

# Modelling with PDEs – Supplementary Notes

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These notes provide supplementary explanations and examples to support the material covered in the *Modelling with PDEs* lectures. For any questions, please contact [fp409@cam.ac.uk](mailto:fp409@cam.ac.uk).

## Contents

<b>1</b>	<b>What are PDEs?</b>	<b>1</b>
1.1	From ODEs to PDEs . . . . .	1
1.2	Definition and examples of PDEs . . . . .	2
1.3	Reaction-Diffusion systems and Turing’s insight . . . . .	2
<b>2</b>	<b>Operators in differential equations</b>	<b>3</b>
2.1	The $\Delta$ and $\nabla$ notation . . . . .	3
2.2	Intuition behind the Laplacian . . . . .	4
<b>3</b>	<b>Reaction equations</b>	<b>5</b>
3.1	Law of mass action . . . . .	5
3.2	Examples . . . . .	5
<b>4</b>	<b>Diffusion equations</b>	<b>6</b>
4.1	Derivation of the diffusion equation . . . . .	6
4.2	Fick’s laws of diffusion . . . . .	8
4.3	Solving the one-dimensional diffusion equation . . . . .	9
<b>5</b>	<b>Reaction-diffusion</b>	<b>13</b>
5.1	Linear stability analysis . . . . .	13
5.2	Example: plankton survival . . . . .	16
5.3	Going beyond: multiple species and higher dimensions . . . . .	17
<b>6</b>	<b>Conclusions and take-home messages</b>	<b>19</b>

## 1 What are PDEs?

Partial Differential Equations (PDEs) are one of the central mathematical tools for describing how quantities change in both space and time. They are used to model a wide range of natural and engineered systems, from heat conduction and population dynamics to chemical reactions and fluid flow.

### 1.1 From ODEs to PDEs

To understand PDEs, it is helpful to start with *ordinary differential equations* (ODEs). An ODE describes how a quantity changes with respect to a single independent variable, usually time. For example, if  $u(t)$  represents the concentration of a substance that decays at a rate proportional to its current value, we can write

$$\frac{du}{dt} = -ku, \tag{1}$$

where  $k > 0$  is a constant. This equation involves only one independent variable,  $t$ , and one derivative. In contrast, many physical and biological systems depend on several independent variables. Temperature, for instance, varies not only with time but also with position in space. Equations involving partial derivatives of a function with respect to multiple variables are called *partial differential equations*. They provide a more complete description of systems that evolve in space and time simultaneously.

## 1.2 Definition and examples of PDEs

A *partial differential equation* (PDE) is an equation that relates a function of several variables to its derivatives with respect to those variables (its *partial derivatives*). For instance, if  $u(x, t)$  represents the concentration of a substance at position  $x$  and time  $t$ , a PDE can express how  $u$  changes both in time and space. The  $k$ -th order *partial derivatives* of  $u$  with respect to  $t$  and  $x$  are denoted by  $\frac{\partial^k u}{\partial t^k}$  and  $\frac{\partial^k u}{\partial x^k}$ , respectively<sup>1</sup>. Mixed partial derivatives can be denoted by  $\frac{\partial^2 u}{\partial x \partial t}$ .

Some of the most common PDEs in mathematical modelling include:

- **Diffusion equation:**

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}, \quad (2)$$

which models the spread of particles or heat due to random motion.

- **Wave equation:**

$$\frac{\partial^2 u}{\partial t^2} = c^2 \frac{\partial^2 u}{\partial x^2}, \quad (3)$$

which describes oscillatory behaviour such as vibrations of a string or sound waves.

- **Advection equation:**

$$\frac{\partial u}{\partial t} + v \frac{\partial u}{\partial x} = 0, \quad (4)$$

representing the transport of a quantity with constant velocity  $v$ .

- **Reaction-diffusion equation:**

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + f(u), \quad (5)$$

which combines diffusion with a reaction term  $f(u)$  describing local production or consumption.

These notes will focus primarily on *reaction-diffusion systems*, which form a bridge between physical transport processes and chemical or biological interactions.

## 1.3 Reaction-Diffusion systems and Turing's insight

Reaction-diffusion systems describe how the concentration of one or more substances evolves under the combined effects of local reactions and diffusion. In general form, for two interacting components  $u(x, t)$  and  $v(x, t)$ , such systems can be generally written as

$$\begin{cases} \frac{\partial u}{\partial t} = f(u, v) + D_u \Delta u, \\ \frac{\partial v}{\partial t} = g(u, v) + D_v \Delta v, \end{cases} \quad (6)$$

where  $f$  and  $g$  define the local reaction kinetics, and  $D_u$  and  $D_v$  are diffusion coefficients. The symbol  $\Delta$  denotes a differential operator, known as the Laplace operator (or Laplacian). In one dimension,  $\Delta$  reduces to  $\frac{\partial^2}{\partial x^2}$ , but in higher dimensions it generalises to

$$\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2}, \quad (7)$$

which captures the diffusion of a quantity across space. A more detailed discussion of  $\Delta$  and related differential operators is provided in Section 2.

The study of these systems was revolutionised by Alan Turing, who in his 1952 paper *The Chemical Basis of Morphogenesis* proposed that spatial patterns in biological systems, such as stripes,

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<sup>1</sup>In practice, more compact notations are often used, such as  $\partial_t u$ ,  $\partial_x u$ , or simply  $u_t$  and  $u_x$  when no ambiguity arises. Similarly,  $u_{xx}$  or  $\partial_{xx} u$  denote the second derivative with respect to  $x$ .

spots, and waves, could emerge spontaneously from a uniform state through the interaction of reaction and diffusion. This idea, known as *Turing instability* or *diffusion-driven instability*, showed that simple chemical or biochemical systems could generate complex spatial organisation without external guidance. Turing called such interacting chemical substances *morphogens*, abstract chemical agents responsible for the emergence of form, that is, for *morphogenesis*.

Turing's work laid the foundation for modern mathematical biology and continues to inspire research in developmental biology, chemistry, ecology, and physics. Reaction-diffusion equations remain a powerful framework for studying how spatial structure arises in natural systems.

## 2 Operators in differential equations

### 2.1 The $\Delta$ and $\nabla$ notation

In the study of partial differential equations, two related notations are commonly used to express spatial derivatives in compact form.

#### The nabla operator $\nabla$

The *nabla operator* represents the vector differential operator

$$\nabla = \left( \frac{\partial}{\partial x}, \frac{\partial}{\partial y}, \frac{\partial}{\partial z} \right), \quad (8)$$

which acts on scalar or vector fields.

- For a **scalar field**  $u(x, y, z)$ ,

$$\nabla u = \left( \frac{\partial u}{\partial x}, \frac{\partial u}{\partial y}, \frac{\partial u}{\partial z} \right), \quad (9)$$

which gives the *gradient* of  $u$ .

- For a **vector field**  $\mathbf{F} = (F_x, F_y, F_z)$ ,

$$\nabla \cdot \mathbf{F} = \frac{\partial F_x}{\partial x} + \frac{\partial F_y}{\partial y} + \frac{\partial F_z}{\partial z}, \quad (10)$$

which gives the *divergence* of  $\mathbf{F}$ .  $\nabla \cdot \mathbf{F}$  is also sometimes written as  $\text{div } \mathbf{F}$ .

#### The Laplacian $\Delta$ or $\nabla^2$

The *Laplacian* is a scalar operator obtained by applying  $\nabla \cdot$  to  $\nabla u$

$$\Delta u = \nabla \cdot (\nabla u) = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + \frac{\partial^2 u}{\partial z^2}. \quad (11)$$

It measures how the value of  $u$  at a point compares with the average of its neighbours, which is a key quantity in diffusion and heat equations. In particular, we have

$$\boxed{\Delta u = \nabla^2 u = \nabla \cdot (\nabla u)} \quad (12)$$

The notation  $\nabla$  provides a unified way to express gradients, divergences, and Laplacians compactly.

