# Chapter 5

# Travelling waves

Huge numbers of phenomena in biology exhibit wave phenomena, where a wave of *e.g.* chemical concentration, mechanical deformation or electrical signal propagates through a domain to effect a process. Examples include the spread of epidemics through susceptible populations, the healing of skin wounds, the invasion of insects and the waves of calcium concentration in early embryo development. In this chapter we will be interested in travelling waves, *i.e.* in waves that move at constant speed and without change in shape. We will learn how to analyse the models and draw useful conclusions about when we might see travelling waves, and how the speed of wave propagation and the shape of the wave depend on the model parameters.

The models we will study will be of reaction-diffusion type *e.g.*

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f(u), \tag{5.1}$$

where $D$ is the diffusion coefficient and $f(u)$ represents the reaction kinetics. In contrast to simple diffusion models of the form

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}, \tag{5.2}$$

we will show that when both reaction and diffusion are present travelling waves can effect a change in system state very much faster than when diffusion alone governs the dynamics.

### 5.1 Fisher–KPP equation: a simple investigation

Fisher's equation, also known as the Kolmogorov–Petrovsky–Piskunov equation, or Fisher–KPP equation, is a simple, classical model that displays travelling waves. In one spatial dimension it can be written as

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru\left(1 - \frac{u}{K}\right) \quad \text{for } x \in (-\infty, \infty) \text{ and } t > 0, \tag{5.3}$$

where $D > 0$ is the diffusion coefficient, $r > 0$ is the population growth rate and $K$ is the population carrying capacity. The model was suggested by Fisher as a model for the spatial spread of a favoured gene through a population. But we can also think of it as the natural extension of the logistic model for population growth to the spatial setting, where the population disperses by diffusion. We will use the Fisher-KPP equation as a paradigm for the study of travelling wave behaviour more generally. All the steps that we will use to analyse the model are relevant in other travelling wave scenarios.

### 5.1.1 Non-dimensionalisation

First, we non-dimensionalise using the following scalings

$$\tilde{u} = \frac{u}{K}, \qquad \tilde{x} = x\sqrt{\frac{r}{D}}, \qquad \tilde{t} = rt. \tag{5.4}$$

Substituting the above scalings into Equation (5.3), and dropping the ˜s for notational convenience, gives

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u) \quad \text{for } x \in (-\infty, \infty) \text{ and } t > 0. \tag{5.5}$$

Clearly the solution of the Fisher–KPP equation will depend on the initial and boundary conditions we impose. For the time being, we will state these conditions as

$$u(x,t) \to u_{\pm\infty} \quad \text{as} \quad x \to \pm\infty \quad \text{and} \quad u(x,0) = u_0(x), \tag{5.6}$$

where $u_{\pm\infty}$ are constants.

### 5.1.2 Change to travelling wave coordinates

We will investigate whether a solution exists for Equation (5.5) which propagates without a change in shape and at a constant (but as yet unknown) speed, $c$. Such wave solutions are defined to be *travelling wave solutions*. Our investigation of the existence of a travelling wave solution will be substantially easier if we first transform to the moving coordinate frame $z = x - ct$ as, by the definition of a travelling wave, the wave profile will be independent of time in a frame moving at speed $c$.

We will make the change of variables $z = x - ct$ and $\tau = t$. Using the chain rule we have

$$\frac{\partial}{\partial t} = \frac{\partial \tau}{\partial t}\frac{\partial}{\partial \tau} + \frac{\partial z}{\partial t}\frac{\partial}{\partial z} \quad \text{and} \quad \frac{\partial}{\partial x} = \frac{\partial \tau}{\partial x}\frac{\partial}{\partial \tau} + \frac{\partial z}{\partial x}\frac{\partial}{\partial x}, \tag{5.7}$$

*i.e.*

$$\frac{\partial}{\partial t} \mapsto \frac{\partial}{\partial \tau} - c\frac{\partial}{\partial x} \quad \text{and} \quad \frac{\partial}{\partial x} \mapsto \frac{\partial}{\partial z}. \tag{5.8}$$

Letting $u(x,t) = \hat{u}(z,\tau)$, the transformed Fisher–KPP equation, Equation (5.5), then becomes

$$\frac{\partial \hat{u}}{\partial \tau} - c\frac{\partial \hat{u}}{\partial z} = \frac{\partial^2 \hat{u}}{\partial z^2} + \hat{u}(1-\hat{u}) \quad \text{for } z \in (-\infty,\infty) \text{ and } \tau > 0. \tag{5.9}$$

