of their location or social network. That is why the total rate of infection is simply proportional to both S and I, which is also known as the *mass-action dynamics*, a concept taken over from the modelling of chemical reactions.
3. No vaccinations: The SIR model assumes that there are no vaccinations available for the disease, and that individuals can only become immune to the disease by recovering from the infection.

4. No incubation period: The SIR model assumes that there is no incubation period, which means that individuals move directly from the susceptible compartment to the infectious compartment once they become infected. This assumption is often referred to as the "instantaneous transmission" assumption.

   However, in reality, many infectious diseases have an *incubation period*, during which the person is infected but not yet infectious to others. We will later discuss an extension of the SIR model called the SEIR model in which a new compartment is added, called the exposed (E) compartment. The exposed compartment represents individuals who have been infected but are not yet infectious.

5. Constant transmission and recovery rates: The SIR model assumes that the transmission rate β and the recovery rate γ remain constant over time. Constant β means that the probability of an infected individual transmitting the disease to a susceptible individual is the same at any point during the epidemic as well as at any point during an individual's illness. Similarly, constant γ means that the probability of and infected individual recovering from the illness is the same at any time.

   In reality, the transmission rate and recovery rate of an infectious disease can vary over time due to factors such as changes in behavior and public health interventions, or evolution of the virus.

6. No loss of immunity: The SIR model assumes that individuals who recover from the disease become permanently immune to the disease and do not lose their immunity over time. This means that individuals who have recovered from the disease cannot become re-infected. We will however later make modifications of the model that allow for loss of immunity.

7. No age structure: The SIR model assumes that the population is homogeneous, meaning that all individuals have the same susceptibility, infectiousness, and recovery rates. This means that the model does not take into account the age structure of the population, which can affect disease transmission.

8. No spatial structure: The SIR model does not model how the disease spreads spatially. We will however later introduce spatial structure and model the movement of infected individuals so that we can study how the disease spreads through space.

Even though the assumptions made by the SIR model may not be true in the real world, the model still provides a useful framework for understanding the spread of infectious diseases and how different interventions can affect the course of an outbreak.

6.1.3 Condition for an epidemic

Let us investigate the possibility of an epidemic. So we start with initial conditions where the number of infecteds is small and the number of susceptibles is high. There are no recovereds yet. We'll write the initial conditions as

$$S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0, \tag{6.3}$$

with $S_0 \approx N$ and $I_0 << N$.

In order for an epidemic to start we need a positive rate of increase in the number of infecteds. Thus we need

$$\left.\frac{dI}{dt}\right|_{t=0} = \beta I_0 S_0/N - \gamma I_0 > 0. \tag{6.4}$$

This happens when

$$R_0 := \frac{\beta S_0}{\gamma N} > 1. \tag{6.5}$$

We have introduced the **basic reproduction ratio** R_0. It is a key parameter in infectious disease epidemiology that measures the average number of secondary infections that a single infectious individual will produce. It is a useful metric for understanding the potential for an infectious disease to spread through a population, because if R_0 is greater than 1, then an epidemic can occur, as each infectious individual will produce more than one secondary infection on average, leading to a sustained increase in the number of infected individuals. IfR_0 is less than 1, then an epidemic can not occur, as each infectious individual will produce less than one secondary infection on average, leading to a decline in the number of infected individuals over time.

The basic reproduction ratio is also sometimes referred to as the *basic reproductive number*. Do not call it the *basic reproductive rate* because it is not a rate. There is also potential confusion due to the notation between R_0 and $R(0)$.

It is interesting to observe there are three ways an epidemic can start:

1) The infectiousness of the illness can increases until $\beta > \gamma \frac{N}{S_0}$.
2) The recovery rate drops until $\gamma < \beta \frac{S_0}{N}$
3) The number of infecteds rises until $S_0 > \frac{\gamma}{\beta} N$.

6.2 How an epidemic unfolds

Let us think about how an epidemic unfolds, once started. The epidemic begins with an initial number of infectious individuals, and as these individuals come into contact with susceptible individuals, the number of infectious individuals increases, and the number of susceptible individuals decreases. The number of individuals in the recovered compartment also increases as more individuals recover from the infection and become immune to the disease.

The epidemic reaches its peak when the number of infectious individuals in the population is at its maximum. After this point, the number of infectious individuals begins to decrease, and the number of recovered individuals continues to increase. The epidemic ends when the number of infectious individuals reaches zero and the disease is no longer spreading in the population.

As is usual with non-linear models, a direct solution of the set of differential equations in Eq. 6.1 is only possible numerically. Such a numerical solution is displayed in Figure 6.2.

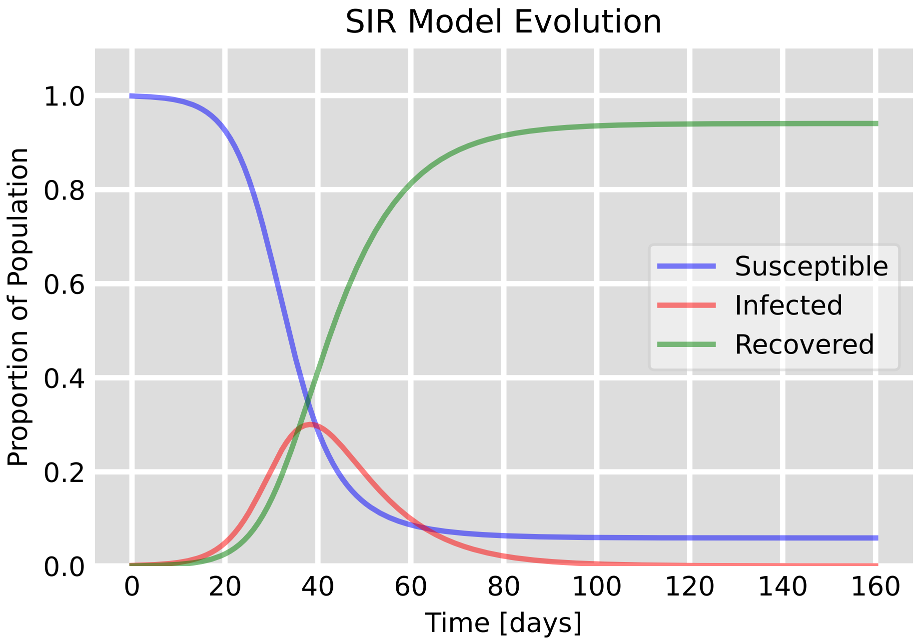

Figure 6.2: Evolution of an epidemic as described by the SIR model. The graph shows the dynamics of the susceptible S, infected I, and recovered R population fractions over time. In this scenario, we start with a single infected individual in a population of 1000, with a contact rate of $\beta = 0.3$ and a recovery rate of $\gamma = 0.1$. The plot demonstrates how the infection spreads through the population, peaks, and eventually declines as individuals recover and gain immunity.

We however are interested in analytic insights. It turns out that it is easy to determine the shape of the trajectories in the SIR phase space.

6.2.1 Trajectory in S-I plane

First we will determine how the number of infecteds changes with the number of susceptibles. This is described by the differential equation

$$\frac{dI}{dS} = \frac{dI/dt}{dS/dt} = \frac{\beta IS - \gamma IN}{-\beta IS} = -1 + \frac{\gamma}{\beta}\frac{N}{S} \tag{6.6}$$

We can easily integrate this equation:

$$\int_{I_0}^{I(S)} d\tilde{I} = \int_{S_0}^{S} \left(-1 + \frac{\gamma N}{\beta \tilde{S}}\right) d\tilde{S} \tag{6.7}$$

gives

$$I(S) - I_0 = -S + S_0 + \frac{\gamma N}{\beta} \log\left(\frac{S}{S_0}\right), \tag{6.8}$$

which we can rewrite as

$$I(S) = N - S + \frac{\gamma N}{\beta} \log \frac{S}{S_0}, \tag{6.9}$$

where we used that $N = S_0 + I_0$.

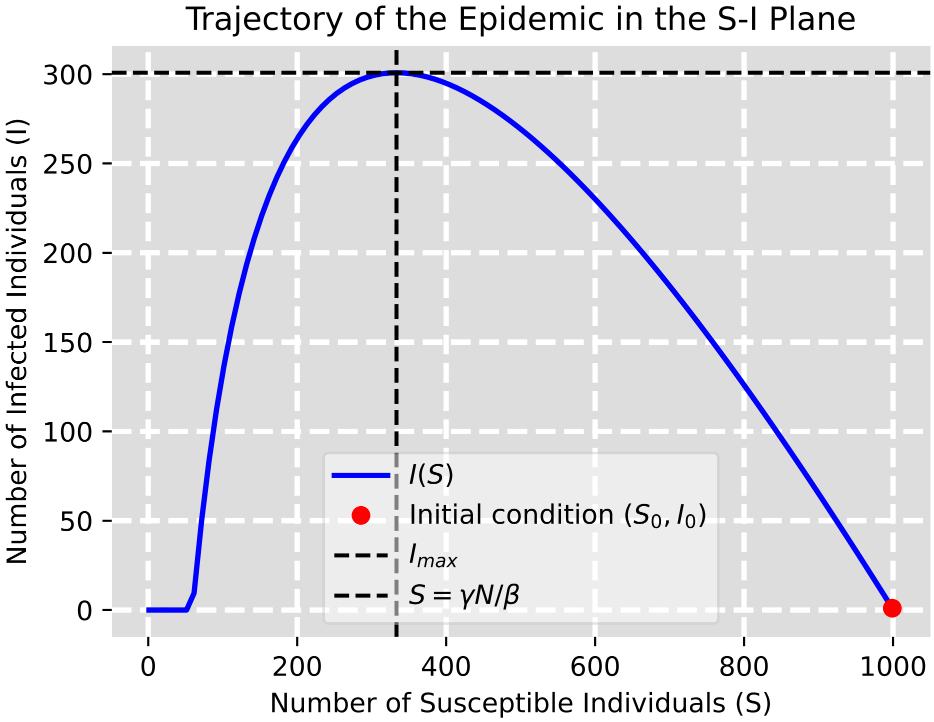

Figure 6.3: Shape of epidemic in S-I plane

This is depicted in Figure 6.3. It agrees with our earlier intuitive description of how an epidemic unfolds. The number of infecteds increases with the number of susceptibles until the number of susceptibles is low enough that the number of infecteds reaches its maximum. After this point, the number of infecteds begins to decrease as the number of susceptibles decreases further.

We can use this result to determine the number I_{max} of infected individuals at the peak of the epidemic.

6.2.2 Peak of an epidemic

Knowing the maximum number of infected individuals can help public health officials plan for the allocation of resources such as hospital beds, medical staff, and equipment. This information can be used to anticipate the surge in demand for healthcare services and to prepare for the management of large numbers of patients. It can also be used to guide the planning of interventions such as vaccinations in order to avoid overstretching the health system at the peak of the epidemic. We will discuss that in Section 6.3.

The peak is where $dI/dS = 0$, which according to Eq. 6.6 happens at $S = \gamma N/\beta$. Thus according to Eq. 6.9

$$I_{max} = I\left(\frac{\gamma}{\beta}N\right) = N - \frac{\gamma}{\beta}N\left(1 - \log\frac{\gamma N}{\beta S_0}\right) \tag{6.10}$$

We can express this in terms of the basic reproduction ratio R_0 as

$$I_{max} = N - \frac{S_0}{R_0}(1 + \log R_0) \tag{6.11}$$

6.2.3 Trajectory in R-S plane

Next we will determine the relationship between the number of susceptibles and the number of recovereds, by using

$$\frac{dS}{dR} = \frac{dS/dt}{dR/dt} = -\frac{\beta}{\gamma}\frac{S}{N}. \tag{6.12}$$

This is solved by

$$S(R) = S_0 \exp\left(-\frac{\beta}{\gamma}\frac{R}{N}\right) \tag{6.13}$$

This is depicted in Figure 6.4. We see in particular that the number of susceptibles decreases exponentially with the number of recovereds but never reaches zero. This means that at the time where the last infected individual recovers and the epidemic ends, there are still individuals that never caught the disease.

6.2.4 Size of an epidemic

By the size of an epidemic we mean the total number of individuals that catches the disease in the course of the epidemic. As we saw above, this will be less than the total population

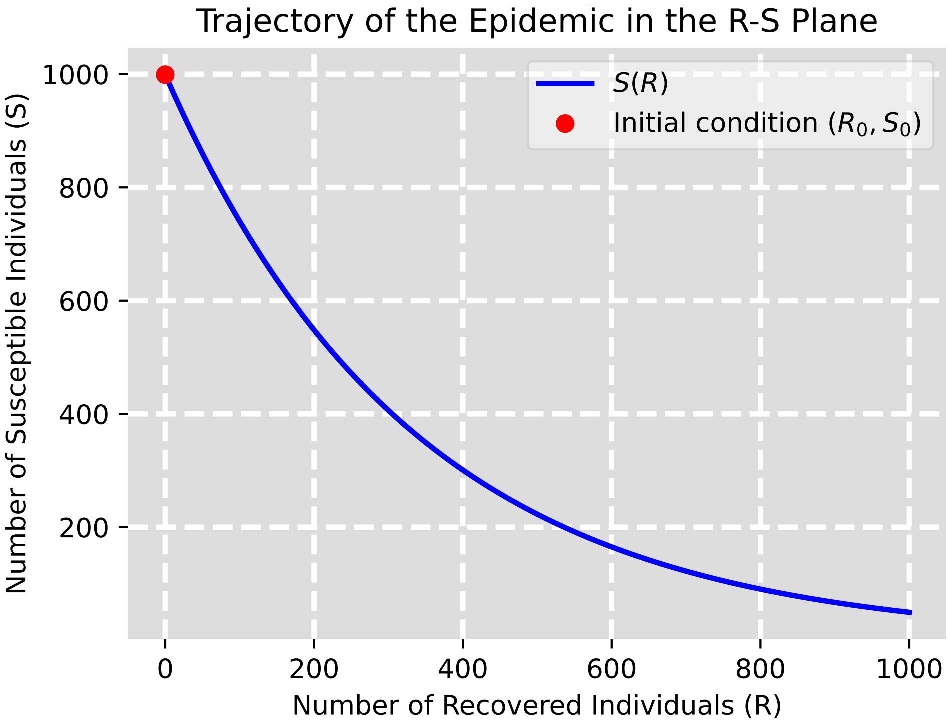

Figure 6.4: Shape of epidemic in R-S plane

number. Let us denote the numbers at the end of the epidemic by a subscript ∞. We have that $I(\infty) = 0$ and $S(\infty)$ is the solution to the equation

$$\begin{aligned} S_\infty = S(R_\infty) &= S_0 \exp\left(-\frac{\beta}{\gamma N} R_\infty\right) \\ &= S_0 \exp\left(-\frac{\beta}{\gamma N}(N - S_\infty)\right) \\ &= S_0 \exp\left(-\frac{\beta}{\gamma}\right) \exp\left(\frac{\beta}{\gamma N} S_\infty\right). \end{aligned} \tag{6.14}$$