**Remark 1.** *It is common to express the Laplacian on the operator level as a dot product,  $\Delta = \nabla \cdot \nabla$*

$$\nabla \cdot \nabla = \left( \frac{\partial}{\partial x}, \frac{\partial}{\partial y}, \frac{\partial}{\partial z} \right) \cdot \left( \frac{\partial}{\partial x}, \frac{\partial}{\partial y}, \frac{\partial}{\partial z} \right) = \frac{\partial}{\partial x} \frac{\partial}{\partial x} + \frac{\partial}{\partial y} \frac{\partial}{\partial y} + \frac{\partial}{\partial z} \frac{\partial}{\partial z} = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2} = \Delta. \quad (13)$$

*Strictly speaking, this is an abuse of notation, since  $\nabla$  is not a true vector but a differential operator. Nevertheless, this shorthand is widely used and convenient in compact expressions.*

**Remark 2.** *Note that  $\Delta$ , the Laplace operator, should not be confused with the small increments of a quantity  $u$ , also written  $\Delta u$ , seen in other contexts.*

## 2.2 Intuition behind the Laplacian

To understand the effect of the Laplacian, it is helpful to begin with the one-dimensional case.

### One-dimensional case

In one dimension, the Laplacian reduces to the second derivative

$$\Delta u = \frac{d^2 u}{dx^2}. \quad (14)$$

The second derivative measures how the slope of a function changes (Figure 1). If  $\frac{d^2 u}{dx^2} > 0$  at a point, the function is locally concave upwards: the value of  $u$  there is smaller than the average of nearby points. Conversely, if  $\frac{d^2 u}{dx^2} < 0$ , the function is concave downwards: the value of  $u$  is greater than the local average. Thus, the Laplacian quantifies how a point differs from its surroundings, which explains its role in diffusion equations: diffusion tends to reduce these differences over time, as per the equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2}. \quad (15)$$

### Higher dimensions

In higher dimensions, the Laplacian generalises this idea by summing the second derivatives along each spatial direction

$$\Delta u = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + \frac{\partial^2 u}{\partial z^2}. \quad (16)$$

Equivalently, it can be expressed as the divergence of the gradient

$$\Delta u = \operatorname{div}(\nabla u). \quad (17)$$

Here,  $\nabla u$  gives the direction and rate of steepest increase of  $u$ , while the divergence  $\operatorname{div}(\nabla u)$  measures how that quantity flows into or out of a point. A positive Laplacian indicates that  $u$  is lower than the average of its neighbours (a local minimum), and a negative Laplacian indicates the opposite (a local maximum). In physical terms, this captures how quantities such as heat, concentration, or potential spread or equilibrate in space.

**Remark 3.** For a visual explanation and further intuition in the multi-dimensional case, see this video: <https://www.youtube.com/watch?v=EW08rD-GFh0>.

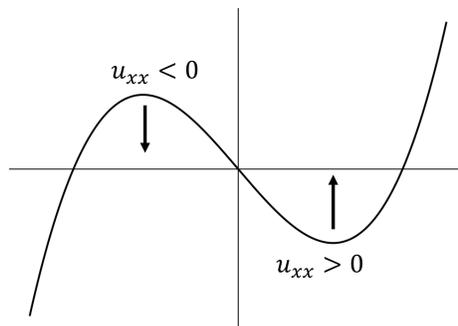


Figure 1: Illustration of the Laplacian in one spatial dimension. The second derivative  $u_{xx}$  measures the local curvature of a function  $u$ : where  $u_t = u_{xx} < 0$ , the function is concave down (a local maximum), and where  $u_t = u_{xx} > 0$ , it is concave up (a local minimum). In diffusion, these curvature differences drive the smoothing of the profile over time. The same ideas extend to other dimensions (see Remark 3).

### 3 Reaction equations

Reaction equations arise from the *law of mass action*, a fundamental principle of chemical kinetics stating that the rate of a reaction is proportional to the product of the concentrations of its reactants, each raised to a power equal to its stoichiometric coefficient. For a simple reaction  $A + B \rightarrow C$  with rate constant  $k$ , the rate of production of  $C$  is given by  $\frac{d[C]}{dt} = k[A][B]$ . Extending this idea to multiple interacting species leads to systems of ordinary differential equations that describe how concentrations change over time. Below, we present the general statement and show how the reaction term describing the temporal change in concentration can be derived.

#### 3.1 Law of mass action

We consider a well-mixed system of species  $X_1, \dots, X_n$  with concentrations  $u_i(t)$ . A generic reaction  $r$  has the form



where  $k_r > 0$  is the rate constant for reaction  $r$ , and  $\nu_{ir}^-, \nu_{ir}^+ \in \mathbb{N}_0$  are the stoichiometric coefficients of reactants and products. Define the stoichiometric change

$$s_{ir} = \nu_{ir}^+ - \nu_{ir}^-. \quad (19)$$

#### Mass-action rate for a single reaction.

The *law of mass action* assumes that the reaction *event rate* (per unit volume) is proportional to the product of reactant concentrations, each raised to its stoichiometric power

$$R_r(u_1, \dots, u_n) = k_r \prod_{j=1}^n u_j^{\nu_{jr}^-}. \quad (20)$$

The time evolution for species  $i$  due to reaction  $r$  follows

$$\left. \frac{du_i}{dt} \right|_r = \underbrace{s_{ir}}_{\text{net change per event}} \times \underbrace{R_r(u)}_{\text{rate of events}}. \quad (21)$$

#### Mass-action system with multiple reactions.

For a network with reactions  $r = 1, \dots, m$  the contributions add:

$$\frac{du_i}{dt} = \sum_{r=1}^m s_{ir} k_r \prod_{j=1}^n u_j^{\nu_{jr}^-}, \quad i = 1, \dots, n. \quad (22)$$

**Remark 4.** *The law of mass action relies on several simplifying assumptions. We consider a well-mixed compartment of fixed volume and constant temperature, where all molecules are uniformly distributed and react through random encounters. Moreover, the number of molecules is assumed to be sufficiently large that fluctuations can be neglected, allowing a deterministic description in terms of concentrations. By working with concentrations rather than molecule counts, the usual volume-scaling factors for bimolecular and higher-order reactions are absorbed into the rate constants.*

#### 3.2 Examples

##### Example 1: one-species exponential growth

Autocatalytic reproduction:



Here  $\nu^- = \{U : 1\}$ ,  $\nu^+ = \{U : 2\}$ , so  $s = \nu^+ - \nu^- = \{U : 1\}$  and the mass-action rate is  $R = \alpha u$ . Hence

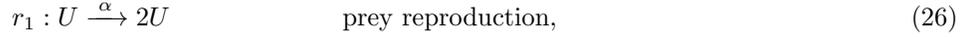
$$\frac{du}{dt} = (+1) \times (\alpha u) = \alpha u, \quad (24)$$

with solution

$$u(t) = u_0 e^{\alpha t}. \quad (25)$$

**Example 2: two-species predator-prey (Lotka-Volterra)**

Let  $u(t)$  be prey and  $v(t)$  be predators. Use the reaction set



Mass-action rates:

$$R_1 = \alpha u, \quad R_2 = \beta uv, \quad R_3 = \delta uv, \quad R_4 = \gamma v. \quad (30)$$

Stoichiometric changes per reaction:

	$r_1$	$r_2$	$r_3$	$r_4$
$\Delta U$	+1	-1	0	0
$\Delta V$	0	0	+1	-1

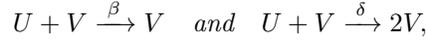
Therefore,

$$\frac{du}{dt} = (+1)R_1 + (-1)R_2 + 0 \cdot R_3 + 0 \cdot R_4 = \alpha u - \beta uv, \quad (31)$$

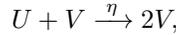
$$\frac{dv}{dt} = 0 \cdot R_1 + 0 \cdot R_2 + (+1)R_3 + (-1)R_4 = \delta uv - \gamma v. \quad (32)$$

These are the standard Lotka-Volterra equations shown in the slides.