Further noting that we seek a solution that is *time independent* in the $(z,\tau)$ coordinate system, we seek solutions $\hat{u}(z,\tau) = U(z)$, so that, letting $'$ denote differentiation with respect to $z$, $U$ satisfies the ordinary differential equation

$$U'' + cU' + U(1-U) = 0 \quad \text{for } z \in (-\infty,\infty). \tag{5.10}$$

We need to choose appropriate boundary conditions as $z \to \pm\infty$ for Equation (5.10). These are the same as the boundary conditions for the full partial differential equation, Equation (5.5), but re-written in terms of $z$:

$$U(z) \to u_{\pm\infty} \quad \text{as} \quad z \to \pm\infty, \tag{5.11}$$

where the constants $u_{\pm\infty}$ are identical to those specified in Equation (5.6).

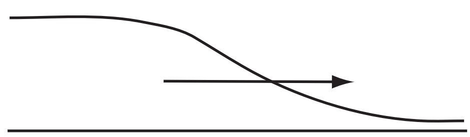
For the non-dimensionalised version of the Fisher-KPP equation, Equation (5.5), we require that $u_{\pm\infty}$ only take the values zero or unity: integrating Equation (5.10) with respect to $z$ from $-\infty$ to $\infty$ gives

$$\int_{-\infty}^{\infty} \left[U'' + cU' + U(1-U)\right] \mathrm{d}z = 0, \tag{5.12}$$

*i.e.*

$$\left[U' + cU\right]_{-\infty}^{\infty} + \int_{-\infty}^{\infty} U(1-U)\, \mathrm{d}z = 0. \tag{5.13}$$

If we want $U \to$ constant as $z \to \pm\infty$ and $U$, $U'$ finite for $\forall z$ we must have either $U \to 0$ or $U \to 1$ as $z \to \infty$ and similarly for $z \to -\infty$. For the particular choice of $U(-\infty) = 1$ and $U(\infty)) = 0$, we anticipate $c > 0$.



Indeed there are no solutions of the Fisher–KPP travelling wave equations with these boundary conditions and $c \leq 0$.

**Notes.**

- Solutions to Equations (5.5) and (5.6) are unique. The proof is an exercise in the theory of partial differential equations.
- The solutions of the travelling wave equation are not unique. One may have solutions for different values of the unknown $c$. Also, if $U(z)$ solves Equation (5.10) for any fixed value of $c$ then, for the same value of $c$, so does $U(z + A)$, where $A$ is any constant. For both $c$ and $A$ fixed the solution of the travelling wave equations are normally unique.
- Note that the solutions of the travelling wave equation, Equation (5.10), can only be solutions of the full partial differential equation, Equation (5.5), when considered on an infinite domain. Realistically one requires that the length scale of variation of the system in question is much less than the length scale of the physical domain for a travelling wave to (have the potential to) be an excellent approximation to the reaction-diffusion wave solutions on a physical, *i.e.* finite, domain.
- By seeking a travelling wave solution one "loses" the initial conditions associated with Equations (5.5) and (5.6). A solution of the travelling wave equation, Equation (5.10), is only a solution of the full partial differential equation, Equation (5.5), for all time if the travelling wave solution is consistent with the initial conditions specified in Equation (5.6). For a very large class of initial conditions, however, one finds instead that a solution of the full partial differential equation system, Equations (5.5) and (5.6), tends, as $t \to \infty$, to a solution of the travelling wave equation, Equation (5.10), with fixed $c$ and $A$.
- The Russian mathematician Kolmogorov proved that, for a large class of initial conditions, solutions of the full partial differential equation system, Equations (5.5) and (5.6), tend, as $t \to \infty$, to a solution of the travelling wave equations with $c = 2$.

### 5.1.3 Phase plane analysis

We will first use phase plane analysis to investigate the nature of solutions of the Fisher–KPP equation, Equation (5.10), restated here for convenience,

$$U'' + cU' + U(1 - U) = 0 \quad \text{for } z \in (-\infty, \infty),$$

with the boundary conditions $U(-\infty) = 1$ and $U(\infty) = 0$ and $c > 0$.