This equation can be solved numerically. We can also get an approximate analytic solution in the case where the epidemic is large so that the fraction of the population that never gets infected is small compared to γ/β, $S_\infty/N << \gamma/\beta$. In this case we can expand the last exponential in the equation above to first order in S_∞/N to get the approximate equation

$$S_\infty \approx S_0 \exp\left(-\frac{\beta}{\gamma}\right)\left(1 + \frac{\beta}{\gamma N} S_\infty\right) \tag{6.15}$$

This we can now easily solve for S_∞ to get

$$S_\infty \approx \frac{S_0 e^{-\beta/\gamma}}{1 - \frac{\beta}{\gamma}\frac{S_0}{N} e^{-\beta/\gamma}}. \tag{6.16}$$

We can express this in terms of the basic reproduction ratio R_0 as

$$\frac{S_\infty}{S_0} \approx \frac{1}{e^{\beta/\gamma} - R_0}. \tag{6.17}$$

6.2.5 Initial exponential growth

At the start of the epidemic when the number of infecteds is small and hence the number of susceptibles is close to N, we can approximate

$$\frac{dI}{dt} = \beta I \frac{S}{N} - \gamma I \approx (\beta - \gamma) I \tag{6.18}$$

and hence

$$I(t) \approx I_0 e^{(\beta - \gamma)t}. \tag{6.19}$$

We can also get an equation for $R(t)$ by using the equation for $S(R)$ as follows:

$$\begin{aligned} \frac{dR}{dt} &= \gamma I = \gamma\,(N - R - S) \\ &= \gamma\left(N - R - S_0 \exp\left(-\frac{\beta}{\gamma}\frac{R}{N}\right)\right) \end{aligned} \tag{6.20}$$

At the initial stages of the epidemic while the number of recovereds is small we can expand the exponential and keep only the first-order term to get

$$\begin{aligned}\frac{dR}{dt} &\approx \gamma\left(N - R - S_0\left(1 - \frac{\beta}{\gamma}\frac{R}{N}\right)\right) \\ &= \gamma I_0 - \gamma(1 + R_0)R\end{aligned} \tag{6.21}$$

where we used that $N - S_0 = I_0$. Again we must not be confused by the notation: R_0 is the basic reproduction number, not the number of recovered at time 0. We have a linear differential equation for $R(t)$ that can be solved to give

$$R(t) = \frac{I_0}{1 + R_0}\left(1 - e^{-(1+R_0)\gamma t}\right). \tag{6.22}$$

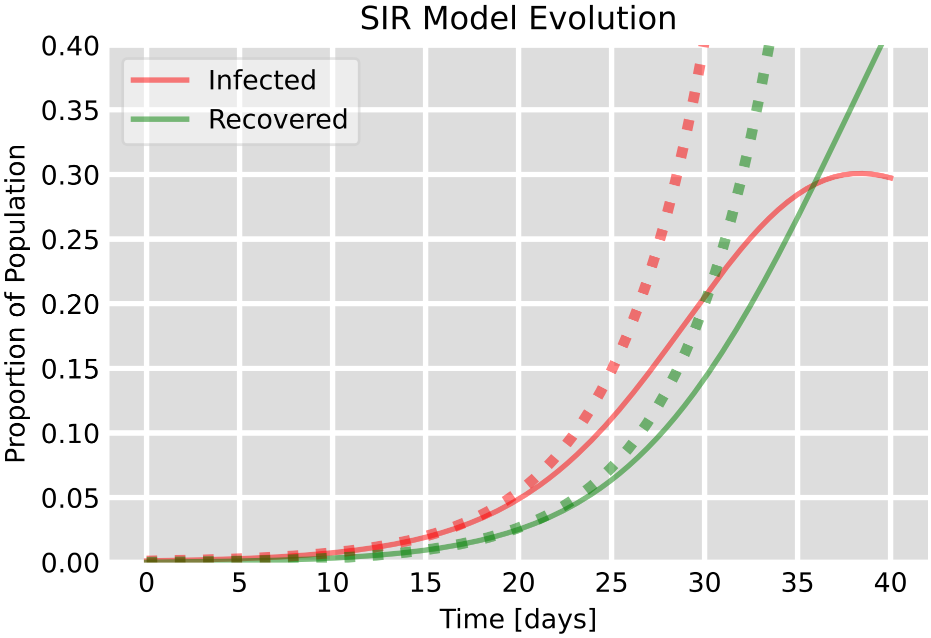

Figure 6.5: Exponential approximation of initial growth of an epidemic. The solid lines are the numeric solutions and the dotted lines are the exponential approximations.

Figure 6.5 compares the approximate expressions Eq. 6.19 and Eq. 6.22 that we have derived above with the numerical solution of the SIR model for the choice of parameters from Figure 6.2. We see that the exponential approximation is very good for the initial stages of the epidemic.

6.2.6 Doubling time

The doubling time of an epidemic is the time it takes for the number of infected individuals to double. It is an important metric for understanding the rate of spread of an infectious disease and can help public health officials anticipate the growth of an epidemic and plan for the allocation of resources such as hospital beds, medical staff, and equipment.

From our initial exponential approximation for $I(t)$ in Eq. 6.19, we see that the number of infecteds doubles in a time t_d when

$$2I_0 = I_0 e^{(\beta-\gamma)t_d}, \tag{6.23}$$

which gives the doubling time

$$t_d = \frac{\log 2}{\beta - \gamma}. \tag{6.24}$$

6.3 Effect of vaccination

Vaccination is a way to move individuals directly from the S component to the R component. This is illustrated in Figure 6.6 .

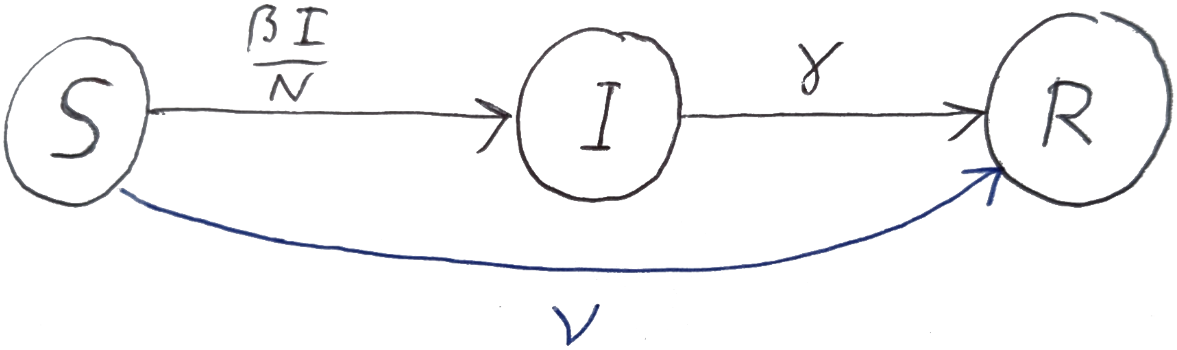

Figure 6.6: Graphical representation of the SIR model with vaccination.

The extra flow from S to R adds a negative term to the equation for dS/dt and a positive term to the equation for dR/dt. The equations become

$$\begin{aligned} \frac{dS}{dt} &= -\beta IS/N - \nu S, \\ \frac{dI}{dt} &= \beta IS/N - \gamma I, \\ \frac{dR}{dt} &= \gamma I + \nu S, \end{aligned} \tag{6.25}$$

where ν is the per-capita vaccination rate.

The modified model still has the feature that the total population size is constant, $dN/dt = 0$. This is because the vaccinated individuals simply move from the S compartment to the R compartment and stay part of the total population.

Also the expression for the basic reproduction number R_0 is the same as before: $R_0 = \beta S_0/\gamma N$. The condition for an epidemic to start is also the same: $R_0 > 1$. However, if a vaccination program has already been in place before the start of an epidemic, the number S_0 of susceptibles is reduced and hence the basic reproduction number is reduced. If the proportion of unvaccinated individuals in the population S_0/N is less than γ/β, then the basic reproduction number is below 1 and the epidemic will not start. Said differently, one needs to only vaccinate a proportion $1 - \gamma/\beta$ of the population to prevent an epidemic from starting.

But even a vaccination program that does not prevent an epidemic from starting can have a large effect on the size of the epidemic. This is because the number of susceptibles is reduced and hence the number of infecteds at the peak of the epidemic is reduced. To understand this in detail we will repeat the analysis from sections Section 6.2.1 and Section 6.2.2 but with the modified equations Eq. 6.25.

We now have

$$\frac{dI}{dS} = \frac{\beta IS - \gamma IN}{-\beta IS - \nu S} = \frac{\beta - \gamma N/S}{-\beta - \nu N/I}. \tag{6.26}$$

This is easily solved by separation of variables:

$$\int_{I_0}^{I(S)} \left(-\beta - \frac{\nu N}{\tilde{I}}\right) d\tilde{I} = \int_{S_0}^{S} \left(\beta - \frac{\gamma N}{\tilde{S}}\right) d\tilde{S}. \tag{6.27}$$

These integrals are easy to perform, and we get

$$I(S) + \frac{\nu N}{\beta} \log \frac{I(S)}{I_0} = N - S + \frac{\gamma N}{\beta} \log \frac{S}{S_0}. \tag{6.28}$$

As before, the peak of the epidemic is where $dI/dS = 0$, which still happens at $S = \gamma N/\beta$, as in the case without vaccination, because vaccination did not affect the equation for dI/dt. Thus we again get the number of infecteds at the peak of the epidemic as $I(\gamma N/\beta)$. Thus

$$I_{max} + \frac{\nu N}{\beta} \log \frac{I_{max}}{I_0} = N - \frac{\gamma N}{\beta}\left(1 - \log \frac{\gamma N}{\beta S_0}\right) = I_{max}(\nu = 0), \tag{6.29}$$

where we have recognised the right-hand side as the expression for the peak of the epdidemic in the absence of vaccinations. We can see that the number of infecteds at the peak of the epidemic is reduced by the vaccination rate ν.

6.4 Effect of loss of immunity

Unfortunately, immunity to many infectious diseases is not permanent, and individuals who have recovered from the disease can lose their immunity over time. This means that individuals

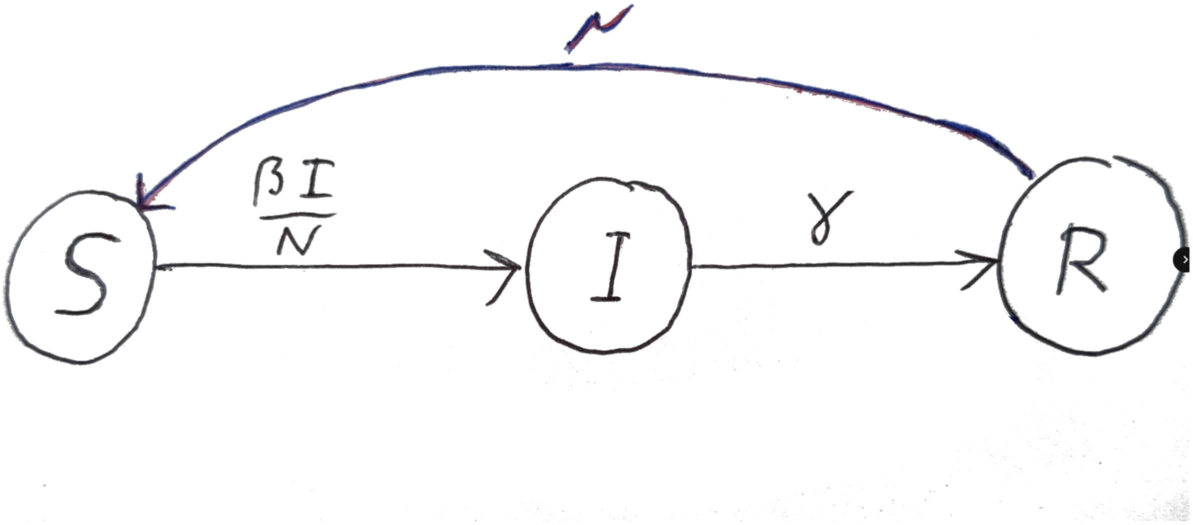

Figure 6.7: Graphical representation of the SIR model with loss of immunity.

who have recovered from the disease can become susceptible to the disease again and can be reinfected. This is illustrated in Figure 6.7 where we have added a flow from the R compartment back to the S compartment with a per-capita rate of μ.

The equations for the SIR model with loss of immunity are

$$\begin{aligned}\frac{dS}{dt} &= -\beta IS/N + \mu R,\\ \frac{dI}{dt} &= \beta IS/N - \gamma I,\\ \frac{dR}{dt} &= \gamma I - \mu R.\end{aligned} \tag{6.30}$$

We will now look at the steady states of the SIR model with loss of immunity. There is of course the disease-free state where the number of infecteds is $I^* = 0$ and everyone has lost their immunity, so $R^* = 0$ and $S^* = N$. But now there is also a new steady state where the number of infecteds is non-zero and the number of recovereds is non-zero. We can find this steady state by setting the time derivatives in Eq. 6.30 to zero. From $dR/dt = 0$ we get

$$R^* = \frac{\gamma}{\mu} I^*. \tag{6.31}$$

From $dI/dt = 0$ we get

$$S^* = \frac{\gamma}{\beta} N. \tag{6.32}$$

From $N = S^* + I^* + R^*$ we get

$$I^* = N \frac{1 - \frac{\gamma}{\beta}}{1 + \frac{\gamma}{\mu}}. \tag{6.33}$$

This is the endemic steady state of the SIR model with loss of immunity. We see that the number of infecteds at the endemic steady state is reduced by the loss of immunity rate μ.

We now want to determine whether this endemic state is stable or not. We will do this by linearising the equations Eq. 6.30 around the endemic steady state. We will then determine the eigenvalues of the Jacobian matrix at the endemic steady state. If all eigenvalues have negative real parts, the endemic steady state is stable. If at least one eigenvalue has a positive real part, the endemic steady state is unstable.