**Remark 5.** *It is often convenient to combine the two intermediate reactions,*



*into a single effective process*



*where  $\eta$  represents the overall efficiency of converting prey encounters into new predators. This formulation absorbs the separate effects of prey removal and predator reproduction into one interaction term. Although the general model involves two independent rates ( $\beta$  and  $\delta$ ), its qualitative behaviour can still be captured by the reduced form through a suitable rescaling.*

## 4 Diffusion equations

Diffusion originates from the concept of *Brownian motion*, first observed by Robert Brown in 1827 while examining pollen grains suspended in water. This motion, characterised by random, erratic displacements of microscopic particles resulting from collisions with the molecules of the surrounding medium, was later explained theoretically by Einstein, who described how the probability distribution of particle positions evolves over time, connecting microscopic randomness to macroscopic diffusion. In this section, we derive the diffusion equation in one dimension from a random walk and solve it.

### 4.1 Derivation of the diffusion equation

Let  $u(x, t)$  denote the expected number (or concentration) of particles at position  $x$  and time  $t$ . The diffusion equation in one dimension reads

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} \quad (33)$$

We provide a full derivation of this equation below.

First, consider a discretisation of space and time, with small increments  $h$  in space and  $\tau$  in time. During a small time step  $\tau$ , we assume each particle moves either one step of length  $h$  to the right with probability  $p$  or one step to the left with probability  $1 - p$  (Figure 2). We assume no probability of remaining in place, particles do not interact, and consider the symmetric (unbiased) case  $p = \frac{1}{2}$ .

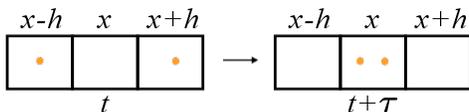


Figure 2: Schematic of particle motion in the discrete random walk model. During each time step  $\tau$ , particles move from neighbouring sites  $x - h$  and  $x + h$  to  $x$  with equal probability  $1/2$ .

### Expected number of particles at a given site

Let  $N(x, t)$  denote the random variable representing the number of particles located at position  $x$  at time  $t$ . We define

$$u(x, t) = \mathbb{E}[N(x, t)], \quad (34)$$

the expected number (or average density) of particles at that site. During each time step  $\tau$ , each particle moves independently either to the right or to the left by a distance  $h$ :

$$\text{left with probability } 1 - p, \quad \text{right with probability } p.$$

The expected number of particles at position  $x$  at time  $t + \tau$  is determined by those that were at  $x - h$  and moved right, together with those that were at  $x + h$  and moved left. At time  $t + \tau$ , the expected number of particles at  $x$  is given by the contributions from neighbouring sites, by the law of total expectation (why? See Remark 6)

$$u(x, t + \tau) = \frac{1}{2} [u(x + h, t) + u(x - h, t)]. \quad (35)$$

### Finite-difference formulation

Subtracting  $u(x, t)$  from both sides of equation (35) and dividing by  $\tau$  leads to

$$\frac{u(x, t + \tau) - u(x, t)}{\tau} = \frac{1}{2\tau} [u(x + h, t) + u(x - h, t) - 2u(x, t)]. \quad (36)$$

Multiplying the right-hand side by  $h^2/h^2$  gives

$$\frac{u(x, t + \tau) - u(x, t)}{\tau} = \frac{h^2}{2\tau} \frac{u(x + h, t) - 2u(x, t) + u(x - h, t)}{h^2}. \quad (37)$$

### Continuum limit

Letting

$$D = \frac{h^2}{2\tau}, \quad (38)$$

and taking the limits  $h, \tau \rightarrow 0$ , the difference quotients become partial derivatives by definition

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}, \quad (39)$$

which is the *one-dimensional diffusion equation* with *diffusion coefficient*  $D$ , assuming  $u$  is differentiable.

### Interpretation

Here  $D$  is the diffusion coefficient, which depends on the microscopic step length  $h$  and time step  $\tau$ . If space is measured in metres (m) and time in seconds (s), then  $D$  has units of  $\text{m}^2\text{s}^{-1}$ . This derivation shows that diffusion arises naturally as the continuum limit of a symmetric random walk where each particle always moves, with equal probability, left or right at each time step.

**Remark 6** (Law of total expectation). *Suppose that at time  $t = 0$ , the sites at  $x - h$  and  $x + h$  contain  $N(x - h, 0)$  and  $N(x + h, 0)$  particles, respectively. During one time step of length  $\tau$ , each particle independently moves towards  $x$  with probability  $p = \frac{1}{2}$ . For simplicity, we assume a deterministic distribution of particles at  $t = 0$ , for all  $x$ .*

Let  $N_l(x, t + \tau)$  and  $N_r(x, t + \tau)$  denote the random numbers of particles that arrive at  $x$  from the left and from the right, respectively, within the interval  $[t, t + \tau]$ . After one time step  $\tau$ , we have

$$N_l(x, \tau) \sim \text{Bin}(N(x - h, 0), \frac{1}{2}), \quad N_r(x, \tau) \sim \text{Bin}(N(x + h, 0), \frac{1}{2}) \quad (40)$$

since each particle moves independently and has a probability  $\frac{1}{2}$  of moving towards  $x$ , so the number of such moves is the count of “successes” in  $N(x \pm h, 0)$  independent Bernoulli trials, which follows a binomial distribution. Therefore, the total number of particles at position  $x$  after one time step is

$$N(x, \tau) = N_l(x, \tau) + N_r(x, \tau). \quad (41)$$

Recall that, for a random variable  $X \sim \text{Bin}(n, p)$ , we have  $\mathbb{E}[X] = np$ . Then, taking expectations and using the linearity of expectation,

$$u(x, \tau) = \mathbb{E}[N(x, \tau)] = \mathbb{E}[N_l(x, \tau)] + \mathbb{E}[N_r(x, \tau)] = \frac{1}{2}N(x + h, 0) + \frac{1}{2}N(x - h, 0). \quad (42)$$

Thus, after a single time step  $\tau$ , the expected number of particles at  $x$  is the sum of the incoming contributions from the neighbouring sites, each weighted by the probability  $\frac{1}{2}$  of moving towards  $x$ .

Following the same logic, the total number of particles at position  $x$  at  $t + \tau$  is then

$$N(x, t + \tau) = N_l(x, t + \tau) + N_r(x, t + \tau). \quad (43)$$

However, now  $N_l(x, t + \tau)$  and  $N_r(x, t + \tau)$  depend on how many particles were at either lateral position in the previous time step,  $N(x \pm h, t)$ , which are themselves random variables. So, in fact, what we know is that, conditional on the value of those random variables,

$$N_l(x, t + \tau) \mid N(x - h, t) \sim \text{Bin}(N(x - h, t), \frac{1}{2}), \quad (44)$$

$$N_r(x, t + \tau) \mid N(x + h, t) \sim \text{Bin}(N(x + h, t), \frac{1}{2}). \quad (45)$$

To compute the expectation of  $N(x, t + \tau)$ , we use the law of total expectation, which states that for random variables  $X$  and  $Y$ ,

$$\mathbb{E}[X] = \mathbb{E}[\mathbb{E}[X \mid Y]]. \quad (46)$$

Then, from (43),

$$u(x, t + \tau) = \mathbb{E}[N(x, t + \tau)] \quad (47)$$

$$= \mathbb{E}[N_l(x, t + \tau)] + \mathbb{E}[N_r(x, t + \tau)] \quad (48)$$

$$= \mathbb{E}[\mathbb{E}[N_l(x, t + \tau) \mid N(x - h, t)]] + \mathbb{E}[\mathbb{E}[N_r(x, t + \tau) \mid N(x + h, t)]] \quad (49)$$

$$= \frac{1}{2}\mathbb{E}[N(x - h, t)] + \frac{1}{2}\mathbb{E}[N(x + h, t)] \quad (50)$$

$$= \frac{1}{2}[u(x - h, t) + u(x + h, t)] \quad (51)$$

which is the discrete evolution equation (35) used in the derivation of the diffusion equation. Note that alternative derivations are possible, interpreting  $u$  as a concentration or probability, where in this case one would use the law of total probability.

