Lecture slides

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Lecture 1

- Introduction to MA42002
- Conservation equations
- Examples of spatially homogeneous models

Conservation equations

$$\begin{pmatrix} \text{rate of change} \\ \text{in the population density} \end{pmatrix} = (\text{spatial movement}) + \begin{pmatrix} \text{birth, growth, death,} \\ \text{production or degradation} \\ \text{due to chemical reactions} \end{pmatrix}$$

Spatially homogeneous models (MA32009 revision)

Example problem - bacteria in a dish

$$N(t + \Delta t) = \quad N(t) + \quad KN(t)\Delta t.$$

A model for cell growth under nutrient depletion

$$
\begin{aligned}
\frac{dN}{dt} &= K(c)N = \kappa c N, \\
\frac{dc}{dt} &= -\alpha \frac{dN}{dt} = -\alpha \kappa c N,
\end{aligned}
\tag{1}
$$

Leading to the logistic growth equation

The last equation can be rewritten as

$$\frac{dN}{dt} = \rho N \, (1 - \frac{N}{B}) \qquad\qquad N(0) = N_0, \tag{2}$$

Can also consider other biological processes

Exercise

Consider a well mixed bio reactor.

A biologist cultures an initial cell population of size N_0 in the bioreactor for 72 h.

Cells undergo division with a period of 14 h.

Each cell produces a non-degradable waste product, W, at rate k_1.

When total waste levels exceed a threshold, W^*, cell division stops. Otherwise the cell population grows exponentially.

How many cells are there at the end of the experiment?

Model development

Model checklist

1. Variables (dependent, indepedent ?)
2. Schematic diagram - what processes are being modelled?
3. Governing equations?
4. Define model parameters?
5. Initial conditions?

Exercise solution

Recap

- Is course layout clear
- Introduction to conservation equation
- Deriving spatially homogeneous models

Lecture 2

- Continue example
- Introduce SIR model
- Introduce an activator inhibitor model
- Derive a conservation equation

Exercise

Consider a well mixed bio reactor.

A biologist cultures an initial cell population of size N_0 in the bioreactor for 72 h.

Cells undergo division with a period of 14 h.

Each cell produces a non-degradable waste product, W, at rate k_1.

When total waste levels exceed a threshold, W^*, cell division stops. Otherwise the cell population grows exponentially.

How many cells are there at the end of the experiment?

The SIR model (used in Chapter 7)

Consider the SIR model equations:

$$\frac{dS}{dt} = -rIS,$$
$$\frac{dI}{dt} = rIS - aI,$$
$$\frac{dR}{dt} = aI.$$

What are the variables? What are the parameters?

Identify an expression for the reproduction number, R_0.

Hence explain why the condition $R_0 < 1$ is necessary to avoid an epidemic?

SIR model Calculations

$$\frac{dS}{dt} = -rIS,$$
$$\frac{dI}{dt} = rIS - aI,$$
$$\frac{dR}{dt} = aI.$$

An activator inhibitor model (used in Chapter 6)

Assume that species A is produced at constant rate k_1 and degrades at rate k_2.

Assume that B is produced at a constant rate, k_4.

Consider the reaction schematic

$$2A + B \rightarrow 3A,$$

with reaction rate k_3.

Write down governing ODEs.

Activator-inhibitor model

Consider the ODEs

$$\frac{da}{dt} = k_1 - k_2 a + k_3 a^2 b,$$
$$\frac{db}{dt} = k_4 - k_3 a^2 b,$$

Identify the steady state of the ODEs. How would you compute linear stability of the steady state?

Recap

- Introduced SIR and activator-inhibitor models
- Computed steady states and stability analysis

Lecture 3 Spatiotemporal models

- Derive conservation PDEs
- Consider different models of fluxes

Spatiotemporal models - derivation

Consider a spatial domain V. A conservation equation can be written either in terms of the mass or number of particles of a species as follows:

$$\begin{aligned}\begin{pmatrix}\text{rate of change of}\\ \text{number of particles}\\ \text{per unit time}\end{pmatrix} &= \begin{pmatrix}\text{rate of entry of}\\ \text{particles into } V\\ \text{per unit time}\end{pmatrix} - \begin{pmatrix}\text{rate of exit of}\\ \text{particles from } V\\ \text{per unit time}\end{pmatrix}\\ &+ \begin{pmatrix}\text{rate of degradation}\\ \text{or creation of particles}\\ \text{in } V \text{ per unit time}\end{pmatrix}\end{aligned}$$