We choose to view the SIR model with loss of immunity as a two-dimensional model for the variables I and R. We can then write the equations Eq. 6.30 as

$$\begin{aligned} \frac{dI}{dt} &= \beta \frac{I(N-I-R)}{N} - \gamma I, \\ \frac{dR}{dt} &= \gamma I - \mu R. \end{aligned} \tag{6.34}$$

We now write $I(t) = I^* + i(t)$ and $R(t) = R^* + r(t)$ where $i(t)$ and $r(t)$ are small perturbations around the endemic steady state. We then linearise the equations Eq. 6.34 around the endemic steady state by keeping only terms linear in $i(t)$ and $r(t)$. We get

$$\begin{aligned} \frac{di(t)}{dt} &= \frac{\beta}{N}\left(N - 2I^* - R^*\right) i(t) - \gamma\, i(t) - \frac{\beta I^*}{N} r(t), \\ \frac{dr(t)}{dt} &= \gamma\, i(t) - \mu\, r(t). \end{aligned} \tag{6.35}$$

We solve this by making the Ansatz $i(t) = v_1 e^{\lambda t}$ and $r(t) = v_2 e^{\lambda t}$. Substituting this into Eq. 6.35 and dividing by $e^{\lambda t}$ gives

$$\begin{aligned} \lambda v_1 &= \frac{\beta}{N}\left(N - 2I^* - R^*\right) v_1 - \gamma v_1 - \frac{\beta I^*}{N} v_2, \\ \lambda v_2 &= \gamma v_1 - \mu v_2. \end{aligned} \tag{6.36}$$

We can write this as a matrix equation

$$\lambda \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = A \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}, \tag{6.37}$$

where

$$A = \begin{pmatrix} \frac{\beta}{N}\left(N - 2I^* - R^*\right) - \gamma & -\frac{\beta I^*}{N} \\ \gamma & -\mu \end{pmatrix}. \tag{6.38}$$

When we evaluate this Jacobian matrix A at the disease-free state we get

$$A(0,0) = \begin{pmatrix} \beta - \gamma & 0 \\ \gamma & -\mu \end{pmatrix}. \tag{6.39}$$

The eigenvalues of this matrix are $\lambda_1 = \beta - \gamma$ and $\lambda_2 = -\mu$. If $\beta > \gamma$ then one of the eigenvalues is positive and one negative, meaning that the disease-free steady state is unstable. If $\beta < \gamma$ then both eigenvalues are negative, meaning that the disease-free steady state is stable.

When we evaluate the Jacobian matrix A at the endemic steady state we can use the relation $\beta(N - I^* - R^*)/N - \gamma = 0$ to get

$$A(I^*, R^*) = \begin{pmatrix} -\frac{\beta I^*}{N} & -\frac{\beta I^*}{N} \\ \gamma & -\mu \end{pmatrix}. \tag{6.40}$$

This time we can not easily read off the eigenvalues, so we calculate the trace and the determinant:

$$\begin{aligned} \mathrm{Tr}(A) &= -\frac{\beta I^*}{N} - \mu, \\ \mathrm{Det}(A) &= \frac{\beta I^*}{N}(\mu + \gamma). \end{aligned} \tag{6.41}$$

We see that the trace is negative and the determinant is positive, meaning that both eigenvalues have negative real parts and the endemic steady state is stable.

6.5 Exercises

6.5.0.1 * SIR with vaccination and loss of immunity

Exercise 6.1.

In the lectures we studied the SIR model with vaccination rate ν and the SIR model with loss of immunity at a rate μ. Now consider the SIR model with both vaccination and loss of immunity. For simplicity assume that the minimum immunity time is $T = 0$.

1. Write down the differential equations for the numbers of susceptibles S, infecteds I and recovereds R.
2. Find the disease-free steady state.
3. Find the endemic steady state and give the condition on the parameters needed for its existence.
4. Now view this model as a two-dimensional model for the variables I and R. Determine the Jacobian matrix A for this model.
5. Evaluate A at the disease-free steady state and use this to classify this fixed point.
6. Evaluate A at the endemic steady state and use this to classify this fixed point.

You will want to compare your results to the results from the lecture and make sure that they make sense.

6.5.0.2 SIR with recrudescence

Exercise 6.2. Imagine a disease that, even after an individual has recovered from it, stays in the body in a dormant state and can be reactivated. Model this as a modification of the SIR model where recovereds can become infected again at a per-capita rate δ.

1. Determine the number of infecteds in the endemic state.
2. Is the endemic state stable for all positive values of the parameters?

6.5.0.3 SIR model with reinfections

Exercise 6.3. In Section 6.4 we studied the SIR model where recovered individuals lose their immunity at a per-capita rate μ so that they can then become infected again at a per-capita rate $\beta I/N$. The question was raised whether the same effect could be achieved by direct reinfections, i.e., a flow from the R component directly into the I component at a per-capita rate $\mu\beta I/N$. Settle this question by determining the number of infecteds in the steady state for the SIR model with direct reinfections and compare it to the corresponding result from Eq. 6.33.

6.5.0.4 Sex-structured SIR model

Exercise 6.4.

In a mathematical model for a certain venereal disease the male population is divided into susceptibles S, infectives I and removeds R. The female population is similarly divided; the three groups being denoted S', I' and R' (note that we use the prime to distinguish between male and female, not to indicate differentiation). The equations are

$$\begin{aligned} \frac{dS}{dt} &= -rSI', \quad & \frac{dI}{dt} &= rSI' - aI, \quad & \frac{dR}{dt} &= aI, \\ \frac{dS'}{dt} &= -r'S'I, \quad & \frac{dI'}{dt} &= r'S'I - a'I', \quad & \frac{dR'}{dt} &= a'I' \end{aligned} \tag{6.42}$$

where r, r' and a, a' are positive constants. The equations are with initial conditions $S(0) = S_0$, $I(0) = I_0$, $S'(0) = S'_0$, $I'(0) = I'_0$, $R(0) = R'(0) = 0$. The total male population is $N = S + I + R$ and the total female population $N' = S' + I' + R'$.

a) Show that N and N' are both constant.

b) Show that $S(t) = S_0 \exp\left(-\frac{r}{a'} R'(t)\right)$ and obtain another similar equation for S'.

c) Assuming that $I(\infty) = I'(\infty) = 0$ show that $S(\infty)$ and $S'(\infty)$ are found by solving simultaneously the equations

$$\begin{aligned} S(\infty) &= S_0 \exp\left(-\frac{r}{a'}(N' - S'(\infty))\right), \\ S'(\infty) &= S'_0 \exp\left(-\frac{r'}{a}(N - S(\infty))\right). \end{aligned} \tag{6.43}$$

7 Spatially-structured populations

We now want to keep track of how individuals are distributed over space. So instead of describing a population by its total number of individuals $N(t)$ we describe it by a population density $u(x,t)$, where $u(x,t)dx$ is the number of individuals in the interval $[x, x+dx]$ at time t. We can recover the total number of individuals by integrating the density over the entire spatial domain.

7.1 Derivation of PDE

In the non-spatial case we described the time evolution of the population by the equation

$$\frac{dN}{dt} = f(N), \tag{7.1}$$

where $f(N)$ is the net growth rate that encodes the difference between birth and death rates for the population as a whole. In the spatial case we have to consider the net growth rate of the population in a small interval $[x, x+dx]$. This is again given by a function f that encodes the births and deaths, but now we also have movement of individuals into or out of the interval. We write the rate of change of the number of individuals in the interval as

$$\frac{\partial}{\partial t}\int_{x_0}^{x_0+\Delta x} u(x,t)dx = \int_{x_0}^{x_0+\Delta x} f(u(x,t),x)dx + J(x_0) - J(x_0+\Delta x). \tag{7.2}$$

The flux $J(x)$ is defined as the net rate at which individuals move through point x from left to right. If more individuals move from right to left than from left to right, the flux is negative. We have indicated explicitly that f can depend on both the population density u at x as well as the position x itself. This is because the birth and death rates can depend on the local environment, for example the availability of resources or the presence of predators. The flux J can also depend on the local population density and the position. We did not indicate this explicitly to simplify the notation.

We now use the integral mean value theorem that states that for a continuous function $g(x)$ the integral over $g(x)$ over an interval $[a,b]$ is equal to $g(\xi)(b-a)$ for some $\xi \in [a,b]$. We apply this to the integrals in Eq. 7.2 to get

$$\partial_t u(\xi_1,t)\Delta x = f(u(\xi_2,t),\xi_2)\Delta x + J(x_0) - J(x_0+\Delta x) \tag{7.3}$$

for some $\xi_1, \xi_2 \in [x_0, x_0 + \Delta x]$. We now divide both sides by Δx,

$$\partial_t u(\xi_1, t) = f(u(\xi_2, t), \xi_2)x + \frac{J(x_0) - J(x_0 + \Delta x)}{\Delta x} \tag{7.4}$$

and take the limit $\Delta x \to 0$, where $\xi_1 \to x$ and $\xi_2 \to x$ and the difference quotient becomes the derivative, to get

$$\partial_t u(x, t) = f(u(x, t), x) - \partial_x J(x). \tag{7.5}$$

As discussed above, the flux J can depend on x both directly and through the population density $u(x, t)$. An important example is the case where the flux is proportional to the gradient of the population density,

$$J(x) = -D\partial_x u(x), \tag{7.6}$$

where D is the diffusion coefficient. This models random motion of the individuals. Each individual is equally likely to move right or left, but if there are more individuals on the left and less on the right, then the result is a net movement to the right. That is why the flux has the opposite sign of the gradient of the density.

This random motion gives us the reaction-diffusion equation

$$\partial_t u = f(u) + D\,\partial_x^2 u. \tag{7.7}$$

If there is no local population dynamics, the equation simplifies to the diffusion equation, also known as the heat equation. The diffusion term has the effect of smoothing out spatial inhomogeneities in the population density. Therefore the heat equation by itself is rather boring. However, as we will see later, the reaction term in combination with the diffusion term can lead to the formation of spatial patterns, such as travelling waves or stationary patterns.

7.2 Fishing model with diffusion

We now consider a model for a population of fish that is subject to fishing and that moves around randomly. We want to model a marine protected area where fishing is limited to avoid a collapse of the fish population. Figure 7.1 shows the spatial setup. The x-axis runs perpendicular to the shore, which is at $x = 0$. A marine protected area runs out upto a distance L from the shore. We assume that the marine protected area has infinite extension in the y-direction, so that we can ignore the y-coordinate and model the fish population as a function of x only.

Beyond $x = L$ there is no management of the fishing activity. We assume that the fishers are so efficient that they catch all fish that venture outside the protected area. So we set $u(x, t) = 0$ for $x \geq L$. This is of course an idealisation, but it allows us to focus on the dynamics within the protected area.

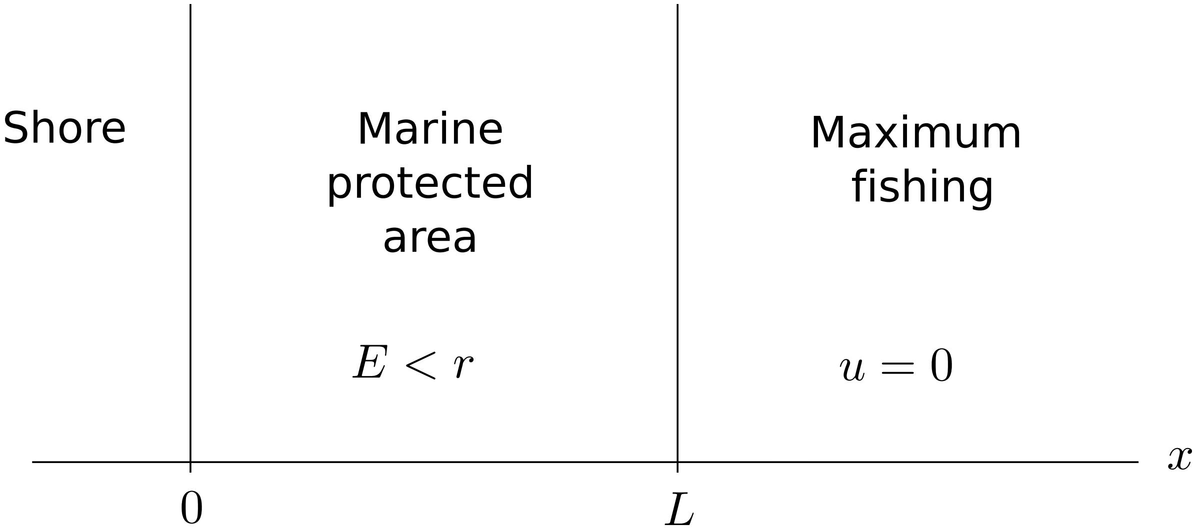

Figure 7.1: Sketch of the marine protected area

We assume that in the absence of fishing the population has a logistic growth rate. The population density $u(x,t)$ satisfies the equation

$$\partial_t u = ru\left(1 - \frac{u}{K}\right) - Eu + D\partial_x^2 u, \tag{7.8}$$

where r is the intrinsic growth rate, K is the carrying capacity, E is the fishing rate and D is the diffusion coefficient. The first term on the right-hand side describes the logistic growth, the second term the fishing and the third term the random motion of the fish.

In the protected area, the fishing rate E must certainly be below the intrinsic growth rate r, otherwise the population is guaranteed to die out. However we must also take into account that some fish will be lost when they randomly move out of the protected area and are then fished immediately. We expect this extra loss to be proportionally larger when the protected area is smaller. So when the marine protected area is planned, there will be a trade-off between the width L of the protected area and the allowed rate of fishing E. Our aim is to describe this trade-off precisely by finding the condition on E and L such that the population does not collapse.

To achieve our aim, we will need to solve the PDE. But before solving a PDE we always need to be clear about the boundary conditions on the solution. We have already discussed that we assume that $u(x,t) = 0$ for $x \geq L$, i.e., we have a Dirichlet boundary condition at $x = L$. At $x = 0$ we impose a no-flux boundary condition, which means that there are no fish moving from the sea onto the shore or the other way around. The no-flux boundary condition is the Neumann boundary condition $\partial_x u(0,t) = 0$.

The PDE in Eq. 7.81 is a nonlinear PDE, so we cannot solve it analytically in general. However, we can still make progress by realising that before the population goes extinct, it will get small.

We can then linearise the PDE around the extinction state $u = 0$ and solve the linearised equation. If the extinction steady state is linearly unstable, then the population will not go extinct.

Linearising the PDE Eq. 7.81 around the extinction state $u = 0$ means that we neglect the term u^2 in the logistic growth term. We then have the linearised equation

$$\partial_t u = (r - E)u + D\partial_x^2 u. \tag{7.9}$$

We can now solve this linear PDE with the method of separation of variables. We make the Ansatz $u(x,t) = X(x)T(t)$ and plug this into Eq. 7.9. We get

$$XT' = (r - E)XT + DX''T \tag{7.10}$$

and after dividing by XT we get

$$\frac{T'}{T} = r - E + D\frac{X''}{X}. \tag{7.11}$$

The left-hand side depends only on t and the right-hand side only on x. Therefore both sides must be equal to a constant, which we call γ. We then have the two ODEs

$$T' = \gamma T, \quad X'' = \frac{\gamma - r + E}{D}X = -\rho^2 X, \tag{7.12}$$

where, in order to save writing, we have introduced

$$\rho^2 = (r - E - \gamma)/D. \tag{7.13}$$

The solution of the time ODE is

$$T(t) = T(0)e^{\gamma t} \tag{7.14}$$

and the solution of the spatial ODE is

$$X(x) = A\cos(\rho x) + B\sin(\rho x), \tag{7.15}$$

where A and B are constants to be determined by the boundary conditions.