## 4.2 Fick’s laws of diffusion

Equation (33) is commonly known as *Fick’s second law of diffusion*. It describes how the concentration of a substance changes over time as a result of diffusion, formalising the idea that fluxes driven by concentration gradients lead to temporal variations in concentration.

Fick’s description of diffusion is based on two related laws:

- **Fick's first law** states that the diffusive flux  $J$  is proportional to the spatial gradient of concentration, directed from regions of high to low concentration:

$$\boxed{J = -D \frac{\partial u}{\partial x}} \quad (52)$$

where  $D$  is the diffusion coefficient and the negative sign indicates movement down the concentration gradient.

- **Fick's second law** expresses how the concentration  $u(x, t)$  evolves in time due to this flux:

$$\boxed{\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}} \quad (53)$$

It follows directly from combining the first law with the principle of mass conservation.

**Remark 7.** *Fick's second law can be derived from the first by applying the law of conservation of mass. Considering that any local change in concentration must equal the negative spatial divergence of the flux,*

$$\frac{\partial u}{\partial t} = -\frac{\partial J}{\partial x}, \quad (54)$$

and substituting Fick's first law,  $J = -D \frac{\partial u}{\partial x}$ , yields

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}. \quad (55)$$

*This relation connects microscopic flux behaviour to macroscopic concentration changes, providing the physical basis for diffusion dynamics.*

### 4.3 Solving the one-dimensional diffusion equation

We consider one-dimensional diffusion in a pipe of length  $L$ . The concentration  $u(x, t)$  satisfies

$$u_t = D u_{xx}, \quad 0 < x < L, \quad t > 0, \quad (56)$$

with boundary conditions (at both ends of the pipe)

$$u(0, t) = 0, \quad u(L, t) = 0, \quad t > 0, \quad (57)$$

and an initial condition (at  $t = 0$ )

$$u(x, 0) = f(x), \quad 0 \leq x \leq L. \quad (58)$$

Here  $D > 0$  is the diffusion coefficient. The notation  $u_t$  and  $u_{xx}$  is a shorthand for the partial derivatives  $\partial u / \partial t$  and  $\partial^2 u / \partial x^2$ .

#### Separation of variables

The method of separation of variables assumes that the solution can be written as a product of a purely spatial part and a purely temporal part<sup>2</sup>

$$u(x, t) = X(x)T(t). \quad (59)$$

Substituting this into the diffusion equation gives

$$X(x)T'(t) = DX''(x)T(t), \quad (60)$$

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<sup>2</sup>Naturally, one might ask why these are the only possible forms of solutions we consider. This question leads to deeper topics such as existence, uniqueness, and completeness of solutions to partial differential equations. In general, finding and classifying solutions to PDEs is a far more intricate problem that often requires advanced analytical or numerical methods, and lies beyond the scope of these lectures. For those wishing to delve deeper, the book *Partial Differential Equations* by Lawrence C. Evans provides a comprehensive and accessible introduction to the topic.

where primes denote ordinary derivatives with respect to the single argument. Assuming  $X$  and  $T$  are not identically zero, we divide both sides by  $DX(x)T(t)$  to obtain

$$\frac{T'(t)}{DT(t)} = \frac{X''(x)}{X(x)}. \quad (61)$$

The left-hand side depends only on  $t$ , and the right-hand side only on  $x$ . Therefore both sides must be equal to the same constant, which we call  $-\lambda$ , and where the minus sign is used for convenience

$$\frac{T'(t)}{DT(t)} = \frac{X''(x)}{X(x)} = -\lambda. \quad (62)$$

This allows us to separate the PDE into a pair of ordinary differential equations

$$T'(t) + D\lambda T(t) = 0, \quad (63)$$

$$X''(x) + \lambda X(x) = 0. \quad (64)$$

The boundary conditions on  $u$  translate into boundary conditions for  $X$ . From

$$u(0, t) = X(0)T(t) = 0, \quad u(L, t) = X(L)T(t) = 0, \quad (65)$$

and the fact that we seek non-trivial solutions with  $T(t) \neq 0$ , we must have

$$X(0) = 0, \quad X(L) = 0. \quad (66)$$

We therefore solve the boundary value problem for  $X(x)$ :

$$X''(x) + \lambda X(x) = 0, \quad X(0) = 0, \quad X(L) = 0. \quad (67)$$

### Solving the spatial problem

We consider the possible signs of  $\lambda$ .

**Case  $\lambda = 0$ .** Equation (64) becomes

$$X''(x) = 0, \quad (68)$$

so

$$X(x) = A + Bx. \quad (69)$$

The boundary conditions  $X(0) = 0$  and  $X(L) = 0$  give  $A = 0$  and  $BL = 0$ , hence  $B = 0$ . This implies  $X(x) \equiv 0$ , the trivial solution, which we discard.

**Case  $\lambda < 0$ .** Write  $\lambda = -\mu^2$  with  $\mu > 0$ . Then (64) becomes

$$X''(x) - \mu^2 X(x) = 0, \quad (70)$$

with general solution (see Remark 8)

$$X(x) = Ae^{\mu x} + Be^{-\mu x}. \quad (71)$$

Applying  $X(0) = 0$  gives  $A + B = 0$ , so  $B = -A$  and

$$X(x) = A(e^{\mu x} - e^{-\mu x}). \quad (72)$$

Then  $X(L) = 0$  implies  $e^{\mu L} = e^{-\mu L}$ , which can only happen if  $A = 0$  or  $\mu = 0$ . Since  $\mu > 0$  by assumption, we again obtain only the trivial solution  $X \equiv 0$ , which we discard.

**Case  $\lambda > 0$ .** Write  $\lambda = \omega^2$  with  $\omega > 0$ . Then (64) becomes

$$X''(x) + \omega^2 X(x) = 0, \quad (73)$$

with general solution

$$X(x) = A \cos(\omega x) + B \sin(\omega x). \quad (74)$$

The boundary condition  $X(0) = 0$  implies  $A = 0$ , so

$$X(x) = B \sin(\omega x). \quad (75)$$

The second boundary condition  $X(L) = 0$  then requires

$$B \sin(\omega L) = 0. \quad (76)$$

For non-trivial solutions we need  $B \neq 0$ , so

$$\sin(\omega L) = 0 \quad \Rightarrow \quad \omega L = n\pi, \quad (77)$$

for integers  $n = 1, 2, 3, \dots$ . Hence

$$\omega_n = \frac{n\pi}{L}, \quad \lambda_n = \omega_n^2 = \left(\frac{n\pi}{L}\right)^2, \quad (78)$$

and the corresponding eigenfunctions are

$$X_n(x) = \sin\left(\frac{n\pi x}{L}\right), \quad n = 1, 2, 3, \dots \quad (79)$$

### Solving the temporal problem

For each  $\lambda_n$ , the temporal equation (63) is

$$T_n'(t) + D\lambda_n T_n(t) = 0. \quad (80)$$

This is a first-order linear ODE with solution (see Remark 9)

$$T_n(t) = b_n \exp(-D\lambda_n t) = b_n \exp\left(-D\left(\frac{n\pi}{L}\right)^2 t\right), \quad (81)$$

where  $b_n$  is a constant. Thus, for each  $n$ , we obtain a separated solution

$$u_n(x, t) = X_n(x)T_n(t) = b_n \sin\left(\frac{n\pi x}{L}\right) \exp\left(-D\left(\frac{n\pi}{L}\right)^2 t\right). \quad (82)$$

### Superposition and the initial condition

The diffusion equation is linear and homogeneous, so any linear combination of separated solutions is also a solution. We therefore consider

$$u(x, t) = \sum_{n=1}^{\infty} b_n \sin\left(\frac{n\pi x}{L}\right) \exp\left(-D\left(\frac{n\pi}{L}\right)^2 t\right). \quad (83)$$

To determine the coefficients  $b_n$ , we impose the initial condition  $u(x, 0) = f(x)$ :

$$f(x) = u(x, 0) = \sum_{n=1}^{\infty} b_n \sin\left(\frac{n\pi x}{L}\right). \quad (84)$$

This is known as the *Fourier sine series* of  $f$  on the interval  $(0, L)$ . In simple terms, this means that any sufficiently well-behaved function  $f(x)$  can be represented as a sum of sine waves with different wavelengths and amplitudes (one may think of it like an audio signal composed of many simpler frequencies). Each sine function,  $\sin\left(\frac{n\pi x}{L}\right)$ , captures a particular spatial pattern, and the coefficient  $b_n$  determines how much of that pattern contributes to the overall shape of  $f(x)$ .