Deriving a conservation equation in 1D

$$\begin{aligned}\frac{\partial}{\partial t}\int_{x}^{x+\Delta x} c(\tilde{x},t)A d\tilde{x} = J(x,t)\,A - J(x+\Delta x,t)\,A \\ + \int_{x}^{x+\Delta x} f(\tilde{x},t,c(\tilde{x},t))\,A\,d\tilde{x}.\end{aligned} \tag{3}$$

A conservation PDE in 1D

$$\frac{\partial}{\partial t}c(x,t) = -\frac{\partial}{\partial x}J(x,t) + f(x,t,c(x,t)). \tag{4}$$

Generalising to R^n

$$\frac{\partial}{\partial t}\int_V c(x,t)\,dx = -\int_S J(x,t)\cdot\mathbf{n}\,d\sigma + \int_V f(x,t,c)dx.$$

Fluxes - Fickian diffusion

$$\mathbf{J} = -D\nabla c, \tag{5}$$

Fluxes - Nonlinear diffusion

$$D = D(c), \qquad \text{e.g. } D(c) = D_0 c^m, \quad D_0 > 0,$$

Hence

$$J = -D(c)\nabla c$$

Fluxes - Convection/advection

$$\mathbf{J} = \mathbf{v}c, \tag{6}$$

Fluxes - Taxis

$$\mathbf{J} = \chi(a)c\nabla a,$$

Domain of definition of the problem

Lecture 4

- Boundary and initial conditions
- Nondimensionalisation
- Model formulation

Boundary conditions

- Dirichlet
- Neumann
- Robin

Initial conditions

Formulating a model

Lecture 5

- Introduce a linear reaction diffusion model
- Diffusion

Linear reaction diffusion equation

$$\frac{\partial c}{\partial t} = D\nabla^2 c + f(c), \quad c \equiv c(\mathbf{x}, t), \ \ \mathbf{x} \in \mathbb{R}^n, \ t > 0.$$

so in 1D Cartesian coordinates

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + f(c), \quad x \in \mathbb{R}, \ t > 0.$$

1D diffusion equation with delta IC

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2}, \quad x \in \mathbb{R},\ t > 0. \tag{7}$$

$$c(x_0, 0) = \delta_0(x) \qquad x \in \mathbb{R}, \tag{8}$$

where δ_0 is a *Dirac delta distribution* (Dirac measure) satisfying

$$\int_{-\infty}^{+\infty} \delta_0(x) = 1 \quad \text{and} \quad \int_{-\infty}^{+\infty} f(x)\delta_0(x) = f(0),\ \text{for continuous } f.$$

Numerical solution

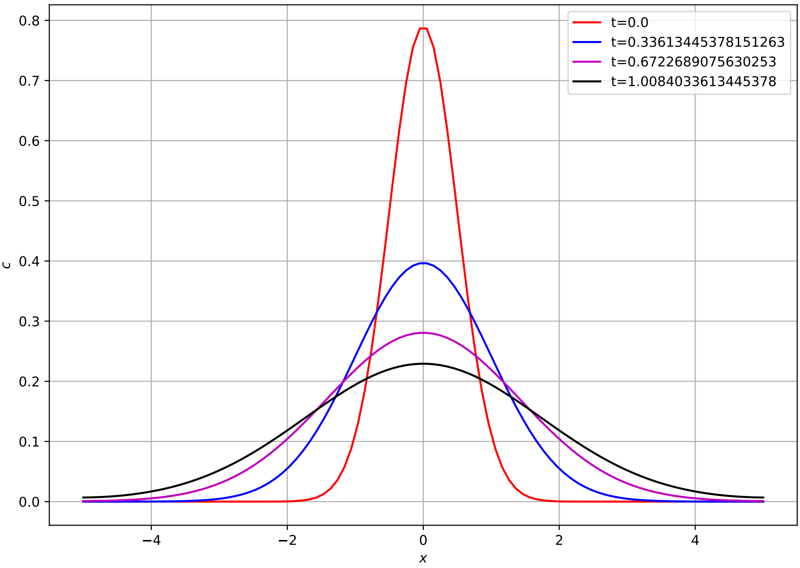


Figure 1: Numerical solution of diffusion equation.

An exact solution computed using a *similarity* variable

Consider the diffusion Equation 7 with initial condition Equation 8.