Imposing the no-flux boundary condition $\partial_x u(0,t)$ gives

$$X'(0) = -A\rho\sin(\rho 0) + B\rho\cos(\rho 0) = B\rho = 0. \tag{7.16}$$

So either $\rho = 0$ or $B = 0$. The case $\rho = 0$ gives the trivial solution $X(x) = A$, which is not interesting. So we take $B = 0$ and get $X(x) = A\cos(\rho x)$.

The Dirichlet boundary condition at $x = L$ gives $X(L) = A\cos(\rho L) = 0$. So either $A = 0$ or $\cos(\rho L) = 0$. The former gives rise to the zero solution, so we want the latter, which requires ρL to be an odd multiple of $\pi/2$, i.e.,

$$\rho = \rho_n = \frac{(2n+1)\pi}{2L} \tag{7.17}$$

for $n = 0, 1, 2, ...$ To each of these ρ_n there corresponds, according to Eq. 7.13, a

$$\gamma_n = r - E - D\rho_n^2 \tag{7.18}$$

and a solution

$$u_n(x,t) = X_n(x)T_n(t) = A_n e^{\gamma_n t}\cos(\rho_n x) \tag{7.19}$$

The general solution is then a linear combination of these solutions,

$$u(x,t) = \sum_{n=0}^{\infty} A_n e^{\gamma_n t}\cos(\rho_n x). \tag{7.20}$$

The condition for the population not to go extinct is that the extinction steady state is linearly unstable. This means that there is at least one γ_n with positive real part. We see from Eq. 7.18 that γ_n increases with n. So the condition for the population not to go extinct is that γ_0 is positive. This gives the condition

$$\gamma_0 = r - E - D\rho_0^2 = r - E - \frac{D\pi^2}{4L^2} > 0. \tag{7.21}$$

We can now solve this inequality for L to get the condition on the width of the marine protected area that ensures the population does not collapse.

$$L > \frac{\pi}{2}\sqrt{\frac{D}{r-E}}. \tag{7.22}$$

Alternatively we can solve the inequality for E to get the condition on the fishing rate that ensures the population does not collapse.

$$E < r - \frac{D\pi^2}{4L^2}. \tag{7.23}$$

This can now be used to inform policy decisions on the width of the marine protected area and the allowed fishing rate.

7.3 Invasion waves in SIR model

We now want to use our spatial modelling skills to study the spread of an infectious disease through space. For concreteness, think of a situation where rabies has infected foxes in Dover and we want to get an idea of how soon we will have rabid foxes in York. We model the fox population by the SIR model, where $S(x,t)$ is the density of susceptible foxes, $I(x,t)$ is the density of infected foxes and $R(x,t)$ is the density of removed foxes (which for rabies unfortunately means dead foxes). So where in Section 6.1 we had ordinary differential equations for the total number of susceptible, infected and removed foxes, we now have partial differential equations for the densities of susceptible, infected and removed foxes in space.

While foxes are usually very territorial and stay in their own territory, infected foxes become a bit insane and move around randomly. This is modelled by a diffusion term in the equation for the infected foxes. The equations are

$$\begin{aligned}\partial_t S &= -\beta \frac{SI}{N},\\ \partial_t I &= \beta \frac{SI}{N} - \gamma I + D\partial_x^2 I,\\ \partial_t R &= \gamma I,\end{aligned} \tag{7.24}$$

where $N = S + I + R$ is the total fox population density, β is the infection rate, γ is the recovery rate and D is the diffusion coefficient. For simplicity we study the movement in the x direction only. The above equations are valid for all x. We will later concentrate on the equations for I and S only, as R can then be calculated from $N = S + I + R$.

Before analysing these equations further, let us think about what we expect to happen. The infected foxes in Dover will infect more and more susceptible foxes. The infected foxes will then move around and infect susceptible foxes in neighbouring territories. This will lead to a wave of infection spreading out from Dover. The wave will move at a speed that depends on the infection rate, the recovery rate and the diffusion coefficient. The wave will have a front where the infected foxes are and a tail where the epidemic has died out.

To make the further analysis easier, we will non-dimensionalise the equations. We introduce the non-dimensional variables

$$u = S/N, \quad v = I/N, \quad \tilde{t} = \beta t, \tag{7.25}$$

Then the equations become

$$\begin{aligned}\partial_{\tilde{t}} u &= -uv\\ \partial_{\tilde{t}} v &= uv - \frac{\gamma}{\beta} v + \frac{D}{\beta}\partial_x^2 v.\end{aligned} \tag{7.26}$$

We now also introduce the non-dimensional spatial variable $\tilde{x} = \sqrt{\frac{\beta}{D}}x$ and the non-dimensional parameter $r = \frac{\gamma}{\beta}$. We now drop the tildes to avoid clutter and write the equations as

$$\begin{aligned}\partial_t u &= -uv\\ \partial_t v &= uv - rv + \partial_x^2 v.\end{aligned} \tag{7.27}$$

7.3.1 Travelling wave Ansatz and boundary conditions

We are looking for a solution describing the spread of the infection from Dover to York. We make the Ansatz that the solution is a travelling wave, i.e., that it is of the form

$$u(x, t) = U(z), \quad v(x, t) = V(z) \tag{7.28}$$

with $z = x - ct$ for some $c > 0$. This means that the wave is a right-moving wave. We plug this into Eq. 7.27 and get the system of ODEs

$$\begin{aligned} -cU' &= -UV, \\ -cV' &= UV - rV + V''. \end{aligned} \tag{7.29}$$

Next let us think about the boundary conditions. We expect that ahead of the wave all the individuals are still susceptible and there are no infecteds yet. So to the far right at $z = infty$ we have $u(\infty) = 1$ (corresponding to S=N) and $v(\infty) = 0$. Behind the wave the epidemic will have run its course and so $u(-\infty) = S_\infty/N =: a$ and $v(-\infty) = 0$. In other words, the travelling wave interpolates between the state before an epidemic (at $z = \infty$) and the state after an epidemic (at $z = -\infty$). We also have that the solution becomes flat as $z \to \pm\infty$, so in particular $V'(\pm\infty) = 0$.

We now massage the equations a bit to get them into a form that we can integrate more easily. From the first equation we see that $UV = cU'$ and also that $V = cU'/U = c(\log U)'$. We plug this into the second equation and get

$$-cV' = cU' - rc(\log U)' + V''. \tag{7.30}$$

Now that each term in the equation is a total derivative, we can integrate it by just removing the differentiations:

$$-cV = cU - rc\log U + V' + A, \tag{7.31}$$

where A is a constant of integration. We use the boundary condition at $z \to \infty$ to determine A:

$$0 = c - rc\log 1 + 0 + A \Rightarrow A = -c. \tag{7.32}$$

At $z \to -\infty$ we get

$$0 = ca - rc\log a + 0 - c \Rightarrow a - 1 = r\log a. \tag{7.33}$$

This equation is equivalent to Eq. 6.14 for S_∞ in the case where $S_0 = N$. Again this transcendental equation can only be solved numerically.

7.3.2 Wave speed

Next we want to learn about the wave speed c. We do this by linearising the equation around the leading edge of the wave, where V is very small and U is close to 1, i.e, $U = 1 - \epsilon$ for small ϵ. Substituting this into the second equation in 7.29 we get

$$-cV' = (1 - \epsilon)V - rV + V''. \tag{7.34}$$

Because both ϵ and V are small, we can neglect the product ϵV and get

$$-cV' = (1 - r)V + V''. \tag{7.35}$$

This is a linear ODE with constant coefficients and can thus be solved with the Ansatz $V(z) = e^{-\lambda z}$. Substituting this into the ODE and dividing by $e^{-\lambda z}$ gives

$$\lambda^2 - c\lambda + 1 - r = 0. \tag{7.36}$$

The solution of this quadratic equation is

$$\lambda = \frac{c \pm \sqrt{c^2 - 4(1-r)}}{2}. \tag{7.37}$$

We need λ to be real so that our solution correctly describes the exponential growth at the start of an epidemic, so we need the discriminant to be non-negative, i.e.,

$$c^2 - 4(1-r) \geq 0 \tag{7.38}$$

and thus we get a lower bound on the wave speed:

$$c \geq 2\sqrt{1-r}. \tag{7.39}$$

7.4 Turing instabilities

We now come to a very intriguing question: how can the complicated spatial patterns arise that one can observe in nature. One might have thought that to explain complicated patterns one would need complicated models that encode all that complexity. However, it turns out that patterns can arise from very simple, translation-invariant models. The key idea is that the spatially uniform steady state in a translation-invariant model can be unstable to small perturbations, which then grow and form spatial patterns. This is called a Turing instability.

We consider a system of two species, described by densities $u(x,t)$ and $v(x,t)$, that interact with each other locally but also move around randomly. The system is described by the reaction-diffusion equations

$$\begin{aligned} \frac{\partial u}{\partial t} &= f(u,v) + D_1 \frac{\partial^2 u}{\partial x^2}, \\ \frac{\partial v}{\partial t} &= g(u,v) + D_2 \frac{\partial^2 v}{\partial x^2}, \end{aligned} \tag{7.40}$$

where f and g are functions that describe the local dynamics of the two species. The diffusion terms model random motion of the individuals.

For values (u^*, v^*) of the densities that satisfy $f(u^*, v^*) = g(u^*, v^*) = 0$, the spatially homogeneous steady state $u(x,t) = u^*$, $v(x,t) = v^*$ is a solution of the system. Assume that in the absence of diffusion, this steady state is stable. Thus without diffusion, any perturbations to the spatially homogeneous steady state will decay. One would then expect that the spatially homogeneous steady state is stable also in the presence of diffusion, given that diffusion has the tendency to spread individuals out away from regions of higher concentration. The result would be the absence of any spatial structure in the solution. However, we will now see that this is not always the case. Rather counter-intuitively, the random motion of the individuals can destabilise the spatially homogeneous steady state and give rise to spatial patterns.

7.4.1 Deriving conditions for Turing instabilities

Mathematics is a great tool for dealing with counter-intuitive phenomena. We just have to do the maths and see what it tells us. So we now derive the equations that describe the time-evolution of small perturbations and solve them and see whether the perturbations grow or not. So we set

$$u(x,t) = u^* + \xi(x,t), \quad v(x,t) = v^* + \eta(x,t) \tag{7.41}$$

where $\xi(x,t)$ and $\eta(x,t)$ are small perturbations. If we plug this into Eq. 7.40 we get equations for the time evolution of the small perturbations:

$$\begin{aligned} \frac{\partial \xi}{\partial t} &= f(u^* + \xi(x,t), v^* + \eta(x,t))\xi + D_1 \frac{\partial^2 \xi}{\partial x^2}, \\ \frac{\partial \eta}{\partial t} &= g(u^* + \xi(x,t), v^* + \eta(x,t))\xi + D_2 \frac{\partial^2 \eta}{\partial x^2}. \end{aligned} \tag{7.42}$$

We now use Taylor expansions to linearise the equations. We expand f and g around (u^*, v^*) to first order and drop all terms that are higher order in ξ and/or η. This gives the linear PDEs

$$\begin{aligned} \frac{\partial \xi}{\partial t} &= \frac{\partial f}{\partial u}(u^*, v^*)\xi + \frac{\partial f}{\partial v}(u^*, v^*)\eta + D_1 \frac{\partial^2 \xi}{\partial x^2} \\ &= a_{11}\xi + a_{12}\eta + D_1 \frac{\partial^2 \xi}{\partial x^2}, \\ \frac{\partial \eta}{\partial t} &= \frac{\partial g}{\partial u}(u^*, v^*)\xi + \frac{\partial g}{\partial v}(u^*, v^*)\eta + D_2 \frac{\partial^2 \eta}{\partial x^2} \\ &= a_{21}\xi + a_{22}\eta + D_1 \frac{\partial^2 \xi}{\partial x^2}. \end{aligned} \tag{7.43}$$

Those partial derivatives of f and g with respect to u and v are familiar to us from the stability analysis in non-spatial models as the entries of the Jacobian matrix and we are using the same shorthand notation for them here.

We now make the harmonic wave Ansatz

$$\begin{aligned} \xi(x,t) &= B_1 e^{\sigma_k t} \sin(kx + \alpha), \\ \eta(x,t) &= B_2 e^{\sigma_k t} \sin(kx + \alpha). \end{aligned} \tag{7.44}$$

During your studies you will have seen this easy way to solve linear PDEs with constant coefficients already several times. Plugging this Ansatz into Eq. 7.43 and dividing by $e^{\sigma_k t} \sin(kx+\alpha)$ we get

$$\begin{aligned} \sigma_k B_1 &= a_{11}B_1 + a_{12}B_2 - k^2 D_1 B_1 \\ \sigma_k B_2 &= a_{21}B_1 + a_{22}B_2 k^2 D_2 B_2. \end{aligned} \tag{7.45}$$

We can write this in matrix form as

$$\sigma_k \begin{pmatrix} B_1 \\ B_2 \end{pmatrix} = A(k) \begin{pmatrix} B_1 \\ B_2 \end{pmatrix}. \tag{7.46}$$

where

$$A(k) = \begin{pmatrix} a_{11} - D_1k^2 & a_{12} \\ a_{21} & a_{22} - D_2k^2 \end{pmatrix}. \tag{7.47}$$

This looks very similar to what we get when we do the stability analysis of a non-spatial model, except that now we have a whole family of matrices $A(k)$, one for each k. The condition for the spatially homogeneous steady state to be stable is that all the eigenvalues σ_k of all the matrices $A(k)$ are negative. The spatially homogeneous steady state to be unstable is that there is at least one k for which the real part of σ_k is positive.

As we know from studying the stability of non-spatial models of two interacting species, an easy way to determine the stability is to look at the signs of the trace and the determinant of the matrix $A(k)$. For the trace we find

$$\operatorname{tr}(A(k)) = a_{11} - k^2D_1 + a_{22} - k^2D_2 = \operatorname{tr}(A(0)) - k^2(D_1 + D_2). \tag{7.48}$$

We are interested in the case where the steady state is stable in the absence of diffusion and is destabilised by the diffusion. Stability in the absence of diffusion requires $\operatorname{tr}(A(0)) < 0$. We see that in that case also $\operatorname{tr}(A(k)) < 0$ for all k because the k-dependent term $-k^2(D_1 + D_2)$ is negative. So the trace is not yet giving us a hint that there might be an instability. So next we look at the determinant.