Under suitable regularity assumptions on  $f$ , the coefficients  $b_n$  can be computed explicitly, in order to reconstruct the original function  $f(x)$  entirely. In this sense, the Fourier sine series provides both a decomposition of  $f(x)$  into simple oscillatory components and a means to recover  $f(x)$  from those components, as follows

$$b_n = \frac{2}{L} \int_0^L f(x) \sin\left(\frac{n\pi x}{L}\right) dx, \quad n = 1, 2, 3, \dots \quad (85)$$

In summary, plugging the coefficients  $b_n$  given by (85) into (82), we have that the solution of the one-dimensional diffusion equation with homogeneous boundary conditions is

$$u(x, t) = \sum_{n=1}^{\infty} \left( \frac{2}{L} \int_0^L f(x') \sin\left(\frac{n\pi x'}{L}\right) dx' \right) \sin\left(\frac{n\pi x}{L}\right) \exp\left(-D \left(\frac{n\pi}{L}\right)^2 t\right). \quad (86)$$

This representation shows how the initial concentration profile  $f(x)$  is decomposed into spatial modes that each decay over time at a rate proportional to  $D(n\pi/L)^2$ .

**Remark 8.** For readers less familiar with differential equations, it is helpful to understand why we use these general forms for  $X(x)$  when solving

$$X''(x) + \lambda X(x) = 0. \quad (87)$$

The goal is to find all functions whose second derivative is proportional to the function itself.

When  $\lambda < 0$ , say  $\lambda = -\mu^2$ , the equation becomes

$$X''(x) - \mu^2 X(x) = 0. \quad (88)$$

The functions whose second derivative equals a positive multiple of themselves are exponential functions, so the general solution is

$$X(x) = Ae^{\mu x} + Be^{-\mu x}. \quad (89)$$

However, this form cannot satisfy boundary conditions such as  $X(0) = X(L) = 0$  unless  $A = B = 0$ , yielding only the trivial solution.

When  $\lambda > 0$ , say  $\lambda = \omega^2$ , the equation becomes

$$X''(x) + \omega^2 X(x) = 0. \quad (90)$$

In this case, the second derivative of the function is the negative of a constant times the function itself. Functions with this property are sine and cosine waves, since differentiating them twice produces  $-\omega^2$  times the original function. Hence, the general solution is

$$X(x) = A \cos(\omega x) + B \sin(\omega x). \quad (91)$$

We now apply the boundary conditions at the ends of the pipe. The condition at  $x = 0$  gives

$$X(0) = A \cos(0) + B \sin(0) = A = 0, \quad (92)$$

so the cosine term vanishes and  $X(x) = B \sin(\omega x)$ . The condition at  $x = L$  then requires

$$X(L) = B \sin(\omega L) = 0. \quad (93)$$

For a non-trivial solution, we need  $B \neq 0$ , so

$$\sin(\omega L) = 0 \quad \Rightarrow \quad \omega L = n\pi, \quad n = 1, 2, 3, \dots \quad (94)$$

which gives

$$\omega_n = \frac{n\pi}{L}, \quad X_n(x) = B \sin\left(\frac{n\pi x}{L}\right). \quad (95)$$

Here  $B$  can be any arbitrary constant, since the equation is linear and homogeneous, and multiplying a solution by a constant yields another valid solution. The constant simply scales the amplitude of the mode. Without loss of generality, we may take  $B = 1$ , as this will later be captured by the initial condition (see Remark 9 and ‘Superposition and the initial condition’).

**Remark 9.** In general, an ordinary differential equation of the form

$$f'(t) = Cf(t), \tag{96}$$

where  $C$  is a constant, has the exponential solution (think of it like this: what is a function which derivative is proportional to itself?)

$$f(t) = f(0)e^{Ct}. \tag{97}$$

In our case, the equation

$$T'_n(t) + D\lambda_n T_n(t) = 0 \tag{98}$$

can be written as  $T'_n(t) = -D\lambda_n T_n(t)$ , which corresponds to  $C = -D\lambda_n$ . Therefore, the solution is

$$T_n(t) = b_n e^{-D\lambda_n t} = b_n \exp\left(-D\left(\frac{n\pi}{L}\right)^2 t\right), \tag{99}$$

where  $b_n = T_n(0)$  is determined by the initial condition.

## 5 Reaction-diffusion

We now turn to the study of *stability* in reaction-diffusion systems, a key concept for understanding how patterns form or disappear in space and time. The idea behind stability analysis is to understand how a system behaves when it is slightly disturbed from a steady state, that is, a state in which all variables remain constant in time because the effects of reaction and diffusion are exactly balanced.

Mathematically, this is done by introducing a small perturbation to the steady solution and studying whether it grows or decays over time. If the perturbation vanishes, the system naturally returns to equilibrium and the steady state is said to be *stable*. If the perturbation grows, the system moves further away, indicating *instability*. Intuitively, one can think of this in terms of a ball resting on a surface: if the ball sits at the bottom of a valley (a local minimum of potential energy), a small push only makes it roll back to its original position, meaning the state is stable. In contrast, if the ball balances at the top of a hill (a local maximum), any small displacement makes it roll away, so the state is unstable. In the same way, a stable steady state of a differential equation resists small perturbations, while an unstable one amplifies them.

Understanding stability is essential when studying *Turing patterns*. Alan Turing showed that in certain reaction-diffusion systems, diffusion can paradoxically destabilise a uniform steady state and lead to the spontaneous formation of spatial structures such as spots, stripes, or waves. This process is now called *diffusion-driven instability*. Intuitively, one can think of two interacting chemical substances: if one diffuses much faster than the other, small fluctuations in their concentrations can grow instead of disappearing, creating stable and repeating patterns in space. These patterns provide a mathematical explanation for many forms observed in nature, from animal coat markings to chemical reactions and biological morphogenesis.

### 5.1 Linear stability analysis

#### Reaction stability

We again consider a model for the concentration of a chemical,  $u$ , along a one-dimensional spatial domain  $0 \leq x \leq L$ . The concentration at both ends of the domain is fixed at a constant value  $u_0$ , and the chemical is produced or removed by a reaction term  $f(u)$ . If we ignore spatial effects for a moment and think of the system as well mixed, a simple model is

$$\frac{du}{dt} = f(u). \tag{100}$$

Assume that there is a value  $u_0$  such that

$$f(u_0) = 0. \tag{101}$$

Then  $u(t) = u_0$  is a *steady-state solution*, since  $du/dt = 0$  (it doesn't change over time). We now ask whether this steady state is stable, that is, whether small perturbations decay over time or grow away from equilibrium. To study this, we perturb the solution slightly and write

$$u(t) = u_0 + \hat{u}(t), \quad (102)$$

where  $\hat{u}(t)$  is a small deviation from the steady state. Using a first-order Taylor expansion of  $f(u)$  around  $u_0$ ,

$$f(u) \approx f(u_0) + (u - u_0)f'(u_0), \quad (103)$$

and using  $f(u_0) = 0$ , we obtain the linearised equation (meaning that only terms up to first order in the Taylor expansion are retained)

$$\frac{du}{dt} = (u - u_0)f'(u_0). \quad (104)$$

In terms of the perturbation  $\hat{u} = u - u_0$ , this becomes

$$\frac{d\hat{u}}{dt} = f'(u_0)\hat{u}. \quad (105)$$

This is an ordinary differential equation of the type

$$y'(t) = Cy(t), \quad (106)$$

which solution is

$$y(t) = y(0)e^{Ct}. \quad (107)$$

Applying this to  $\hat{u}$  with  $C = f'(u_0)$  gives

$$u(t) = u_0 + Ae^{f'(u_0)t}, \quad (108)$$

where  $A$  is determined by the initial perturbation. If  $f'(u_0) < 0$ , the exponential term decays in time and the steady state is stable. If  $f'(u_0) > 0$ , the perturbation grows and the steady state is unstable.