To make progress we first transform to a system of first order ordinary differential equations by writing $U' = V$ to give

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} U \\ V \end{pmatrix} = \frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} U \\ U' \end{pmatrix} = \begin{pmatrix} V \\ -cV - U(1-U) \end{pmatrix} = \begin{pmatrix} f(U,V) \\ g(U,V) \end{pmatrix}. \tag{5.14}$$

This system has two steady states: at $(U, V) = (0, 0)$ and $(U, V) = (1, 0)$. To determine their linear stability, we linearise around the steady state, writing $U = U_s + \tilde{U}$ and $V = V_s + \tilde{V}$, where $\tilde{U}$ and $\tilde{V}$ are small perturbations and $(U_s, V_s)$ the steady state, to write

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} \tilde{U} \\ \tilde{V} \end{pmatrix} = \boldsymbol{J}\begin{pmatrix} \tilde{U} \\ \tilde{V} \end{pmatrix}, \tag{5.15}$$

where $\boldsymbol{J}$ is the Jacobian matrix given by

$$\boldsymbol{J} = \left.\begin{pmatrix} \frac{\partial f}{\partial U} & \frac{\partial f}{\partial V} \\ \frac{\partial g}{\partial U} & \frac{\partial g}{\partial V} \end{pmatrix}\right|_{(U_s,V_s)} = \begin{pmatrix} 0 & 1 \\ -1 + 2U_s & -c \end{pmatrix}. \tag{5.16}$$

At $(0, 0)$ we have

$$\det(\boldsymbol{J} - \lambda\boldsymbol{I}) = \det\begin{pmatrix} -\lambda & 1 \\ -1 & -c-\lambda \end{pmatrix} \quad\Longrightarrow\quad \lambda^2 + c\lambda + 1 = 0, \tag{5.17}$$

and hence

$$\lambda = \frac{-c \pm \sqrt{c^2 - 4}}{2}. \tag{5.18}$$

Therefore:

- if $c < 2$ we have $\lambda = -c/2 \pm i\mu$ and hence a stable spiral;
- if $c > 2$ we have $\lambda = -c/2 \pm \mu$ and hence a stable node;
- if $c = 2$ we have $\lambda = -1$ and hence a stable node.

At $(1, 0)$ we have

$$\det(\boldsymbol{J} - \lambda\boldsymbol{I}) = \det\begin{pmatrix} -\lambda & 1 \\ 1 & -c-\lambda \end{pmatrix} \quad\Longrightarrow\quad \lambda^2 + c\lambda - 1 = 0, \tag{5.19}$$

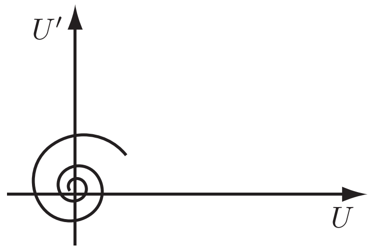
and hence

$$\lambda = \frac{-c \pm \sqrt{c^2 + 4}}{2}. \tag{5.20}$$

Therefore $(1, 0)$ is a saddle point.

**Note 1.** Solutions of the Fisher–KPP travelling wave equations must tend to phase plane stationary points as $z \to \pm\infty$. This is because $(U, V) = (U, U')$ will change as $z$ increases, unless at a stationary point. Therefore they will keep moving along a phase space trajectory as $z \to \infty$ unless the $z \to \infty$ limit evolves to a stationary point. To satisfy $\lim_{z\to\infty} U(z) = 0$, we need to be on a phase space trajectory which "stops" at $U = 0$. Therefore we must be on a trajectory which tends to a stationary point with $U = 0$ as $z \to \infty$. Hence $(U, U')$ must tend to $(0, 0)$ as $z \to \infty$ to satisfy $\lim_{z\to\infty} U(z) = 0$ as $z \to \infty$. An analogous argument holds as $z \to -\infty$.

**Note 2.** Solutions of Equation (5.10) with $c < 2$ are unphysical because if $c < 2$ then $U < 0$ at some point on the trajectory (close to the origin the solution looks like a spiral).




### 5.1.4 Existence and uniqueness

We will now investigate the existence and uniqueness of solutions of the Fisher–KPP equation, Equation (5.5), for $c \geq 2$ (so that we are considering only physically realistic travelling waves).