Introduce the similarity variable

$$\eta = \frac{x}{\sqrt{Dt}}$$

and look for solution of the form

$$c(x,t) = \frac{1}{\sqrt{Dt}} F(\eta).$$

Hence it can be shown that the explicit (analytic) solution is given by

$$c(x,t) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(-\frac{x^2}{4Dt}\right). \tag{9}$$

The 1D diffusion equation for arbitrary initial condition

For a general initial condition $c(x,0) = c_0(x)$ for $x \in \mathbb{R}$:

$$c(x,t) = \int_{-\infty}^{+\infty} \frac{c_0(y)}{\sqrt{4\pi D t}} \exp\left(-\frac{(x-y)^2}{4Dt}\right) dy.$$

Key properties of the (linear) diffusion equation (heat equation)

- The solution is infinitely smooth.
- The solution $c(x,t)$ stays positive for all $t > 0$ and $x \in \mathbb{R}$ if $c(x,0) > 0$ for $x \in \mathbb{R}$.
- The solution "propagates'' with infinite speed i.e. for any $t > 0$, the solution is everywhere in $\mathbb{R}$.
- If we change the initial data $c(x,0)$ (continuously) then the solution also changes (continuously).

Diffusive transit time

$$D\frac{d^2c}{dx^2} = 0 \quad \text{in } (0, L), \quad c(0) = C_0,\, c(L) = 0.$$

Diffusion as a description of random walk

Suppose that the probability of a particle hopping distance Δx to the right in time Δt is

$$\lambda_R \Delta t.$$

Similarly, the probability of hopping a distance Δx to the left is

$$\lambda_L \Delta t.$$

Numerical simulation

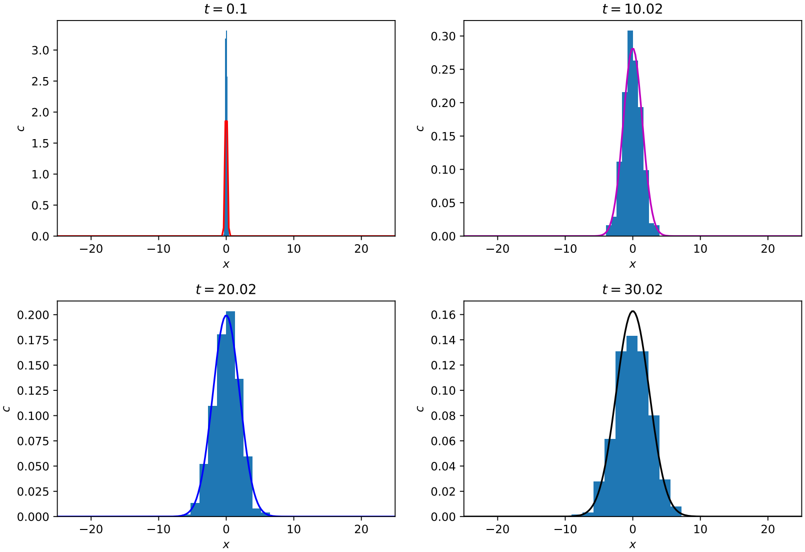


Figure 3: Numerical implementation of random walk

Derivation

Let $c(x,t)$ represent the particle density at spatial location x and time t.

A conservation equation for c is given by

$$c(x,t+\Delta t) = c(x,t) + \lambda_R \Delta t c(x-\Delta x,t) - \lambda_R \Delta t c(x,t) + \\ \lambda_L \Delta t c(x+\Delta x,t) - \lambda_L \Delta t c(x,t).$$

Lecture 6

- Random walk as a model for the diffusion equation
- Linear reaction diffusion

Recap from last week

A conservation equation for c is given by

$$c(x, t + \Delta t) = c(x, t) + \lambda_R \Delta t c(x - \Delta x, t) - \lambda_R \Delta t c(x, t) + \\ \lambda_L \Delta t c(x + \Delta x, t) - \lambda_L \Delta t c(x, t).$$