### Including diffusion

We now introduce diffusion. The concentration  $u(x, t)$  depends on both space and time and satisfies

$$\frac{\partial u}{\partial t} = f(u) + D \frac{\partial^2 u}{\partial x^2}, \quad (109)$$

for  $0 < x < L$ , with boundary conditions

$$u(0, t) = u(L, t) = u_0. \quad (110)$$

As before, we assume there is a homogeneous steady state  $u(x, t) = u_0$  with  $f(u_0) = 0$ . To examine its stability, we introduce a small spatially varying perturbation

$$u(x, t) = u_0 + \hat{u}(x, t), \quad (111)$$

with

$$\hat{u}(0, t) = \hat{u}(L, t) = 0. \quad (112)$$

Linearising  $f(u)$  around  $u_0$  as before,

$$f(u) \approx f(u_0) + \hat{u}f'(u_0) = \hat{u}f'(u_0), \quad (113)$$

we obtain the linear PDE for the perturbation

$$\frac{\partial \hat{u}}{\partial t} = f'(u_0)\hat{u} + D \frac{\partial^2 \hat{u}}{\partial x^2}. \quad (114)$$

To solve this, we again use separation of variables and assume

$$\hat{u}(x, t) = X(x)T(t). \quad (115)$$

Substituting into the PDE gives

$$X(x)T'(t) = f'(u_0)X(x)T(t) + DX''(x)T(t). \quad (116)$$

Dividing by  $X(x)T(t)$  (assuming they are not zero) yields

$$\frac{T'(t)}{T(t)} = f'(u_0) + D\frac{X''(x)}{X(x)}. \quad (117)$$

The left-hand side depends only on  $t$ , and the right-hand side only on  $x$ , so both sides must be equal to the same constant, which we denote by  $\lambda$

$$\frac{T'(t)}{T(t)} = f'(u_0) + D\frac{X''(x)}{X(x)} = \lambda. \quad (118)$$

This gives two ordinary differential equations

$$T'(t) = \lambda T(t), \quad (119)$$

$$DX''(x) + (f'(u_0) - \lambda)X(x) = 0. \quad (120)$$

The time equation has the solution

$$T(t) = Ae^{\lambda t}, \quad (121)$$

where  $A$  is a constant. For the spatial part, we write

$$DX''(x) + (f'(u_0) - \lambda)X(x) = 0 \implies X''(x) + \omega^2 X(x) = 0, \quad (122)$$

where

$$\omega^2 = \frac{1}{D}(f'(u_0) - \lambda). \quad (123)$$

As before, the general solution of

$$X''(x) + \omega^2 X(x) = 0 \quad (124)$$

is, after applying the boundary conditions, given by

$$X(x) = B \sin(\omega x). \quad (125)$$

From  $X(L) = 0$  we obtain

$$B \sin(\omega L) = 0. \quad (126)$$

For a non-trivial solution we require  $B \neq 0$ , hence

$$\sin(\omega L) = 0 \implies \omega L = n\pi, \quad n = 1, 2, 3, \dots \quad (127)$$

and therefore

$$\omega_n = \frac{n\pi}{L}. \quad (128)$$

Substituting back, we find

$$\frac{1}{D}(f'(u_0) - \lambda_n) = \left(\frac{n\pi}{L}\right)^2, \quad (129)$$

so

$$\lambda_n = f'(u_0) - D\left(\frac{n\pi}{L}\right)^2. \quad (130)$$

Hence, a solution of the system for the perturbation  $\hat{u}$  is

$$\hat{u}_n(x, t) = b_n \sin\left(\frac{n\pi x}{L}\right) e^{\lambda_n t}, \quad (131)$$

and by superposition the general perturbation is

$$\hat{u}(x, t) = \sum_{n=1}^{\infty} b_n \sin\left(\frac{n\pi x}{L}\right) e^{\lambda_n t}, \quad (132)$$

where the coefficients  $b_n$  are determined by the initial perturbation.

The effect of diffusion is now visible in the expression for  $\lambda_n$ . For each mode  $n$  we have

$$\lambda_n = f'(u_0) - D \left( \frac{n\pi}{L} \right)^2. \quad (133)$$

If  $D$  is sufficiently large, then  $D(n\pi/L)^2$  dominates  $f'(u_0)$  and every  $\lambda_n$  is negative. In that case, all perturbations decay in time, whatever their spatial shape, and the homogeneous steady state  $u(x, t) = u_0$  is stable. In this sense, diffusion has a stabilising effect: it smooths out spatial variations and prevents small perturbations from growing.

## 5.2 Example: plankton survival

To illustrate the effect of diffusion on stability, let us consider a simple biological example involving plankton. Suppose  $u(x, t)$  represents the concentration of plankton along a one-dimensional water column of length  $L$ . The population grows locally at a rate proportional to its concentration and diffuses through the water. A simple model combining these effects is

$$\frac{\partial u}{\partial t} = ku + D \frac{\partial^2 u}{\partial x^2}, \quad (134)$$

where  $D$  is the diffusion coefficient and  $k$  is the intrinsic growth (or reproduction) rate of the plankton. We assume that the boundaries are inhospitable, so that

$$u(0, t) = u(L, t) = 0. \quad (135)$$

This model captures the competition between two effects: local reproduction tends to increase the concentration of plankton, while diffusion tends to spread and dilute it. The question is whether the population can survive or whether it decays to zero over time. In particular, what is the critical length,  $L = L_c$ , for which the concentration of plankton is stable?

### Perturbation analysis

We consider the behaviour of small perturbations and recall that the general perturbation solution of the diffusion-reaction equation, as seen in (131), can be written as

$$\hat{u}(x, t) = \sum_{n=1}^{\infty} b_n \sin\left(\frac{n\pi x}{L}\right) e^{\lambda_n t}, \quad (136)$$

where  $\lambda_n$  is the growth rate associated with each spatial mode. The solution decays if  $\lambda_n < 0$  and grows if  $\lambda_n > 0$ . Substituting this form into the governing equation gives the dispersion relation

$$\lambda_n = k - D \left( \frac{n\pi}{L} \right)^2 \quad (137)$$

as deduced generally in (130), where  $f'(u_0) = k$  in this case. Each mode corresponds to a spatial oscillation across the domain, and its stability depends on the sign of  $\lambda_n$ .

### Critical length and stability

The first mode ( $n = 1$ ) represents the *dominant behaviour* of the system, meaning the part of the solution that determines what happens as time tends to infinity. Each mode in the solution evolves as an exponential function  $e^{\lambda_n t}$ , where

$$\lambda_n = k - D \left( \frac{n\pi}{L} \right)^2. \quad (138)$$

As  $n$  increases, the term  $(n\pi/L)^2$  grows, making  $\lambda_n$  smaller:

$$\lambda_1 > \lambda_2 > \lambda_3 > \dots \quad (139)$$

This means that higher modes ( $n = 2, 3, \dots$ ) decay faster because their exponential terms  $e^{\lambda_n t}$  approach zero more quickly. Even if some modes initially contribute to the shape of the solution, they vanish with time, leaving only the slowest-decaying or fastest-growing mode: the first mode ( $n = 1$ ). Hence, when we analyse stability, we focus on  $\lambda_1$  because it determines the long-term outcome: if  $\lambda_1 < 0$ , all modes decay and the population dies out; if  $\lambda_1 > 0$ , the system grows without bound and the plankton population survives.