First, we consider the direction in which the trajectory leaving $(U, V) = (0, 1)$ travels. From Section 5.1.3 we know that the eigenvectors of the Jacobian, $\boldsymbol{J}$, at $(1, 0)$ satisfy

$$\begin{pmatrix} 0 & 1 \\ 1 & -c \end{pmatrix} \begin{pmatrix} 1 \\ q_\pm \end{pmatrix} = \lambda_\pm \begin{pmatrix} 1 \\ q_\pm \end{pmatrix} \quad \Longrightarrow \quad q_\pm = \lambda_\pm \quad \text{and} \quad 1 - cq_\pm = \lambda_\pm q_\pm. \tag{5.21}$$

Hence

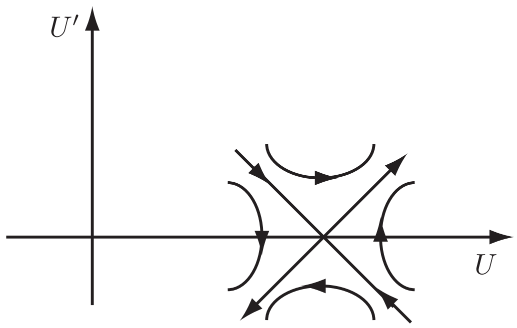
$$\boldsymbol{v}_\pm = \begin{pmatrix} 1 \\ q_\pm \end{pmatrix} = \begin{pmatrix} 1 \\ \frac{1}{2}\left[-c \pm \sqrt{c^2+4}\right] \end{pmatrix}. \tag{5.22}$$

As a result, the gradient of the unstable manifold at $(U, V) = (1, 0)$ is given by

$$\frac{1}{2}\left(-c + \sqrt{c^2+4}\right) < \frac{1}{c}, \tag{5.23}$$

where the last inequality holds for $c \geq 2$ (this will be useful later for drawing the phase plane).

We can sketch the qualitative form of the phase plane trajectories near to the stationary point $(U, V) = (1, 0)$ for $c \geq 2$:



Close to the stationary point $(U, V) = (1, 0)$ we can then write

$$\begin{pmatrix} U \\ U \end{pmatrix} - \begin{pmatrix} U_s \\ V_s \end{pmatrix} = \begin{pmatrix} \tilde{U} \\ \tilde{V} \end{pmatrix} = a_- e^{\lambda_- z} \boldsymbol{v}_- + a_+ e^{\lambda_+ z} \boldsymbol{v}_+. \tag{5.24}$$

As a result, we see that any physically relevant phase plane trajectory must leave the saddle point $(U, V) = (1, 0)$ along the unstable manifold, which corresponds to $a_+$, in the direction of decreasing $U$.

We will now use a "trapping region" argument to demonstrate existence and uniqueness. This involves finding a region such that, for $c$ fixed, the trajectory from the saddle point $(U, V) = (1, 0)$ enters the region, cannot leave, and is "funnelled" towards the stable node at $(U, V) = (0, 0)$.

For the trapping region we will take

$$\mathcal{R} \stackrel{\text{def}}{=} \{(U, V) \,:\, U \in [0, 1],\, V \leq 0,\, -V \leq U\}. \tag{5.25}$$

We begin by analysing the direction in which trajectories that cross the boundaries of $\mathcal{R}$ are moving: we want to establish that they all point into $\mathcal{R}$.

- Along $\mathcal{L}_1 = \{(U, V) \,:\, V = 0,\, U \in (0, 1)\}$ the trajectories point vertically into $\mathcal{R}$ as

$$\left|\frac{\mathrm{d}V}{\mathrm{d}U}\right| \to \infty \quad \text{as we approach } \mathcal{L}_1 \text{ and } cV' = -U(1-U) < 0. \tag{5.26}$$

- Along $\mathcal{L}_2 = \{(U, V) \,:\, U = 1,\, V \in (-1, 0)\}$ we have

$$\left.\frac{\mathrm{d}V}{\mathrm{d}U}\right|_{\mathcal{L}_2} = -c - \frac{U(1-U)}{V} = -c < 0, \tag{5.27}$$

  and so the trajectories point "diagonally upwards" into $\mathcal{R}$.

- Along $\mathcal{L}_3 = \{(U, V) \,:\, U \in [0, 1],\, V = -U\}$ we have

$$\left.\frac{\mathrm{d}V}{\mathrm{d}U}\right|_{\mathcal{L}_3} = -c + (1-U) = (-c + 2) - (1 + U) < -1, \tag{5.28}$$

  and so the trajectories also point "diagonally upwards" into $\mathcal{R}$.