For the determinant we find

$$\begin{aligned} \det(A(k)) &= (a_{11} - D_1k^2)(a_{22} - D_2k^2) - a_{12}a_{21} \\ &= D_1D_2k^4 - (D_1a_{22} + D_2a_{11})k^2 + \det(A(0)) \end{aligned} \tag{7.49}$$

Stability in the absence of diffusion tells us that $\det(A(0)) > 0$. We see that $\det(A(k))$ is a quadratic polynomial in k^2 with positive leading coefficient. Its graph is a parabola. This means that the determinant is positive for small k and for large k but there may be an intermediate region where the parabola dips below the axis and the determinant is negative in that region. Perturbations with wave numbers in that region would grow over time, making the homogeneous steady state unstable and leading to spatial structure. If that region exists, it is bounded by the values $k_\pm$ for which the determinant is zero. Using the quadratic formula we find that

$$k_\pm^2 = \frac{D_1a_{22} + D_2a_{11} \pm \sqrt{(D_1a_{22} + D_2a_{11})^2 - 4D_1D_2\det(A(0))}}{2D_1D_2}. \tag{7.50}$$

The unstable interval exists if $k_\pm^2$ are real and positive. They are real if the discriminant under the square root is non-negative. This gives the condition

$$(D_1a_{22} + D_2a_{11})^2 > 4D_1D_2\det(A(0)). \tag{7.51}$$

They are positive if the numerator is positive. This gives the condition

$$D_1a_{22} + D_2a_{11} > 0. \tag{7.52}$$

The condition for the spatially homogeneous steady state to be unstable is that both Eq. 7.51 and Eq. 7.52 are satisfied.

7.4.2 Understanding the conditions for Turing instabilities

We have now derived the conditions for Turing instabilities in terms of the entries of the Jacobian matrix $A = A(0)$ of the local dynamics of the two species and the diffusion coefficients:

$$\begin{aligned} &a) \qquad a_{11} + a_{22} < 0, \\ &b) \qquad a_{11}a_{22} - a_{12}a_{21} > 0, \\ &c) \qquad D_1 a_{22} + D_2 a_{11} > 0, \\ &d) \qquad (a_{11} + a_{22})^2 > 4(a_{11}a_{22} - a_{12}a_{21}). \end{aligned} \tag{7.53}$$

Conditions a) and b) are the conditions for the spatially homogeneous steady state to be stable in the absence of diffusion. Condition c) and d) are the condition for the spatially homogeneous steady state to be unstable in the presence of diffusion.

We will first look at what these conditions tell us about the sign structure of the Jacobian, which will introduce the concept of activator and inhibitor species. We make three observations:

1. We observe that condition a) implies that at least one of a_{11} and a_{22} is negative. We are free to choose the numbering of our species, so, without loss of generality, let's say that $a_{22} < 0$. This means that species 2 inhibits its own growth above the steady state. We call species 2 an **inhibitor** species.
2. From condition c) we see that if $a_{22} < 0$ then $a_{11} > 0$. This means that species 1 activates its own growth above the steady state. We call species 1 an **activator** species.
3. From condition b) we now observe that, because $a_{11}a_{22} < 0$, we must have that $a_{12}a_{21} < 0$.

Taking these three observations together tells us that there are only two possibilities for the sign structure of the Jacobian matrix:

$$\text{sign}(A) = \begin{pmatrix} + & - \\ + & - \end{pmatrix} \quad \text{or} \quad \text{sign}(A) = \begin{pmatrix} + & + \\ - & - \end{pmatrix}. \tag{7.54}$$

If the signs in the Jacobian are different from both of these possibilites you can immediately rule out a Turing instability.

Next we look at what our conditions a) to d) tell us about the magnitude of the diffusion coefficients. From condition a) we know that $a_{11} < -a_{22}$ and hence $-a_{11}/a_{22} < 1$. From condition c) we see that $D_1/D_2 < -a_{11}/a_{22}$. Putting these together gives $D_1/D_2 < 1$ and hence $D_1 < D_2$: **The inhibitor must diffuse faster than the activator**. This is a necessary condition for a Turing instability.

Exactly how much faster the inhibitor must diffuse than the activator depends on the details of the local interactions and we will next study this in a concrete example.

7.4.3 Example

Let's consider the following concrete reaction-diffusion system:

$$\begin{aligned} \partial_t u &= -u + u^2 v + D_1 \partial_x^2 u = f(u,v) + D_1 \partial_x^2 u, \\ \partial_t v &= b - u^2 v + D_2 \partial_x^2 v = g(u,v) + D_2 \partial_x^2 v. \end{aligned} \tag{7.55}$$

The Jacobian matrix of the local dynamics is

$$A = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} = \begin{pmatrix} -1 + 2uv & u^2 \\ -2uv & -u^2 \end{pmatrix}. \tag{7.56}$$

We are interested in the coexistence steady state (u^*, v^*) where both species coexist. Imposing that $f(u^*, v^*) = 0$ gives us that $u^* v^* = 1$ and then imposing that $g(u^*, v^*) = 0$ gives us that $u^* = b$ and hence $v^* = 1/b$. So the coexistence steady state is

$$(u^*, v^*) = \left(b, \frac{1}{b}\right). \tag{7.57}$$

The Jacobian matrix evaluated at the coexistence steady state is

$$A = \begin{pmatrix} 1 & b^2 \\ -2 & -b^2 \end{pmatrix}. \tag{7.58}$$

We see that the sign structure of this matrix is one of those in Eq. 7.54 that can give rise to a Turing instability. Species u is the activator and species v is the inhibitor.

Now let us check each of the conditions a) to d) from Eq. 7.53. Condition a) becomes $1 - b^2 < 0$ and hence $b^2 > 1$. Condition b) becomes $-b^2 + 2b^2 > 0$ which is automatically satisfied. Condition c) becomes $D_2 - b^2 D_1 > 0$ which implies $D_1 b^2 < D_2$, which means that the ratio $d = D_2/D_1 > b^2$. Condition d) becomes $(D_2 - b^2 D_1)^2 > 4 D_1 D_2 b^2$. Multiplying out the square and bringing everything to one side gives $b^4 D_1^2 - 6 D_1 D_2 + D_2^2 > 0$. We can rewrite this in terms of the ratio $d = D_2/D_1$ as

$$b^4 - 6db^2 + d^2 > 0. \tag{7.59}$$

The graph of the left-hand side against d is a parabola that opens upwards and has roots at

$$d_\pm = 3b^2 \pm \sqrt{9b^4 - b^4} = b^2(3 \pm \sqrt{8}). \tag{7.60}$$

The condition in Eq. 7.59 tells us that d is outside the interval (d_-, d_+). We have also already derived that $d > b^2 > d_-$. So the final condition on the ratio of the diffusion rates is

$$d = \frac{D_2}{D_1} > b^2(3 + \sqrt{8}). \tag{7.61}$$

7.4.4 Finite domain

We now restrict space to a finite interval $[0, L]$ and impose no-flux boundary conditions at the boundaries:

$$\partial_x u(0,t) = \partial_x u(L,t) = 0, \quad \partial_x v(0,t) = \partial_x v(L,t) = 0. \tag{7.62}$$

This implies that also the perturbations away from the homogeneous steady state must satisfy these boundary conditions:

$$\partial_x \xi(0,t) = \partial_x \xi(L,t) = 0, \quad \partial_x \eta(0,t) = \partial_x \eta(L,t) = 0. \tag{7.63}$$

Substituting our harmonic wave Ansatz Eq. 7.44 into the boundary condition $\partial_x \xi(0,t) = 0$ gives $k\cos(\alpha) = 0$ and hence $\alpha = \pi/2$. Substituting it into the boundary condition $\partial_x \xi(L,t) = 0$ gives $k\cos(kL + \pi/2) = 0$. This means that kL must be a multiple of π and hence k must be an integer multiple of π/L. We can write this as

$$k = k_n = \frac{n\pi}{L}, \quad n = 1, 2, ... \tag{7.64}$$

The boundary conditions for η are satisfied for the same set of wave numbers k_n.

We had seen that only perturbations with wave numbers in the interval $[k_-, k_+]$ can grow, with $k_\pm$ given by Eq. 7.50. So the condition for a Turing instability in our bounded domain is that there is at least one n for which k_n is in the interval $[k_-, k_+]$. This gives the condition $k_1 = \pi/L < k_+$ or equivalently $L > \pi/k_+$. Turing instabilities can only occur in domains that are large enough.

7.5 Directed motion

So far we have only discussed random motion. We now want to consider directed motion. There are many reasons for individuals to move in a directed way. For example, they might move towards a food source or away from a predator. This kind of movement is referred to as **taxis**: the movement towards (or away from) a higher concentration of something (prey, predator, light, nutrient). If the something is a chemical this is called **chemotaxis**. Chemotaxis is a very important mechanism in biology. For example, immune cells move towards sites of infection, sperm cells move towards the egg, and bacteria move towards nutrients.

To model this, we introduce the density $n(\mathbf{x}, t)$ of individuals and the density $a(\mathbf{x}, t)$ of the chemical, which we will assume is an attractant, i.e., individuals move towards higher concentrations of the chemical. The individuals move in response to the gradient of the chemical, so the chemotactic movement is described by a flux

$$\mathbf{J}_c = \chi n \, a, \tag{7.65}$$

where $\chi > 0$ is the chemotactic sensitivity. Compare this with the diffusive flux

$$\mathbf{J}_d = -D \; n. \tag{7.66}$$

The equation for the density of individuals is then

$$\partial_t n = f(n) - \quad \cdot \mathbf{J}, \tag{7.67}$$

where $f(n)$ describes the local population dynamics. This is just the higher-dimensional version of Eq. 7.5. We can now plug in the expressions for the fluxes and get

$$\partial_t n = f(n) - \quad \cdot (\chi n \; a) + \quad \cdot (D_n \; n). \tag{7.68}$$

The attractant a is governed by the equation

$$\partial_t a = g(a, n) + \quad \cdot (D_a \; n). \tag{7.69}$$

The local dynamics of the attractant is described by $g(a, n)$ and the diffusion of the attractant has diffusion coefficient D_a.

7.5.1 Slime mould aggregation

A fascinating example of chemotaxis is the aggregation of slime moulds. Slime moulds are single-celled organisms that live in the soil and feed on bacteria. When the food supply runs out, the slime moulds aggregate to form a fruiting body that releases spores. The aggregation is guided by a chemical attractant. The slime moulds move towards higher concentrations of the attractant. The attractant is a chemical that is released by the slime moulds themselves.

When modelling the slime mould aggregation we can neglect the population dynamics which are not relevant for the aggregation process and thus set $f(n) = 0$. For the local dynamics of the attractant we use

$$g(a, n) = hn - qa, \tag{7.70}$$

where $h > 0$ is the rate at which the attractant is produced by the slime moulds and $q > 0$ is the rate at which the attractant is degraded. We assume that the chemotactic sensitivity χ and the diffusion coefficients D_n and D_a are positive constants. We also restrict ourselves again to motion in one dimension. Then the equations for the slime mould aggregation are:

$$\begin{aligned} \partial_t n &= -\chi \partial_x (n \partial_x a) + D_n \partial_x^2 n, \\ \partial_t a &= hn - qa + D_a \partial_x^2 a. \end{aligned} \tag{7.71}$$

The homogeneous steady state where $n(x, t) = n^*$ and $a(x, t) = a^*$ has to satisfies $hn^* = qa^*$. We can now linearise the equations around the homogeneous steady state by setting $n(x, t) = n^* + \xi(x, t)$ and $a(x, t) = a^* + \eta(x, t)$ with ξ and η small. We get

$$\begin{aligned} \partial_t \xi &= -\chi n^* \partial_x^2 \eta + D_n \partial_x^2 \xi, \\ \partial_t \eta &= h\xi - q\eta + D_a \partial_x^2 \eta. \end{aligned} \tag{7.72}$$

We write this linear system in matrix form as

$$\partial_t \begin{pmatrix} \xi \\ \eta \end{pmatrix} = \begin{pmatrix} D_n \partial_x^2 & -\chi n^* \partial_x^2 \\ h & -q + D_a \partial_x^2 \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix}. \tag{7.73}$$

To solve this we make the Ansatz

$$\begin{pmatrix} \xi \\ \eta \end{pmatrix} = \begin{pmatrix} B_1 \\ B_2 \end{pmatrix} e^{\sigma_k t} \sin(kx + \alpha). \tag{7.74}$$

Plugging this into Eq. 7.73 and dividing by $e^{\sigma_k t} \sin(kx + \alpha)$ gives

$$\sigma \begin{pmatrix} B_1 \\ B_2 \end{pmatrix} = \begin{pmatrix} -D_n k^2 & \chi n^* k^2 \\ h & -q - D_a k^2 \end{pmatrix} \begin{pmatrix} B_1 \\ B_2 \end{pmatrix}. \tag{7.75}$$

We again denote the matrix above as $A(k)$. The condition for the homogeneous steady state to be stable is that the real parts of the eigenvalues σ_k are all negative. The condition for the homogeneous steady state to be unstable is that there is at least one k for which the real part of σ_k is positive.

To determine the stability we again calculate the trace and determinant of the matrix in Eq. 7.75. The trace is

$$\mathrm{tr}(A(k)) = -(D_n + D_a)k^2 - q. \tag{7.76}$$

This is manifestly negative for all k, so this does not yet indicate any instability. The determinant is

$$\det(A(k)) = D_n D_a k^4 + D_n q k^2 - h\chi n^* k^2. \tag{7.77}$$

This is negative and hence gives an instability if

$$D_n D_a k^2 < h\chi n^* - D_n q \tag{7.78}$$

Because the left-hand side in this inequality is positive, the right-hand side must be positive as well. This gives us the condition

$$D_n < \frac{h\chi n^*}{q}. \tag{7.79}$$

This makes sense: if the individuals diffuse too fast, the aggregation can not happen. We can also rewrite the condition for the aggregation as

$$h > \frac{q D_n}{\chi n^*}. \tag{7.80}$$

So aggregation only happens if the rate of production of the attractant is larger enough.

7.6 Exercises

7.6.0.1 Fishing model with diffusion

Exercise 7.1.

A population of fish $F(x,t)$ in a river of width L with banks at $x = 0$ and $x = L$ can be modelled by the partial differential equation

$$\frac{\partial F}{\partial t} = rF\left(1 - \frac{F}{K}\right) + D\frac{\partial^2 F}{\partial x^2}, \tag{7.81}$$

where r, K and D are positive constants. No-flux boundary conditions are applied at $x = L$. At precisely $x = 0$ some shore-based fishermen catch all of the fish. We wish to find the minimum width of the river to ensure the fish population does not collapse.