For  $n = 1$ , we have

$$\lambda_1 = k - \frac{\pi^2 D}{L^2}. \quad (140)$$

If  $\lambda_1 > 0$ , the plankton population grows exponentially; if  $\lambda_1 < 0$ , it decays to zero; and if  $\lambda_1 = 0$ , the system is neutrally stable (Figure 3). The critical case  $\lambda_1 = 0$  defines the threshold between growth and extinction, giving the *critical length*  $L_c$  as

$$L_c = \pi \sqrt{\frac{D}{k}}. \quad (141)$$

If the domain is smaller than this critical length ( $L < L_c$ ), diffusion dominates and carries the plankton toward the boundaries faster than reproduction can replenish it, leading to extinction. If the domain is larger ( $L > L_c$ ), reproduction outweighs diffusive loss and the population can persist. Revisiting Eq. (138) it becomes clearer how reaction and diffusion are balanced to determine stability.

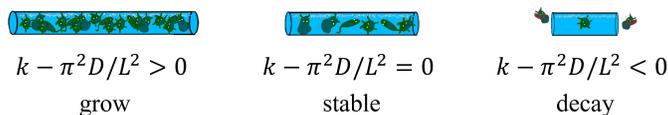


Figure 3: Illustration of the plankton survival model. The balance between diffusion and growth determines whether the population persists or goes extinct. When the domain length  $L$  is large enough ( $k - \pi^2 D / L^2 > 0$ ), the plankton population grows; when diffusion and confinement dominate ( $k - \pi^2 D / L^2 < 0$ ), the population decays to extinction. The critical length  $L_c = \pi \sqrt{D/k}$  marks the transition between survival and extinction.

### Biological interpretation

This simple example demonstrates how diffusion can have a stabilising or destabilising effect depending on the spatial scale of the system. Even if plankton reproduce locally, excessive diffusion in a small region can prevent the population from sustaining itself. The critical length  $L_c$  therefore sets a minimum spatial scale required for survival, showing how spatial constraints and movement play a crucial role in determining whether a population can persist.

### 5.3 Going beyond: multiple species and higher dimensions

So far, we have studied reaction-diffusion equations in one spatial dimension for a single species. In that setting, diffusion tends to smooth out spatial variations and is usually stabilising. In many biological and chemical systems, however, patterns become much more interesting when we consider *multiple* interacting species that diffuse at different rates, and diffusing across multiple spatial dimensions.

Analysing such systems in full generality is beyond the scope of these lectures, but it is helpful to outline the main ideas, since they underpin the prediction of spatial structures known as *Turing patterns*. For clarity, we restrict our attention to two interacting species diffusing in a two-dimensional domain, which already captures the emergence of spatially heterogeneous patterns such as spots and stripes.

We denote the concentrations of the two species by  $u(x, y, t)$  and  $v(x, y, t)$ , where  $(x, y)$  represent spatial coordinates and  $t$  is time. The general reaction-diffusion system is written as

$$\begin{cases} \frac{\partial u}{\partial t} = f(u, v) + D_u \Delta u, \\ \frac{\partial v}{\partial t} = g(u, v) + D_v \Delta v, \end{cases} \quad (142)$$

where  $f$  and  $g$  describe the local reaction kinetics, and  $D_u, D_v$  are the diffusion coefficients. The operator  $\Delta$  denotes the Laplacian in two dimensions,

$$\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}. \quad (143)$$

### Homogeneous steady states and linearisation

We first look for a spatially uniform steady state  $(u_0, v_0)$  that satisfies

$$f(u_0, v_0) = 0, \quad g(u_0, v_0) = 0. \quad (144)$$

This represents a uniform distribution of both species, where local reactions are exactly balanced and diffusion produces no net effect. Again, to study the stability of this steady state, we introduce small perturbations

$$u(x, y, t) = u_0 + \hat{u}(x, y, t), \quad v(x, y, t) = v_0 + \hat{v}(x, y, t), \quad (145)$$

where  $\hat{u}$  and  $\hat{v}$  are small deviations. Substituting these into the system and linearising the reaction terms about  $(u_0, v_0)$  gives

$$f(u, v) \approx f_u \hat{u} + f_v \hat{v}, \quad g(u, v) \approx g_u \hat{u} + g_v \hat{v}, \quad (146)$$

where the partial derivatives are evaluated at the steady state

$$f_u = \left. \frac{\partial f}{\partial u} \right|_{(u_0, v_0)}, \quad f_v = \left. \frac{\partial f}{\partial v} \right|_{(u_0, v_0)}, \quad g_u = \left. \frac{\partial g}{\partial u} \right|_{(u_0, v_0)}, \quad g_v = \left. \frac{\partial g}{\partial v} \right|_{(u_0, v_0)}. \quad (147)$$

The linearised system for the perturbations becomes

$$\begin{cases} \frac{\partial \hat{u}}{\partial t} = D_u \Delta \hat{u} + f_u \hat{u} + f_v \hat{v}, \\ \frac{\partial \hat{v}}{\partial t} = D_v \Delta \hat{v} + g_u \hat{u} + g_v \hat{v}. \end{cases} \quad (148)$$

### Fourier decomposition in space

To understand how these perturbations evolve, we decompose them into spatial Fourier modes of the form

$$\hat{u}(x, y, t) = \tilde{u}(t) e^{i(k_x x + k_y y)}, \quad \hat{v}(x, y, t) = \tilde{v}(t) e^{i(k_x x + k_y y)}, \quad (149)$$

where  $(k_x, k_y)$  are the spatial frequencies, and  $|\mathbf{k}| = \sqrt{k_x^2 + k_y^2}$  is the wavenumber. Each mode represents a sinusoidal pattern with wavelength  $2\pi/|\mathbf{k}|$ . Substituting these forms into the linearised equations yields

$$\Delta e^{i(k_x x + k_y y)} = -|\mathbf{k}|^2 e^{i(k_x x + k_y y)}. \quad (150)$$

Thus, each spatial mode evolves independently in time, and the equations reduce in Fourier space to

$$\frac{d}{dt} \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} = \begin{pmatrix} f_u - D_u |\mathbf{k}|^2 & f_v \\ g_u & g_v - D_v |\mathbf{k}|^2 \end{pmatrix} \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}, \quad (151)$$

where  $\tilde{u}$  and  $\tilde{v}$  denote the Fourier amplitudes of the perturbations.

## Growth rates and diffusion-driven instability

For each wavenumber  $|\mathbf{k}|$ , this system is a set of linear ordinary differential equations with constant coefficients. Its behaviour is governed by the eigenvalues  $\sigma_1(|\mathbf{k}|)$  and  $\sigma_2(|\mathbf{k}|)$  of the coefficient matrix. Each spatial mode then evolves approximately as

$$e^{\sigma_i(|\mathbf{k}|)t}, \quad i = 1, 2. \quad (152)$$

The sign of the real part of  $\sigma_i(|\mathbf{k}|)$  determines whether the mode grows or decays in time:

- If  $\text{Re}(\sigma_i(|\mathbf{k}|)) < 0$ , the mode decays: the steady state is stable.
- If  $\text{Re}(\sigma_i(|\mathbf{k}|)) > 0$ , the mode grows: the steady state is unstable.

The key observation is that diffusion can alter stability. The steady state may be stable in the absence of diffusion but become unstable for certain non-zero wavenumbers when diffusion is introduced. In such cases, diffusion acts as a *destabilising* mechanism, amplifying spatial variations instead of smoothing them out. The resulting instability leads to the formation of stationary spatial patterns, a phenomenon known as a *Turing instability*.

Although the detailed conditions for pattern formation depend on the reaction terms and diffusion rates, this framework captures the essential principle: in two dimensions, as in nature, diffusion can generate strikingly regular patterns (stripes, spots, or labyrinthine structures) from initially uniform states.

## 6 Conclusions and take-home messages

These lectures have introduced the basic ideas behind partial differential equations (PDEs) and their application to modelling biological and physical systems. Below is a summary of the main concepts and how they connect to the study of reaction-diffusion systems and pattern formation.