Together, we have therefore shown that, for fixed $c \geq 2$, the single unstable manifold leaving $(U, V) = (1, 0)$ and entering the region $V < 0$, $U < 1$ enters, and can never leave, the region $\mathcal{R}$. Any trajectory must end at a stationary point, and trajectories are thus forced to the point $(U, V) = (0, 0)$.

As a result, we have shown that that, with $U \geq 0$ there is a solution to Equation 5.10 for every value of $c \geq 2$, and with $c \geq 2$ fixed, the phase space trajectory is unique. Moreover, the solution is monotonic as $V < 0$ throughout $\mathcal{R}$. Figure 5.1 shows the phase plane, with the null clines and travelling wave solution.

**Note.** For $c$ fixed, the phase space trajectory of the Fisher–KPP travelling wave equation is unique. The non-uniqueness associated with the fact that if $U(z)$ solves the Fisher–KPP travelling wave equation then so does $U(z + A)$ for $A$ constant simply corresponds to a shift along the phase space trajectory. This, in turn, corresponds to translation of the travelling wave.

Figure 5.1 shows the results of numerical simulation of the Fisher–KPP equation, Equation (5.5), with initial and boundary conditions given by Equation (5.6) at a series of time points.

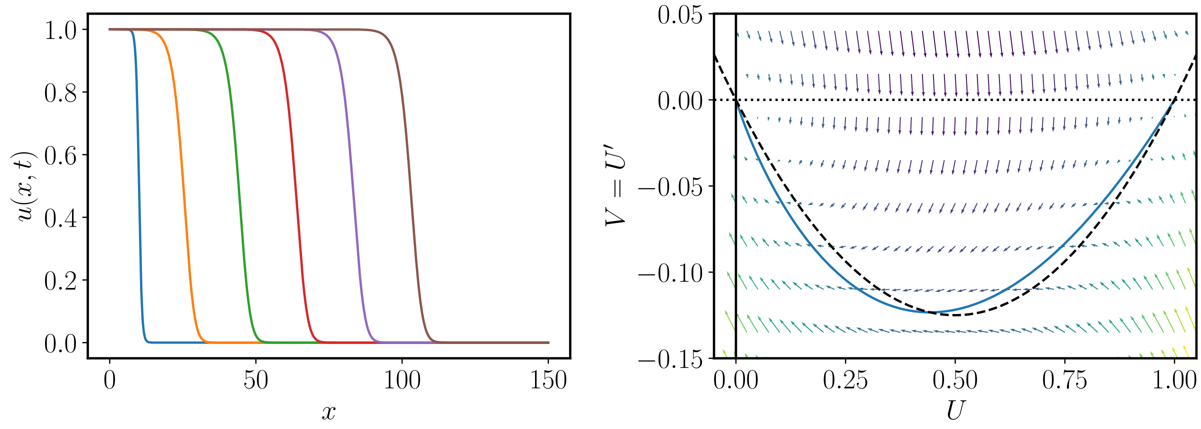



Figure 5.1: Left: Solution of the Fisher–KPP equation, Equation (5.5), with initial and boundary conditions given by Equation (5.6) at non-dimensional times $t = 0, 10, 20, 30, 40, 50$. Right: phase plane with the $U$ null cline (dotted), $V$ null cline (dashed) and the travelling wave solution (blue).

### 5.1.5 Relation between the travelling wave speed and initial conditions

We showed above that when the Fisher–KPP equation possesses a travelling wave solution then its wave speed satisfies $c^2 \geq 4$. When are such travelling wave solutions realised, and with what wave speeds? A rough estimate can be obtained by studying the Fisher–KPP equation near the leading front of the travelling wave where $u$ is small. Linearising Equation (5.5) about $u = 0$ yields the following linear partial differential equation:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u. \tag{5.29}$$

We will assume that

$$u(x, 0) \sim Be^{-ax} \quad \text{as } x \to \infty, \tag{5.30}$$

for $a, B > 0$ and seek travelling solutions of the linearised Fisher–KPP equation of the form

$$u(x,t) \sim Be^{-a(x-ct)}. \tag{5.31}$$

The linearised partial differential equation yields the following *dispersion relation* which defines the wave speed $c$ in terms of the decay rate of the initial data

$$ac = a^2 + 1 \quad \Longrightarrow \quad c = a + \frac{1}{a} \geq 2, \tag{5.32}$$

with equality if and only if $a = 1$. We will consider separately the cases $a > 1$ and $a < 1$.