1. First determine the spatially uniform steady states and indicate their stability.
2. Linearise the system for small F.
3. By considering a solution of the form $F(x,t) = e^{\lambda t}\left(A\cos kx + B\sin kx\right)$ show that

   $$\lambda = \lambda_n =: r - k_n^2 D, \tag{7.82}$$

   where

   $$k = k_n =: \frac{(2n+1)\pi}{2L}, \quad n = 0,\ 1,\ 2, ...$$

4. Hence, determine the condition on L for the fish population not to collapse.

7.6.0.2 Travelling wave in 1-species reaction-diffusion model

Exercise 7.2.

A reaction-diffusion population model has the form

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2} \tag{7.83}$$

where $D > 0$ and where f satisfies $f(0) = f(1) = 0$ and $f(u) > 0$ for $u \in (0,1)$.

a) Convert this equation into travelling wave form by making the Ansatz that $u(x,t) = U(z)$ and $v(x,t) = V(z)$ with $z = x - ct$.

b) Assuming that a solution exists such that $U(-\infty) = 1$, $U(\infty) = 0$ show, by linearising the equation at the leading edge, that for a biologically realistic solution the wave speed c satisfies $c \geq 2\sqrt{Df'(0)}$.

c) Suppose that, instead, $f(u) = 0$. Show that the equation in travelling wave form becomes $DU'' + cU' = 0$. Give the general solution of this. Does the solution look realistic for a function that represents a population?

7.6.0.3 * Travelling wave in 2-species reaction-diffusion model

Exercise 7.3.

Consider the system

$$\begin{aligned} \frac{\partial u}{\partial t} &= -u^2 v \\ \frac{\partial v}{\partial t} &= u^2 v - \rho v + \frac{\partial^2 v}{\partial x^2} \end{aligned} \tag{7.84}$$

where ρ is a positive constant. Convert this system into travelling wave form by making the Ansatz that $u(x,t) = U(z)$ and $v(x,t) = V(z)$ with $z = x - ct$, and show in particular that

$$-c\frac{dV}{dz} = c\frac{dU}{dz} - \frac{\rho c}{U^2}\frac{dU}{dz} + \frac{d^2V}{dz^2}. \tag{7.85}$$

Consider a solution of the travelling wave equations such that $U(\infty) = 1$, $U(-\infty) = a$, $V(\pm\infty) = 0$ for some $a < 1$. By integrating the above equation from $-\infty$ to ∞ and imposing the boundary conditions, determine the value of a. Also determine a lower bound on the wave velocity c by linearising around the leading edge of the wave.

7.6.0.4 SIR model with logistic growth

Exercise 7.4.

Assume that in the absence of rabies, the fox population is described by a logistic model with intrinsic growth rate r and carrying capacity K. Adding this population dynamics to the SIR model gives the equations

$$\begin{aligned} \partial_t S &= rS\left(1 - \frac{S}{K}\right) - \beta SI \\ \partial_t I &= \beta SI - \gamma I. \end{aligned} \tag{7.86}$$

We ignore the removed component R, which in this case would correspond to dead foxes.

a) Show that this model can be written in non-dimensionalised form as

$$\begin{aligned}\partial_{\tilde{t}} u &= bu(1-u) - uv \\ \partial_{\tilde{t}} v &= uv - mv.\end{aligned} \tag{7.87}$$

b) Determine the steady state solutions (fixed points). Under what condition on the parameters is there an endemic state?

Now assume that both susceptible and infected foxes move around randomly, but at different rates. This adds diffusion terms to the SIR model, where now $S = S(x,t)$ and $I = I(x,t)$ denote densities in space.

$$\begin{aligned}\partial_t S &= rS\left(1 - \frac{S}{K}\right) - \beta SI + D_1 \partial_x^2 S \\ \partial_t I &= \beta SI - \gamma I + D_2 \partial_x^2 I.\end{aligned} \tag{7.88}$$

c) Give expressions for $\tilde{x}$ and d such that this model can be written in non-dimensionalised form as

$$\begin{aligned}\partial_{\tilde{t}} u &= bu(1-u) - uv + \partial_{\tilde{x}}^2 u \\ \partial_{\tilde{t}} v &= uv - mv + d\, \partial_{\tilde{x}}^2 v\end{aligned} \tag{7.89}$$

We will now work with these non-dimensional equations but drop the tildes to avoid clutter.

d) Make the travelling wave Ansatz

$$u(x,t) = A(z), \quad v(x,t) = B(z) \tag{7.90}$$

with $z = x - ct$ for some $c > 0$ and derive the system of ODEs describing the functions A and B.

e) If $A(\infty) = 1$, what are $A(-\infty), B(\infty)$ and $B(-\infty)$? Make a sketch of $A(z)$ and $B(z)$ and indicate the direction of travel with an arrow.

f) By linearising about the leading edge of the wave where B is very small, determine a lower limit on the wave speed c.

7.6.0.5 Derive Turing instability

Exercise 7.5. Consider the reaction-diffusion model

$$\begin{aligned} \frac{\partial u}{\partial t} &= a - u + u^2 v + D_1 \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} &= b - u^2 v + D_2 \frac{\partial^2 v}{\partial x^2} \end{aligned} \tag{7.91}$$

where $b > 0$ and $a + b > 0$.

Show that a spatially uniform steady state solution (u^*, v^*) exists for this model and is given by $(u^*, v^*) = (a + b\,,\ b/(a + b)^2)$. Show that the conditions for this steady state to be driven unstable by diffusion are that the three inequalities

$$b - a < (a + b)^3$$

$$\left[D_2 \left(\frac{b - a}{a + b}\right) - D_1 (a + b)^2\right]^2 > 4 D_1 D_2 (a + b)^2 \tag{7.92}$$

$$D_2 \left(\frac{b - a}{a + b}\right) - D_1 (a + b)^2 > 0 \tag{7.93}$$

should all hold simultaneously.

7.6.0.6 * Conditions for Turing instability

Exercise 7.6. Consider the reaction-diffusion model

$$\begin{aligned} \frac{\partial c_1}{\partial t} &= \delta - k c_1 - c_1 c_2^2 + D_1 \frac{\partial^2 c_1}{\partial x^2} \\ \frac{\partial c_2}{\partial t} &= k c_1 + c_1 c_2^2 - c_2 + D_2 \frac{\partial^2 c_2}{\partial x^2} \end{aligned} \tag{7.94}$$

where $k > 0$ and $\delta > 0$.

Show that a spatially uniform steady state solution (c_1^*, c_2^*) exists for this model and give the conditions for this steady state to be driven unstable by diffusion. You may use any results derived in the lectures.

7.6.0.7 Slime mould with boundary

Exercise 7.7. In the model for the aggregation of slime mould amoebae suppose that the spatial domain is $0 \leq x \leq L$ rather than $-\infty < x < \infty$. Show that the conditions for aggregation to occur are $\chi a^* f > k\mu$ and

$$L > \pi\sqrt{\frac{D\mu}{\chi a^* f - k\mu}}. \tag{7.95}$$

A Solutions

This appendix holds the solutions to selected exercises in the book. Please look at these solutions only after having made a serious attempt at solving the exercises and knowing exactly where you got stuck.

A.1 Continuous-time population models

Von Bertalanffy growth

Exercise 1.2:

i) Seeking a steady state we find $\alpha w^{2/3} - \beta w = 0 \implies w^{2/3}(\alpha - \beta w^{1/3}) = 0 \implies w = 0$ or $w^{1/3} = \alpha/\beta$. With the graphical approach in Figure A.1 we see that the non-zero steady state is stable. Hence,

$$\lim_{t\to\infty} w(t) = \left(\frac{\alpha}{\beta}\right)^3 . \tag{A.1}$$

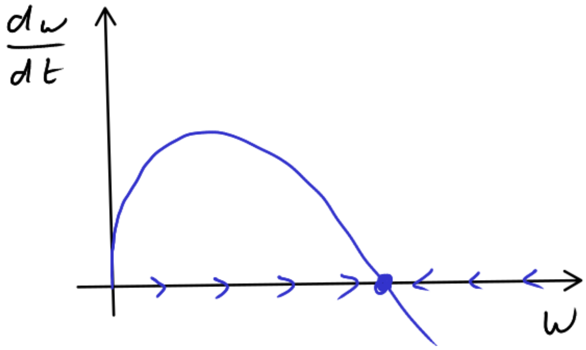

Figure A.1: dw/dt versus w for the von Bertalanffy growth model.

ii) For the time derivative of $u = w^{1/3}$ we find by the chain rule that

$$\frac{du}{dt} = \frac{1}{3} w^{-2/3} \frac{dw}{dt} = \frac{1}{3u^2}\left(\alpha w^{2/3} - \beta w\right). \tag{A.2}$$

Hence

$$3\frac{du}{dt} = \frac{1}{u^2}\left(\alpha u^2 - \beta u^3\right) = \alpha - \beta u. \tag{A.3}$$

So this change of variables has yielded a first-order ODE with linear coefficients, which is easy for us to solve:

$$u(t) = \frac{1}{\beta}\left(\alpha - Ae^{-\beta t/3}\right) \tag{A.4}$$

for some integration constant A. If $u(0) = u_0$ then $A = \alpha - \beta u_0$.

iii) Translating back to w with $w_0 = u_0^3$ we finally have

$$w(t) = u(t)^3 = \frac{1}{\beta^3}\left(\alpha - \left(\alpha - \beta w_0^{1/3}\right)e^{-\beta t/3}\right)^3. \tag{A.5}$$

Solving logistic equation

Exercise 1.3: We separate the variables by dividing both sides of the ODE by $N(1 - N/K)$ and multiplying by dt, and then integrate to get

$$\int_{N_0}^{N(t)} \frac{dN}{N\left(1 - \frac{N}{K}\right)} = \int_0^t r\,dt. \tag{A.6}$$

The right hand side is trivial to integrate, but for the integral on the left-hand side we need to employ the method of partial fractions, using that

$$\frac{dN}{N\left(1 - \frac{N}{K}\right)} = \frac{1}{N} + \frac{1}{K - N}. \tag{A.7}$$

The left-hand side then gives

$$\begin{aligned}&\int_{N_0}^{N(t)} \left(\frac{1}{N} + \frac{1}{K - N(t)}\right) dN \\ &\qquad = \log N(t) - \log N_0 - \log(K - N(t)) + \log(K - N_0).\end{aligned} \tag{A.8}$$

We exponentiate both sides to get

$$\frac{N(t)}{N_0}\frac{K - N_0}{K - N(t)} = e^{rt}. \tag{A.9}$$

Now we just need to solve for $N(t)$:

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}. \tag{A.10}$$

Harvesting with fixed quota

**Exercise 1.5: If we harvest with a fixed quota Q, the population is described by the equation

$$\frac{dN}{dt} = \alpha N \log \frac{K}{N} - Q. \tag{A.11}$$

The subtraction of Q shifts the graph of the right-hand side down by a distance Q. This brings the non-zero fixed points closer together until Q is equal to the maximum of the growth rate of the unfished population. If Q is increased beyond this value the non-zero fixed points disappear and the population will go extinct. is because we are removing Q individuals from the population at a constant rate. Thus the maximum sustainable yield occurs when Q equals the maximum replenishment rate of the unfished population. To find that maximum we first solve

$$0 = \frac{d}{dN}\left(\alpha N \log \frac{K}{N}\right) = \alpha \left(\log \frac{K}{N} - 1\right). \tag{A.12}$$

This tells us that the maximum is at

$$N_{max} = K\, e^{-1}. \tag{A.13}$$

Hence the value at the maximum is

$$MSY = Q_{max} = \alpha N_{max} \log \frac{K}{N_{max}} = \alpha\, K\, e^{-1}. \tag{A.14}$$

Fishing at this quota is not wise, as this reduces the population to the threshold level below which the population will go extinct.

Wasp model

Exercise 1.6: For $0 \leq t \leq t_c$ the number of workers satisfies

$$\frac{dn}{dt} = r\, n. \tag{A.15}$$

Therefore

$$n(t) = n_0 e^{r\,t}. \tag{A.16}$$

For $t_c \leq t \leq T$ the number of reproducers satisfies

$$\frac{dN}{dt} = Rn(t_c) = R\, n_0\, e^{r\,t_c}, \tag{A.17}$$

so that

$$N(T) = (T - t_c) R\, e^{r\,t_c}. \tag{A.18}$$

To find the value of t_c that maximises $N(T)$ we set the derivative of $N(T)$ with respect to t_c to zero:

$$\begin{aligned}0 = \frac{d}{dt_c}N(T) &= \frac{d}{dt_c}(T-t_c)R\,e^{r\,t_c}\\ &= -R\,e^{r\,t_c} + (T-t_c)R\,r\,e^{r\,t_c}\\ &= R\,e^{r\,t_c}(r\,T - r\,t_c - 1).\end{aligned} \tag{A.19}$$

This implies that

$$t_c = T - \frac{1}{r}. \tag{A.20}$$

Wasp model with death

Exercise 1.7: For $0 \le t \le t_c$ the number of workers satisfies

$$\frac{dn}{dt} = (r-d)n. \tag{A.21}$$

Therefore

$$n(t) = e^{(r-d)t}. \tag{A.22}$$

For $t_c \le t \le T$ we have

$$\frac{dn}{dt} = -dn \tag{A.23}$$

so that

$$n(t) = n(t_c)e^{-d(t-t_c)} = e^{(r-d)t}e^{-d(t-t_c)} = e^{r\,t_c}e^{-d\,t}. \tag{A.24}$$

Also for $t_c \le t \le T$ the number of reproducers satisfies

$$\frac{dN}{dt} = Rn(t) = Re^{r\,t_c}e^{-d\,t}, \tag{A.25}$$

so that

$$N(T) = \int_{t_c}^{T} Re^{r\,t_c}e^{-d\,t}dt = \frac{R}{d}e^{r\,t_c}\left(e^{-d\,t_c} - e^{-d\,T}\right). \tag{A.26}$$

To find the value of t_c that maximises $N(T)$ we set the derivative of $N(T)$ with respect to t_c to zero:

$$\begin{aligned}0 = \frac{d}{dt_c}N(T) &= \frac{d}{dt_c}\left(\frac{R}{d}e^{r\,t_c}\left(e^{-d\,t_c} - e^{-d\,T}\right)\right)\\ &= Re^{r\,t_c}\left(\left(\frac{r}{d}-1\right)e^{-d\,t_c} - \frac{r}{d}e^{-d\,T}\right).\end{aligned} \tag{A.27}$$

This is equivalent to

$$e^{-d\,t_c} = \frac{1}{1-d/r}e^{-d\,T} \tag{A.28}$$

and thus

$$t_c = T + \frac{1}{d} \ln \left(1 - \frac{d}{r}\right) . \tag{A.29}$$

A.2 Discrete-time population models

Verhulst model

Exercise 2.1: Let's write the equation as $N_{t+1} = f(N_t)$ with

$$f(N) = rN \left(1 - \frac{N}{K}\right) . \tag{A.30}$$

Because $f(N)$ is positive for all $N < K$, the only way for N_{t+1} to be negative is for N_t to be greater than K. This in turn is only possible if $f(N_{t-1}) > K$. So the function f at its maximum needs to be larger than K. Because the function describes an upside-down parabola with zeros at 0 and K, its maximum is in the middle at $N = K/2$, where $f(K/2) = rK/4$. Thus the population can get negative iff $rK/4 > K$, which is equivalent to $r > 4$.