- **Partial differential equations (PDEs).** PDEs describe how quantities change in both space and time. They generalise ordinary differential equations (ODEs), which depend only on time, by introducing spatial variables and their derivatives. PDEs are essential tools in physics, biology, and engineering because they capture continuous processes such as diffusion, wave propagation, or growth.
- **Physical intuition.** PDEs describe how local processes combine to produce large-scale behaviour. Each term in a PDE corresponds to a physical mechanism that drives change. For example, diffusion represents the spreading of a quantity from high to low concentration, while reaction terms describe local sources, sinks, or interactions. Together, these terms capture how matter, energy, or information moves and transforms in space and time.

A useful way to think about PDEs is that they connect the microscopic and macroscopic worlds. The diffusion equation, for instance, can be derived from the random motion of individual particles (Brownian motion), yet it also describes how temperature or chemical concentration evolves smoothly at larger scales. Similarly, wave equations describe how local forces and inertia give rise to global oscillations, and reaction-diffusion equations show how local interactions between components can generate complex spatial patterns.

In systems that are small or contain few particles, fluctuations can become important and a stochastic description may be required. In contrast, when the system is *well mixed* and involves large numbers of interacting particles, the random microscopic behaviour averages out, and deterministic PDEs provide an accurate description of the macroscopic dynamics.

- **Reaction equations.** Reaction equations describe how the concentration of one or more substances changes over time due to local chemical or biological interactions. In the simplest case, the rate of change of a concentration  $u(t)$  depends on how it reacts with itself or with other substances. These reactions are often modelled using the *law of mass action*, which states that

the rate of a reaction is proportional to the product of the concentrations of the reacting species. For example, in a system with two substances  $u$  and  $v$ , we may write

$$\frac{du}{dt} = f(u, v), \quad \frac{dv}{dt} = g(u, v), \quad (153)$$

where the functions  $f$  and  $g$  describe how the reactions create or consume each component. Reaction equations by themselves do not account for spatial movement; they describe the well-mixed case, where the system is assumed to be uniform in space.

- **The diffusion equation.** The diffusion equation introduces space into the description and models how a quantity spreads out over time. It takes the form

$$\frac{\partial u}{\partial t} = D\Delta u, \quad (154)$$

where  $D$  is the diffusion coefficient and  $\Delta$  is the Laplace operator. Diffusion captures the random motion of particles such as molecules in a liquid or gas, which move from regions of high concentration to regions of low concentration. The key effect of diffusion is to smooth out spatial differences, leading the system toward a uniform distribution over time. Microscopically, this process can be derived from the random (stochastic) movement of particles, known as Brownian motion, which gives rise to the macroscopic diffusion law when averaged over many particles.

- **Reaction-diffusion equations.** When local reactions are combined with diffusion, we obtain *reaction-diffusion systems*. These describe how substances are produced, transformed, or consumed while simultaneously spreading through space:

$$\frac{\partial u}{\partial t} = f(u, v) + D_u\Delta u, \quad \frac{\partial v}{\partial t} = g(u, v) + D_v\Delta v. \quad (155)$$

Here, the reaction terms  $f$  and  $g$  represent local interactions, while the diffusion terms account for spatial transport. Together, they couple space and time, allowing for the emergence of rich dynamics, including steady states, travelling waves, and spatial patterns. Reaction-diffusion models are widely used to describe processes in biology, chemistry, and ecology, from the distribution of morphogens in developing embryos to chemical oscillations and population dispersal.

- **Solving reaction-diffusion equations.** Solving a reaction-diffusion equation means determining how concentrations change both in space and in time, under the combined influence of local reactions and spatial spreading. The mathematical solution depends on the geometry of the system, the reaction terms, and the boundary and initial conditions.

A common starting point is to separate the problem into its main components. The diffusion term tends to smooth spatial variations, while the reaction terms can generate or remove material, often driving the system towards steady states or oscillatory behaviour. In some simple cases, analytical techniques such as the *method of separation of variables* can be used. Here, we assume that the solution can be written as a product of a spatial and a temporal part,  $u(x, t) = X(x)T(t)$ , which reduces the PDE to two ordinary differential equations. Each spatial mode evolves in time at a rate that depends on its wavelength and the parameters of the system. The full solution is obtained as a sum over these modes.

In more complex cases, especially when nonlinear reactions are involved, numerical methods are typically required. These simulate the coupled evolution of reaction and diffusion, revealing behaviours such as the formation of stationary patterns, travelling waves, or oscillations.

Overall, solving a reaction-diffusion equation provides insight into how local processes, such as chemical reactions or population growth, interact with spatial transport to produce global patterns in space and time.

- **The role of boundary and initial conditions.** To determine a unique solution, a PDE must be supplemented with additional information. The *initial condition* specifies the state of the system at the start, for example  $u(x, 0) = u_0(x)$ . The *boundary conditions* describe how the system behaves at its spatial limits, such as fixed values at the boundaries (Dirichlet), no flux

across the boundaries (Neumann), or repeating values (periodic). These conditions determine how diffusion acts and whether material can leave the system, accumulate, or redistribute within a confined space. Different boundary conditions can lead to qualitatively different solutions, even for the same diffusion equation.

- **Interpreting solutions.** The solutions of PDEs represent measurable physical quantities such as temperature, chemical concentration, or population density. For pure diffusion, the interpretation is intuitive: local peaks gradually flatten as material spreads out, eventually approaching a uniform distribution. In systems with both reaction and diffusion, however, the situation is richer. Depending on how reaction and diffusion interact, the system can reach a stable equilibrium, oscillate in time, or form stationary spatial patterns. In this way, PDEs connect simple local rules describing motion and reaction to global behaviours that can be observed in nature.
- **Why study stability.** When studying reaction-diffusion systems, we are often interested not only in finding possible steady states but also in understanding whether these states can persist over time. A *steady state* is a situation where the concentrations of all substances remain constant: the production and consumption through reactions balance perfectly, and diffusion no longer causes any net movement.

However, in real systems, conditions are rarely perfectly uniform. Small fluctuations or perturbations can always occur, whether due to noise, random motion, or external influences. The key question is therefore not just whether a steady state exists, but whether it is *stable*. That is, if the system is slightly disturbed, will it naturally return to its original steady state, or will the disturbance grow and drive the system away from equilibrium?

This is the motivation behind *stability analysis*. It provides a framework for predicting how small deviations evolve in time and helps distinguish between steady states that are physically stable and those that are not. In the context of reaction-diffusion systems, it also reveals how the interaction between reaction and diffusion can sometimes turn a uniform steady state into one that generates rich spatial patterns.

- **The intuition behind stability analysis.** Stability analysis allows us to predict how a system behaves when it is slightly disturbed from a steady state. The idea is to introduce a small perturbation and observe how it evolves in time. If the perturbation fades away, the steady state is stable; if it grows, the steady state is unstable and the system moves towards a new configuration.

To make this idea more concrete, we imagine that any disturbance can be expressed as a combination of simple spatial patterns, such as waves or oscillations. Each of these patterns, often called *modes*, behaves independently and either decays or amplifies over time. This is similar to decomposing a sound into its basic frequencies: some tones may fade quickly, while others dominate and persist.

By analysing how each mode changes, we can determine which spatial patterns the system naturally enhances or suppresses. Diffusion tends to smooth and dampen variations, but the reaction terms can sometimes counteract this smoothing effect and amplify specific modes. The outcome depends on the balance between these two influences. If a particular spatial mode grows instead of decaying, the system becomes unstable to that pattern, and small fluctuations can evolve into large, organised structures.

- **Turing instability and pattern formation.** Alan Turing showed that in systems with two reacting and diffusing substances, diffusion can paradoxically destabilise a uniform steady state. Although diffusion normally smooths differences, when the two species diffuse at different rates, certain spatial patterns can grow instead of fading. The result is the spontaneous emergence of regular structures such as spots, stripes, or labyrinths. These *Turing patterns* provide a powerful example of how complex spatial organisation can arise naturally from simple local interactions between reaction and diffusion.

In summary, partial differential equations form the mathematical language of continuous systems. Reaction-diffusion equations, in particular, illustrate how simple local rules can lead to complex global behaviours and the spontaneous emergence of spatial order. Stability analysis then provides the key to understanding when such order will arise and what forms it will take.