**Case 1:** $a < 1$**.** In this case

$$e^{-ax} > e^{-x}, \tag{5.33}$$

which implies that the initial conditions decay less rapidly than the travelling wave with minimum wave speed $c_{\text{min}} = 2$. As a result, the behaviour is dominated by the initial conditions and $c = a + a^{-1}$.

**Case 2:** $a > 1$**.** In this case

$$e^{-ax} < e^{-x}, \tag{5.34}$$

which implies that the initial conditions decay more rapidly than the travelling wave with minimum wave speed $c_{\text{min}} = 2$. As a result, the behaviour is dominated by the travelling wave with minimum wave speed $c_{\text{min}} = 2$.

**Non-Examinable: initial conditions of compact support**

Kolmogorov considered the Fisher–KPP equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u) \quad \text{for } x \in (-\infty, \infty) \text{ and } t > 0,$$

with the boundary conditions

$$u(x,t) \to 1 \quad \text{as} \quad x \to -\infty \quad \text{and} \quad u(x,t) \to \quad \text{as} \quad x \to \infty, \tag{5.35}$$

and non-negative initial conditions such that there is an $M$, with $0 < M < \infty$, for which

$$u(x,0) = 0 \quad \text{for} \quad x > M \quad \text{and} \quad u(x,0) = 1 \quad \text{for} \quad x < -M. \tag{5.36}$$

He proved that $u(x,t)$ tends to a Fisher–KPP travelling wave solution with $c = 2$ as $t \to \infty$.

## 5.2 Models of epidemics

The study of infectious diseases has a long history and there are numerous detailed models of a variety of epidemics and epizootics (*i.e.* animal epidemics). Here we will only scratch the surface. In what follows we consider a basic model and show how it can be used to make general comments about epidemics and, in fact, approximately describe some specific epidemics.

### 5.2.1 The SIR model

Consider a disease for which the population can be placed into three compartments:

- the susceptible compartment, $S$, who can catch the disease;
- the infective compartment, $I$, who have and transmit the disease;
- the removed compartment, $R$, who have been isolated, or who have recovered and are immune to the disease, or have died due to the disease during the course of the epidemic.

We will make the following assumptions in order to build our model:

- the epidemic is of short duration course so that the population is constant (counting those who have died due to the disease during the course of the epidemic);
- the disease has a negligible incubation period;
- if a person contracts the disease and recovers, they are immune (and hence remain in the removed compartment);
- the numbers involved are sufficiently large to justify a continuum approximation, and there is sufficient population mixing to justify neglecting spatial effects;
- the dynamics of the disease can be described by applying the Law of Mass Action to the following "reactions"

$$S + I \xrightarrow{r} 2I, \quad \text{and} \quad I \xrightarrow{a} R. \tag{5.37}$$

Then the system of ordinary differential equations describing the time evolution of numbers in the susceptible, infective and removed compartments is

$$\frac{\mathrm{d}S}{\mathrm{d}t} = -rIS, \tag{5.38}$$

$$\frac{\mathrm{d}I}{\mathrm{d}t} = rIS - aI, \tag{5.39}$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aI, \tag{5.40}$$

subject to

$$S(0) = S_0, \quad I(0) = I_0, \quad R(0) = 0. \tag{5.41}$$

Note that

$$\frac{\mathrm{d}}{\mathrm{d}t}(S + I + R) = 0 \quad \Longrightarrow \quad S + I + R = S_0 + I_0. \tag{5.42}$$

Key questions in an epidemic situation are, given $r$, $a$, $S_0$ and $I_0$,

1. Will the disease spread, *i.e.* will the number of infectives increase, at least in the short-term?
2. If the disease spreads, what will be the maximum number of infectives at any given time?
3. How many people in total catch the disease?

We can use simple analysis of the model equations to answer them.

First, we have

$$\frac{\mathrm{d}S}{\mathrm{d}t} = -rIS \quad \Longrightarrow \quad S \text{ is decreasing and therefore } S \leq S_0. \tag{5.43}$$

As a result,

$$\frac{\mathrm{d}I}{\mathrm{d}t} = I(rS - a) < I(rS_0 - a). \tag{5.44}$$

Therefore, if $S_0 < a/r$ the number of infectives never increases.