A.3 Sex-structured population models

Dominance structure

Exercise 3.2:

a) The ratio F/Q in the negative term in the equation for the alpha females represents the fact that if the ratio between the subordinate individuals who gather the food and the alpha females who rely on that food is too small, then the alpha females don't get enough food and hence are less fit, leading to either a decreased birth rate or an increased mortality rate.

(b) We derive the ODE:

$$\begin{aligned}\frac{d}{dt}\frac{F}{Q} &= \frac{F'Q - FQ'}{Q^2} \\ &= \frac{(b_F - \mu_F F/Q)FQ - F(b_Q F - \mu_Q Q)}{Q^2} \\ &= (b_F + \mu_Q)\frac{F}{Q}\left(1 - \frac{b_Q + \mu_F}{b_F + \mu_Q}\frac{F}{Q}\right).\end{aligned} \tag{A.31}$$

Ideally you identify this as the logistic equation with initial growth rate r and carrying capacity K given by

$$r = b_F + \mu_Q, \quad K = \frac{b_F + \mu_Q}{b_Q + \mu_F}. \tag{A.32}$$

You can then look up the solution in the lecture notes:

$$\frac{F}{Q}(t) = \frac{\frac{F_0}{Q_0}Ke^{rt}}{K + \frac{F_0}{Q_0}\left(e^{rt} - 1\right)}. \tag{A.33}$$

Otherwise you have to work a bit harder.

(c) Because we have identified $F/Q(t)$ as the solution of a logistic equation it is easy to see that as $t \to \infty$, $F/Q \to K$ with K as in Eq. A.32.

(d) We derive the ODE:

$$\begin{aligned}\frac{d}{dt}\frac{F}{M} &= \frac{F'M - FM'}{M^2} \\ &= \frac{(b_F - \mu_F F/Q)FM - F(b_M F - \mu_M M)}{M^2} \\ &= \frac{F}{M}\left(b_F + \mu_M - \mu_F\frac{F}{Q} - b_M\frac{F}{M}\right).\end{aligned} \tag{A.34}$$

We are only interested in the limit of F/M as $t \to \infty$. Let us denote this limit by R. We already know that the limit of F/Q as $t \to \infty$ is K. The limit of the previous equation gives

$$0 = \frac{d}{dt}R = R\left(b_F + \mu_M - \mu_F K - b_M R\right) \tag{A.35}$$

and hence

$$R = \frac{b_F + \mu_M - \mu_F K}{b_M}. \tag{A.36}$$

Substituting the expression for K and bringing everything on a common denominator gives

$$R = \frac{(b_F + \mu_M)(b_Q + \mu_F) - \mu_F(b_F + \mu_Q)}{b_M(b_Q + \mu_F)} \tag{A.37}$$

To see that this is always positive we multiply out the numerator:

$$R = \frac{b_F b_Q + \mu_M b_Q + \mu_M \mu_F - \mu_F \mu_Q}{b_M(b_Q + \mu_F)} \tag{A.38}$$

This is positive because $b_F b_Q > \mu_F \mu_Q$

(e) The birth rates are linear in the number of alpha females and independent of M and Q. Independence of M is realistic only if M is large. Using a weighted mean might be better, i.e., birth rates given by $b_i FM/(F/n + M)$, where n is the number of females a male can mate with per mating season. Or we could take into account that the alpha females will reproduce less if there are fewer subordinate individuals gathering food for them, for example by choosing birth rates to be given by $b_i FQ/(F/n + Q)$, where n is the number of pregnant females that a subordinate monkey can keep well fed. There are many other possible improvements.

A.4 Age-structured population models

Harvestings an age-structured population

Exercise 4.2: We can start from Eq. 4.14 that gives the expected number of offspring produced by an individual within their lifetime:

$$\phi(0) = \int_0^\infty b(a) \exp\left(-\int_0^a \mu(a')\, da'\right) da. \tag{A.39}$$

This will now simplify when we use the given expressions Eq. 4.46 and Eq. 4.47 for the rates. Because $b(a)$ is non-zero only for $a > a_m$, the outer integral only has to run from a_m to ∞. The inner integral from 0 to a we need to split into two integrals because of the piece-wise nature of $\mu(a)$. Hence

$$\phi(0) = \int_{a_m}^\infty b(a) \exp\left(-\int_0^{a_m} \mu(a')\, da' - \int_{a_m}^a \mu(a')\, da'\right) da. \tag{A.40}$$

We can now substitute the appropriate constants for the rates:

$$\begin{aligned}\phi(0) &= \int_{a_m}^{\infty} b\, \exp\left(-\int_0^{a_m} \mu_0\, da' - \int_{a_m}^{a} (\mu_0 + \mu_F)\, da'\right)\, da \\ &= \int_{a_m}^{\infty} b\, \exp\left(-\mu_0 a_m - (\mu_0 + \mu_F)(a - a_m)\right)\, da \\ &= b\, \exp(-\mu_F a_m) \int_{a_m}^{\infty} \exp\left(-(\mu_0 + \mu_F)a\right)\, da \\ &= b\, \exp(-\mu_F a_m) \left[-\frac{1}{\mu_0 + \mu_F} \exp\left(-(\mu_0 + \mu_F)a\right)\right]_{a_m}^{\infty} \\ &= b\, \exp(-\mu_F a_m) \frac{1}{\mu_0 + \mu_F} \exp\left(-(\mu_0 + \mu_F)a_m\right) \\ &= \frac{b}{\mu_0 + \mu_F} \exp\left(-\mu_0 a_m\right).\end{aligned} \tag{A.41}$$

This expected number of offspring produced by an individual within their lifetime must be greater or equal to 1 for the population to sustain itself. Hence the upper limit on the harvesting rate μ_F is given by

$$\mu_F \leq b \exp\left(-\mu_0 a_m\right) - \mu_0. \tag{A.42}$$

Seasonal mortality

Exercise 4.3:

(a) Substituting $n(t, a) = p(t)r(a)$ into Eq. 4.3 and dividing by $n(t, a)$ gives

$$\frac{p'(t)}{p(t)} + \frac{r'(a)}{r(a)} = -\mu(a) - f(t). \tag{A.43}$$

Separating variables gives

$$\frac{p'(t)}{p(t)} + f(t) = -\frac{r'(a)}{r(a)} - \mu(a). \tag{A.44}$$

As the left-hand side is independent of a and the right-hand side is independent of t, both sides must be equal to some constant γ. This gives us the two ODEs

$$\frac{d}{dt} \log(p(t)) = \gamma - f(t), \quad \frac{d}{da} \log(r(a)) = -\gamma - \mu(t). \tag{A.45}$$

These have the solutions

$$\begin{aligned}p(t) &= p(0)\exp\left(\int_0^t \gamma - f(s)\,ds\right),\\ r(a) &= r(0)\exp\left(-\int_0^a \gamma + \mu(s)\,ds\right)\end{aligned} \tag{A.46}$$

Thus the solution for n is

$$n(t,a) = n(0,0)\exp\left(\int_0^t \gamma - f(s)\,ds\right)\exp\left(-\int_0^a \gamma + \mu(s)\,ds\right). \tag{A.47}$$

(b) Substituting the solution into Eq. 4.4 gives

$$p(t)r(0) = \int_0^\infty b(a)p(t)r(a)\,da. \tag{A.48}$$

After dividing by $p(t)r(0)$ and using our expression for $r(a)$ from the previous part,

$$1 = \int_0^\infty b(a)\exp\left(-\int_0^a \gamma + \mu(s)ds\right)da = \phi(\gamma). \tag{A.49}$$

The factor $\exp(-\gamma a)$ in the integrand decreases monotonically with increasing γ and therefore so does the integral. Hence the function $\phi(\gamma)$ is a monotonically decreasing function.

(c) The end of a season occurs at any $t \in \mathbb{Z}$. At those integer times we can write the integral in the expression for $p(t)$ as

$$\begin{aligned}\int_0^t \gamma - f(s)\,ds &= \sum_{i=1}^t \int_{i-1}^i \gamma - f(s)\,ds\\ &= \sum_{i=1}^t (\gamma - F) = t(\gamma - F).\end{aligned} \tag{A.50}$$

Hence for the population at the end of the season t we have

$$n(t,a) = n(0,0)\exp(t(\gamma - F))r(a). \tag{A.51}$$

This will go to zero in the limit $t \to \infty$ if $\gamma - F < 0$. Thus the criterion for extinction is $\gamma < F$.

(d) Because $\phi(\gamma)$ decreases with γ,

$$\gamma < F \Leftrightarrow \phi(\gamma) > \phi(F). \tag{A.52}$$

Because $\phi(\gamma) = 1$, this is equivalent to the condition $1 > \phi(F)$. Thus the condition for extinction is

$$\int_0^\infty b(a)\exp\left(-\int_0^a F + \mu(s)\,ds\right)da < 1. \tag{A.53}$$

A.5 Interacting populations

A.6 Epidemics

SIR with recrudescence

Exercise 6.2: The modified equations are

$$\begin{aligned} \frac{dS}{dt} &= -\beta SI/N, \\ \frac{dI}{dt} &= \beta SI/N - \gamma I + \delta R, \\ \frac{dR}{dt} &= \gamma I - \delta R. \end{aligned} \tag{A.54}$$

1. At the steady state all these derivatives have to vanish. From the first equation we find $S^* = 0$ or $I^* = 0$. We are not interested in $I^* = 0$ because we are interested in the endemic state which by definition has $I^* > 0$, so we have $S^* = 0$. The third equation gives $R^* = \gamma/\delta I^*$. Then I^* is found from the fact that $N = S^* + I^* + R^*$ which gives $I^* = N - \gamma/\delta I^*$. Soving for I^* gives

   $$I^* = \frac{N\delta}{\delta + \gamma}. \tag{A.55}$$

2. For the stability analysis we reduce the problem to a two-dimensional system by eliminating S from the last two equations. This gives

   $$\begin{aligned} \frac{dI}{dt} &= \frac{\beta I}{N}(N - I - R) - \gamma I + \delta R, \\ \frac{dR}{dt} &= \gamma I - \delta R. \end{aligned} \tag{A.56}$$

   The Jacobian matrix is

   $$A = \begin{pmatrix} \frac{\beta}{N}(N - 2I - R) - \gamma & \delta - \frac{\beta I}{N} \\ \gamma & -\delta \end{pmatrix}. \tag{A.57}$$

   Evaluated at the endemic state this gives

   $$A = \begin{pmatrix} -\frac{\beta}{N} I^* - \gamma & \delta - \frac{\beta}{N} I^* \\ \gamma & -\delta \end{pmatrix}. \tag{A.58}$$

   This has determinant and trace given by

   $$\begin{aligned} \det(A) &= (\delta + \gamma)\frac{\beta}{N} I^* > 0, \\ \operatorname{tr}(A) &= -\frac{\beta}{N} I^* - \gamma - \delta < 0. \end{aligned} \tag{A.59}$$

   so the endemic state is stable for all positive values of the parameters.

SIR model with reinfections

Exercise 6.3: The modified equations are

$$\begin{aligned}\frac{dS}{dt} &= -\beta SI/N,\\ \frac{dI}{dt} &= \beta SI/N - \gamma I + \beta\mu RI/N,\\ \frac{dR}{dt} &= \gamma I - \beta\mu RI/N.\end{aligned} \tag{A.60}$$

At the steady state all these derivatives have to vanish. From the first equation we find $S^* = 0$ or $I^* = 0$. We are not interested in $I^* = 0$ because we are interested in the endemic state which by definition has $I^* > 0$, so we have $S^* = 0$. The third equation gives $R^* = \gamma N/(\beta\mu)$. Then I^* is found from the fact that $N = S^* + I^* + R^*$ which gives

$$I^* = N - R^* = N\left(1 - \frac{\gamma}{\beta\mu}\right). \tag{A.61}$$

This is not the same as the number of infecteds in the endemic state of the model with loss of immunity given in Eq. 6.33.

Sex-structured SIR model

Exercise 6.4:

a. As $N = S + I + R$ we have

$$\frac{dN}{dt} = \frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} = -rSI' + rSI' - aI + aI = 0. \tag{A.62}$$

Hence, N is a constant. Similarly, N' is a constant.

b. We start by deriving an ODE for S as a function of R':

$$\frac{dS}{dR'} = \frac{dS}{dt}\Big/\frac{dR'}{dt} = \frac{-rSI'}{a'I'} = -\frac{r}{a'}S. \tag{A.63}$$

This is easy to solve:

$$S(t) = S_0 e^{-\frac{r}{a'}R'(t)}. \tag{A.64}$$

Similarly,

$$S'(t) = S'_0 e^{-\frac{r'}{a}R(t)}. \tag{A.65}$$

c. At $t = \infty$ we have

$$S(\infty) = S_0 e^{-\frac{r}{a'} R'(\infty)}. \tag{A.66}$$

But at $t = \infty$, $I' = 0$ and $N' = S' + I' + R'$ and so

$$S(\infty) = S_0 e^{-\frac{r}{a'} (N' - S'(\infty))}. \tag{A.67}$$

Similarly,

$$S'(\infty) = S'_0 e^{-\frac{r'}{a} (N - S(\infty))}. \tag{A.68}$$

A.7 Spatially-structured population models

Fishing model with diffusion

Exercise 7.1

1. The spatially uniform steady states are $F^* = 0$ and K. Stability can be determined graphically or from the gradient at the steady state, with the result that $F^* = 0$ is unstable and $F^* = K$ is stable.
2. If F is small then $\frac{\partial F}{\partial t} \approx rF + D\frac{\partial^2 F}{\partial x^2}$.
3. Try $F(x,t) = e^{\lambda t} \left(A \cos kx + B \sin kx\right)$ such that

   $$\frac{\partial F}{\partial x} = k e^{\lambda t} \left(-A \sin kx + B \cos kx\right). \tag{A.69}$$

   The boundary conditions are $F(0,t) = 0 = \frac{\partial F}{\partial x}(L,t)$. The boundary condition at $x = 0$ implies that $A = 0$. The second implies that

   $$\cos kL = 0 \implies k = \frac{(2n+1)\pi}{2L} =: k_n, \quad n = 0,\ 1,\ 2, \ldots. \tag{A.70}$$

   Substituting this solution into the PDE gives

   $$\lambda = \lambda_n =: r - k_n^2 D. \tag{A.71}$$

4. A full solution is a superposition of the above solutions. For the fish population not to collapse we need at least one $\lambda_n > 0$ for some n. The largest λ_n is for the smallest k_n, which occurs when $n = 0$, giving the requirement that $\lambda_0 = r - D\left(\frac{\pi}{2L}\right)^2 > 0$. Hence, we need

   $$L^2 > \frac{D\pi^2}{4r}. \tag{A.72}$$

Travelling wave in 1-species reaction-diffusion model

Exercise 7.2:

a. With $z = x - ct$ we have

$$\frac{\partial}{\partial t} = \frac{\partial z}{\partial t}\frac{\partial}{\partial z} = -c\frac{\partial}{\partial z} \text{ and } \frac{\partial}{\partial x} = \frac{\partial z}{\partial x}\frac{\partial}{\partial z} = \frac{\partial}{\partial z}. \tag{A.73}$$

Substituting this into the PDE gives the ODE

$$-cU' = f(U) + DU''. \tag{A.74}$$

b. For a travelling wave from left to right ($c > 0$) we expect solution at $\pm\infty$ to be at steady state: $U(-\infty) = 1$ and $U(\infty) = 0$, with $U'(\pm\infty) = 0$.

We will now use a slightly different way to approach the linearisation around the leading edge of the travelling wave than the one we used in the lecture. The methods are equivalent, and it is always instructional to look at different ways of doing the same thing.

At the leading edge of the wave we have that U is very small, so we can Taylor-expand $f(U) = f(0) + Uf'(0) + \ldots$. We keep only the first two terms and also use that $f(0) = 0$ to get the linear ODE

$$-cU' = Uf'(0) + DU''. \tag{A.75}$$

Rather than making an Ansatz for U as in the lecture, we convert this second order ODE into a set of first-order ODEs by introducing a second variable V so that $U' = V$ and $V' = -\frac{U}{D}f'(0) - \frac{c}{D}V$. In vector notation this reads

$$\begin{pmatrix} U' \\ V' \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -\frac{f'(0)}{D}U & -\frac{c}{D} \end{pmatrix} \begin{pmatrix} U \\ V \end{pmatrix}. \tag{A.76}$$

The eigenvalues λ of this linear matrix ODE are solutions of

$$\det \begin{pmatrix} -\lambda & 1 \\ -\frac{f'(0)}{D} & -\lambda - \frac{c}{D} \end{pmatrix} = 0 \qquad \Longrightarrow \qquad \lambda^2 + \frac{c}{D}\lambda + \frac{f'(0)}{D} = 0. \tag{A.77}$$

Real eigenvalues and thus realistic biological solutions exist iff

$$\frac{c^2}{D^2} - 4\frac{f'(0)}{D} \geq 0, \qquad \Longrightarrow \qquad c \geq 2\sqrt{Df'(0)}. \tag{A.78}$$

c. If $f(u) = 0$ for all u we get $DU'' + cU' = 0$. Setting $U(z) = e^{\mu z} \implies D\mu^2 + c\mu \implies \mu = 0$ or $-c/D$. The general solution is $U = Ae^{-\frac{c}{D}z} + B$. Clearly $|U| \to \infty$ as $z \to -\infty$. This is not a biologically realistic solution.

SIR model with logistic growth

Exercise 7.4:

a. One can either approach this systematically or one can just try to guess the necessary change of variables. We will use a blended approach: we guess the expressions for u and v by inspecting the equations, and we make a general Ansatz for $\tilde{t}$.

   By comparing the $(1 - S/K)$ factor in the equation for S to the factor $(1 - u)$ in the equation for u we see that $u = S/K$. It is natural to also choose $v = I/K$. We write $\tilde{t} = t/\tau$, where τ is still to be determined. With these we have

   $$\begin{aligned}\partial_{\tilde{t}} u &= \tau/K \partial_t S = \tau/K \left(rKu(1-u) - \beta K^2 uv\right) \\ &= \tau r u(1-u) - \tau\beta K uv\end{aligned} \tag{A.79}$$

   By comparing this with equation for u in the problem statement, we can read off that

   $$\tau = \frac{1}{\beta K}, \quad b = \frac{r}{\beta K}. \tag{A.80}$$

   Then

   $$\begin{aligned}\partial_{\tilde{t}} v &= \tau/K \partial_t I = \tau/K \left(\beta K^2 uv - \gamma K v\right) \\ &= uv - \frac{\gamma}{\beta K} v.\end{aligned} \tag{A.81}$$

   By comparing this with the equation for v in the problem statement we read off that

   $$m = \frac{\gamma}{\beta K}. \tag{A.82}$$

b. By inspection we see that one steady state is $(u(x,t), v(x,t)) = (0,0)$ and that another is

   $$(u(x,t), v(x,t)) = (1,0). \tag{A.83}$$

   The first describes a situation where the foxes are extinct, the second the situation where in the absence of the disease the fox population sits at its carrying capacity. We look for another steady state $(u(x,t), v(x,t)) = (u^*, v^*)$ with $v^* \neq 0$. From the equation for v we read off that $u^* = m$ and then from the equation for u we get $v^* = b(1-m)$. This is the endemic state because the number of infecteds is nonzero. It exists as long as $m < 1$. This tells us that the existence of the endemic state is independent of the intrinsic growth rate r of the fox population but does depend on its carrying capacity.

c. We want $D_1 \partial_x^2 S = \partial_{\tilde{x}}^2 u$, where $u = S/K$. Hence

   $$\tilde{x} = \sqrt{\frac{K\beta}{D_1}} x. \tag{A.84}$$

Then $d\,\partial_{\tilde{x}}^2 v = d\,D_1\partial_x^2 I$ but we want $D_2\partial_x^2 I$ so we need

$$d = \frac{D_2}{D_1}. \tag{A.85}$$

d. Substituting the wave Ansatz into the PDEs for u and v gives

$$-cA' = bA(1-A) - AB + A'', \quad -cB' = AB - mB + dB''. \tag{A.86}$$

e. If $A(\infty) = 1$ (which corresponds to $S = K$) then that means that at $x = \infty$ the system is in the disease-free state and thus $B(\infty) = 0$. At $x = -\infty$ the system must thus be in the endemic state, so $A(-\infty) = u^* = m$ and $B(-\infty) = v^* = b(1-m)$. So the key to this question was the observation that the travelling wave will always have to interpolate between two steady states.

f. At the leading edge where B is very small, A is very close to 1, so $A = 1 - \epsilon$ for a small $\epsilon > 0$. The equations Eq. A.86 can thus be approximated by the linear equations

$$c\epsilon' = b\epsilon - B - \epsilon'', \quad -cB' = B - mB + dB''. \tag{A.87}$$

We obtained this by dropping all terms involving ϵ^2 or ϵB because they are negligible when ϵ and B are both small.

We concentrate on the second equation, which we solve with the Ansatz $B(x) = \exp(\lambda x)$. Substituting this Ansatz into the equation gives the characteristic equation for λ:

$$d\lambda^2 + c\lambda + 1 - m = 0, \tag{A.88}$$

and thus

$$\lambda = \frac{-c \pm \sqrt{c^2 - 4d(1-m)}}{2d}. \tag{A.89}$$

We do not want the solution to oscillate, so we want λ to be real, hence

$$c \geq 2\sqrt{d(1-m)}. \tag{A.90}$$

Derive Turing instability

Exercise 7.5:

Here,

$$f(u,v) = a - u + u^2 v, \quad g(u,v) = b - u^2 v. \tag{A.91}$$

Step 1. Uniform steady state

$$a - u^* + {u^*}^2 v^* = 0 \;\text{ and }\; b - {u^*}^2 v^* = 0 \tag{A.92}$$

implies

$$(u^*,\ v^*) = (a+b,\ b/(a+b)^2). \tag{A.93}$$

Step 2. Linearize

Set $u = u^* + \xi$ and $v = v^* + \eta$ with ξ and η small. Substitute and Taylor expand to get

$$\begin{pmatrix} \frac{\partial \xi}{\partial t} \\ \frac{\partial \eta}{\partial t} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix} + \begin{pmatrix} D_1 \frac{\partial^2 \xi}{\partial x^2} \\ D_2 \frac{\partial^2 \eta}{\partial x^2} \end{pmatrix}, \tag{A.94}$$

where

$$\begin{aligned} a_{11} &= \frac{\partial f}{\partial u}(u^*, v^*) = -1 + 2u^*v^* \\ &\qquad\qquad\quad = -1 + 2(a+b)b/(a+b)^2 \\ &\qquad\qquad\quad = (b-a)/(a+b) \\ a_{12} &= \frac{\partial f}{\partial v}(u^*, v^*) = {u^*}^2 = (a+b)^2 \\ a_{21} &= \frac{\partial g}{\partial u}(u^*, v^*) = -2u^*v^* = -2b/(a+b) \\ a_{22} &= \frac{\partial g}{\partial v}(u^*, v^*) = -{u^*}^2 = -(a+b)^2 \end{aligned} \tag{A.95}$$

Step 3. Solutions

Make the Ansatz $\xi = A_1 e^{\sigma t} \sin(kx + \alpha)$ and $\eta = A_2 e^{\sigma t} \sin(kx + \alpha)$. Substitute to get

$$\begin{pmatrix} \sigma - \frac{b-a}{a+b} + D_1 k^2 & -(a+b)^2 \\ \frac{2b}{a+b} & \sigma + (a+b)^2 + D_2 k^2 \end{pmatrix} \begin{pmatrix} A_1 \\ A_2 \end{pmatrix} = \mathbf{0} \tag{A.96}$$

For a non-trivial solution we require the determinant of this matrix to be zero (otherwise we would be able to find an inverse, etc.). Hence,

$$\sigma^2 + \left[(a+b)^2 - \frac{b-a}{a+b} + (D_1 + D_2)k^2\right]\sigma + h(k^2) = 0, \tag{A.97}$$

where

$$h(k^2) = D_1 D_2 k^4 - \left[D_2 \frac{b-a}{a+b} - D_1 (a+b)^2\right] k^2 + (a+b)^2. \tag{A.98}$$

Step 4. In the absence of diffusion (Put $D_1 = 0 = D_2$.)

$$\sigma^2 + \left[(a+b)^2 - \frac{b-a}{a+b}\right]\sigma + (a+b)^2 = 0. \tag{A.99}$$

For σ to have roots in the left half of the complex plane (giving us a stable steady state) we need $(a+b)^2 - \frac{b-a}{a+b} > 0 \implies b - a < (a+b)^3$ and $(a+b)^2 > 0$ (which it is).

Step 5. With diffusion ($D_1 \neq 0 \neq D_2$.)

We want steady state to be unstable in this case. The coefficient of σ is

$$(a+b)^2 - \frac{b-a}{a+b} + (D_1 + D_2)k^2 > (D_1 + D_2)k^2 > 0 \quad \text{from Step 4} \tag{A.100}$$

Therefore, we require $h(k^2) < 0$ for some k^2 for there to be an instability.

As $h(0) > 0$ we must have two positive real roots of $h(k^2) = 0$ for there to be an instability.

Real distinct roots ($\implies \quad B^2 - 4AC > 0$)

$$\implies \left[D_2 \frac{b-a}{a+b} - D_1(a+b)^2\right]^2 > 4D_1D_2(a+b)^2. \tag{A.101}$$

Both positive ($\implies B < 0$)

$$\implies D_2 \frac{b-a}{a+b} - D_1(a+b)^2 > 0. \tag{A.102}$$

Slime mould with boundary

Exercise 7.7

$$\frac{\partial a}{\partial t} = \frac{\partial}{\partial x}\left(\mu \frac{\partial a}{\partial x} - \chi a \frac{\partial \rho}{\partial x}\right), \quad \text{and} \quad \frac{\partial \rho}{\partial t} = fa - k\rho + D\frac{\partial^2 \rho}{\partial x^2}. \tag{A.103}$$

Steady states are $fa^* = k\rho^*$.

Consider a perturbation $a = a^* + \xi$ and $\rho = \rho^* + \eta$, where ξ and η are small. Substitute and linearize to give

$$\frac{\partial \xi}{\partial t} = \mu \frac{\partial^2 \xi}{\partial x^2} - \chi a^* \frac{\partial^2 \eta}{\partial x^2}, \quad \text{and} \quad \frac{\partial \eta}{\partial t} = f\xi - k\eta + D\frac{\partial^2 \eta}{\partial x^2}. \tag{A.104}$$

Put $\xi = A_1 e^{\sigma t + iqx}$ and $\eta = A_2 e^{\sigma t + iqx}$. Hence,

$$\begin{pmatrix} \sigma + \mu q^2 & -\chi a^* q^2 \\ -f & \sigma + k + Dq^2 \end{pmatrix} \begin{pmatrix} A_1 \\ A_2 \end{pmatrix} = \mathbf{0} \tag{A.105}$$

A non-trivial solution requires the determinant of the matrix to be zero

$$\implies \sigma^2 + g(q^2)\sigma + h(q^2) = 0, \tag{A.106}$$

where $g(q^2) = k + (D+\mu)q^2 > 0$ and $h(q^2) = \mu D q^4 + (k\mu - \chi a^* f)q^2 > 0$.

We need $(k\mu - \chi a^* f) < 0$ for there to be a positive root of $h(q^2) = 0$ and so instability.

If $0 \leq x \leq L$ we need boundary conditions. Assume no flux at $x = 0,\ L$: $\frac{\partial a}{\partial x} = 0 = \frac{\partial \rho}{\partial x}$ at $x = 0,\ L$.

Try $\xi = A_1 e^{\sigma t} \cos qx$ and $\eta = A_2 e^{\sigma t} \cos qx$ to satisfy BCs at $x = 0$.

At $x = L$ we have $\sin qL = 0$ for a non-trivial solution $\implies q = q_n := n\pi/L$, $n = 0, 1, 2, ...$

Aggregation will not occur if $h(q_1^2) > 0$, which implies

$$L < \pi \sqrt{\frac{D\mu}{\chi a^* f - k\mu}}. \tag{A.107}$$

Aggregation will occur if

$$k\mu < \chi a^* f \quad \text{and} \quad L > \pi \sqrt{\frac{D\mu}{\chi a^* f - k\mu}}. \tag{A.108}$$