Second, we can write

$$\frac{\mathrm{d}I}{\mathrm{d}S} = -\frac{(rS - a)}{rS} = -1 + \frac{\rho}{S} \quad \text{where} \quad \rho \overset{\text{def}}{=} \frac{a}{r}. \tag{5.45}$$

Integrating gives

$$I + S - \rho \ln S = I_0 + S_0 - \rho \ln S_0, \tag{5.46}$$

and so, noting that $\mathrm{d}I/\mathrm{d}S = 0$ for $S = \rho$, the maximum number of infectives is given by

$$I_{\text{max}} = \begin{cases} I_0 & S_0 \leq \rho \\ I_0 + S_0 - \rho \ln S_0 - \rho \ln \rho - \rho & S_0 > \rho \end{cases}. \tag{5.47}$$

Third, from Equations (5.43)-(5.44), $I \to 0$ as $t \to \infty$. Therefore the total number who catch the disease is

$$R(\infty) = N_0 - S(\infty) - I(\infty) = N_0 - S(\infty), \tag{5.48}$$

where $S(\infty) < S_0$ is the root of

$$S_\infty - \rho \ln S_\infty = N_0 - \rho \ln S_0, \tag{5.49}$$

obtained by setting $S = S_\infty$ and $N_0 = I_0 + S_0$ in Equation (5.46).

Figure 5.2 shows the phase plane with a number of trajectories marked.

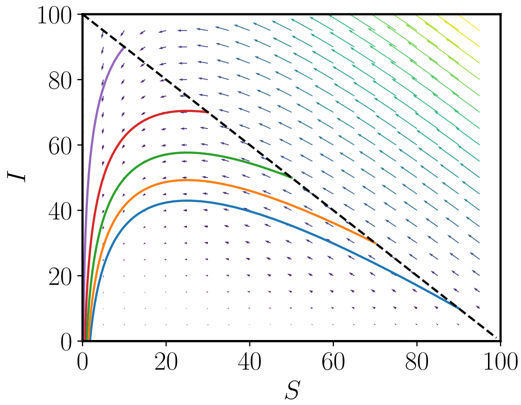



Figure 5.2: Phase space of the SIR model, Equations (5.38)–(5.40), where the solid lines indicate the phase trajectories and the dashed line is $S + I = S_0 + I_0$. Parameters are as follows: $r = 0.01$ and $a = 0.25$.

### 5.2.2 An SIR model with spatial heterogeneity

We now consider an application of the SIR modelling approach to the spread of fox rabies. We will make the same assumptions as for the standard SIR model (except the assumption that it is possible to neglect spatial effects), plus:

- healthy, *i.e.* susceptible, foxes are territorial and, on average, do not move from their territories;
- rabid, *i.e.* infective, foxes undergo behavioural changes and migrate randomly, with an effective, constant, diffusion coefficient $D$;
- rabies is fatal, so that infected foxes do not return to the susceptible compartment but die, and hence the removed compartment does not migrate.

Taking into account random motion of rabid foxes, the SIR equations become

$$\frac{\partial S}{\partial t} = -rIS, \tag{5.50}$$

$$\frac{\partial I}{\partial t} = D\nabla^2 I + rIS - aI, \tag{5.51}$$

$$\frac{\partial R}{\partial t} = aI. \tag{5.52}$$

The $I$ and $S$ equations decouple, and we consider these in more detail. We assume a one-dimensional spatial domain $x \in (-\infty, \infty)$, and non-dimensionalise the model using

$$\tilde{I} = \frac{I}{S_0}, \quad \tilde{S} = \frac{S}{S_0}, \quad \tilde{x} = \sqrt{\frac{rS_0}{D}}x, \quad \tilde{t} = rS_0 t \quad \text{and} \quad \lambda = \frac{a}{rS_0}, \tag{5.53}$$

where $S_0$ is the population density in the absence of rabies. The non-dimensionalised partial differential equations for $I$ and $S$ are then (after dropping the $\tilde{}$s for notational convenience)

$$\frac{\partial S}{\partial t} = -IS, \tag{5.54}$$

$$\frac{\partial I}{\partial t} = \frac{\partial^2 I}{\partial x^2} + I(S - \lambda). \tag{5.55}$$

We will assume $\lambda = a/(rS_0) < 1$ below – this is equivalent to the condition for disease spread in the earlier SIR model.

**Travelling wave analysis**

We seek travelling wave solutions with $S(x,t) = S(z)$ and $I(x,t) = I(z)$ where $z = x - ct$ for $c > 0$. Letting $' = \mathrm{d}/\mathrm{d}z$ gives

$$0 = cS' - IS, \tag{5.56}$$

$$0 = I'' + cI' + I(S - \lambda). \tag{5.57}$$

As boundary conditions, we assume a healthy population as $z \to \infty$

$$S \to 1 \quad \text{and} \quad I \to 0, \tag{5.58}$$

and as $z \to -\infty$ we require

$$I \to 0. \tag{5.59}$$

**Minimum wave speed.** We can establish a lower bound on the travelling wave speed by writing $S = 1 - P$ and linearising about the wavefront:

$$-cP' - I = 0 \quad \text{and} \quad I'' + cI' + I(1 - \lambda). \tag{5.60}$$

The $I$ equation decouples and analysis of this equation gives a stable focus at $(I, I') = (0, 0)$ if the eigenvalues

$$\mu = \frac{-c \pm \sqrt{c^2 - 4(1 - \lambda)}}{2}, \tag{5.61}$$

are real and negative. This requires

$$c \geq c_{\text{min}} = 2\sqrt{1-\lambda}. \tag{5.62}$$

In typical situations the wave evolves to have minimum wave speed, $c_{\text{min}}$.

**Severity of the epidemic.** The number of susceptible individuals left as $t \to \infty$, which is given by $S(-\infty)$ since in transforming to the travelling wave frame time is reversed, is a measure of the severity of the epidemic. We have $I = cS'/S$ and therefore

$$\frac{\mathrm{d}}{\mathrm{d}z}(I' + cI) + cS'\left(\frac{S-\lambda}{S}\right) = 0. \tag{5.63}$$

By integrating and evaluating Equation (5.63) as $z \to \infty$ we have

$$(I' + cI) + c(S - \lambda \ln S) = \text{constant} = c. \tag{5.64}$$

In this case the severity of the equation is given as the solution to

$$S(-\infty) - \lambda \ln S(-\infty) = 1, \quad \text{where} \quad S(-\infty) < 1. \tag{5.65}$$

**Numerical results.** Results from simulation of the full partial differential equation model are shown in Figure 5.3, and illustrate the formation of a travelling wave of infection through the susceptible population.

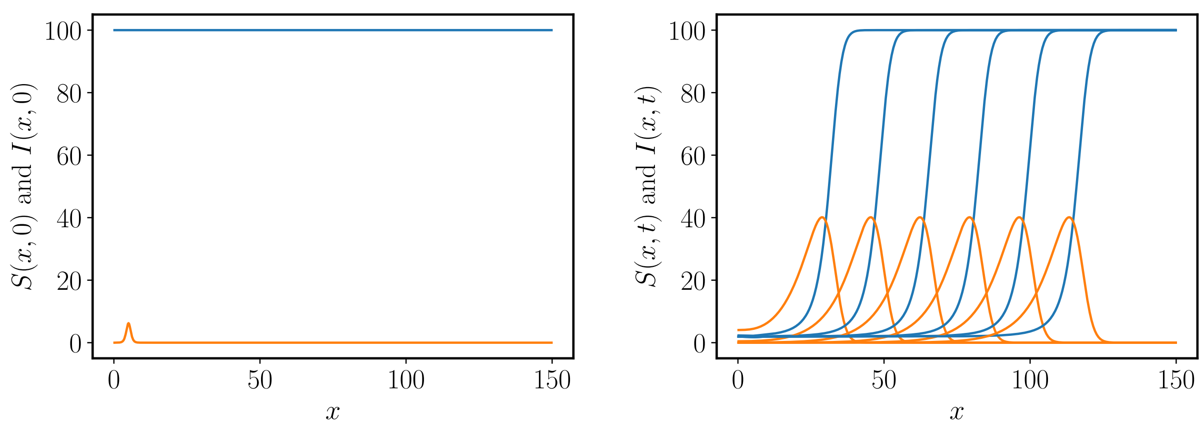



Figure 5.3: Solution of the fox rabies model, Equations (5.50)–(5.51), in one spatial dimension. Left: Initial conditions. Right: at times $t = 20, 30, 40, 50, 60, 70$. $S(x,t)$ is shown in blue and $I(x,t)$ in orange. Zero flux conditions are implemented at both boundaries. Parameters are as follows: $S_0 = 100$, $r = 0.01$ and $a = 0.25$.

**Suggested reading.**

- J. D. Murray, *Mathematical Biology, Volume I* – Chapter 13.
- J. D. Murray, *Mathematical Biology, Volume II* – Chapter 1.
- N. F. Britton, *Essential Mathematical Biology* – Chapter 5.