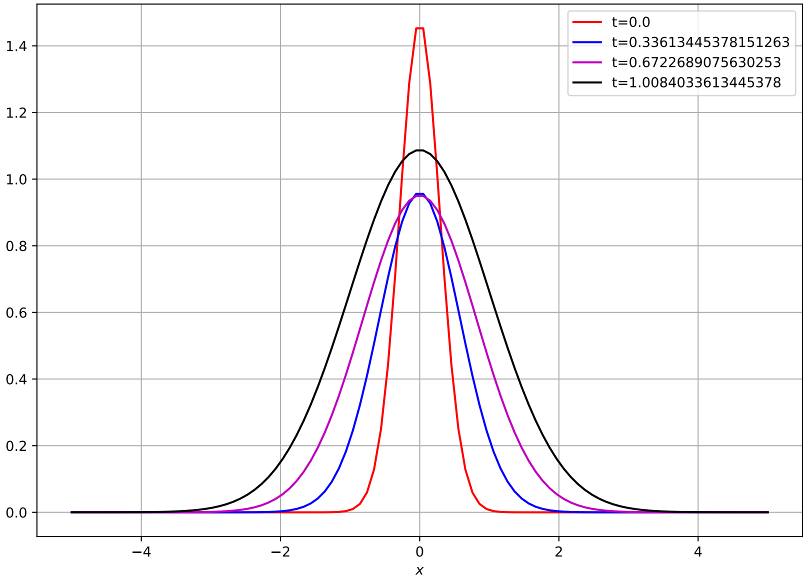
Linear reaction term

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} + \rho\, c, \quad x \in \mathbb{R},\ t > 0, \tag{10}$$

where $\rho \in \mathbb{R}$ is a constant. with initial condition

$$u(x,0) = M\delta_0(x), \quad x \in \mathbb{R}. \tag{11}$$

Numerical solution



Muskrat invasion dynamics

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x_1^2} + \frac{\partial^2 u}{\partial x_2^2}\right) + \rho\, u, \quad \mathbf{x} = (x_1, x_2) \in \mathbb{R}^2,\ t > 0,$$

with initial condition

$$u(\mathbf{x}, 0) = M\delta_0(\mathbf{x}), \quad \mathbf{x} \in \mathbb{R}^2. \tag{12}$$

$$u_1(\mathbf{x}, t) = \frac{M}{4\pi D t} \exp\left(\rho t - \frac{r_1^2}{4Dt}\right).$$

Lecture 7

Travelling waves

Travelling wave

A travelling wave is a solution of a PDE that has a constant profile (shape) and a constant propagation speed.

Fisher's equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \rho u(1 - \frac{u}{K}), \qquad x \in \mathbb{R},\ t > 0$$

with initial condition

$$u(x,0) = u_0(x). \tag{13}$$

Nondimensional form

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u), \qquad x \in \mathbb{R},\ t > 0$$

with initial condition

$$u(x,0) = u_0(x). \tag{14}$$

Numerical solution

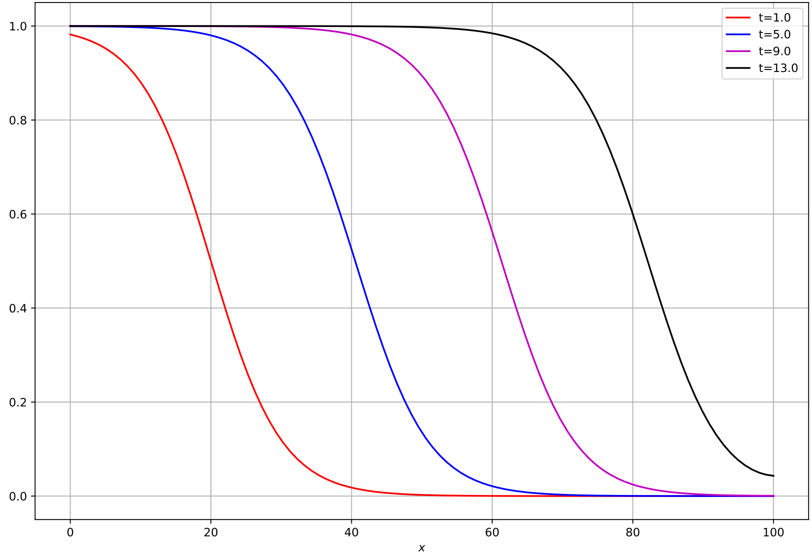


Figure 4: Numerical solution of Fisher's equation.

Spatially homogeneous solutions

Travelling wave solutions

In travelling wave coordinates

$$\frac{d^2W}{dz^2} + v\frac{dW}{dz} + W(1-W) = 0.$$

A pair of first order ODEs

$$\frac{dW}{dz} = P = F(W, P),$$
$$\frac{dP}{dz} = -vP - W(1 - W) = G(W, P).$$

Numerical solution

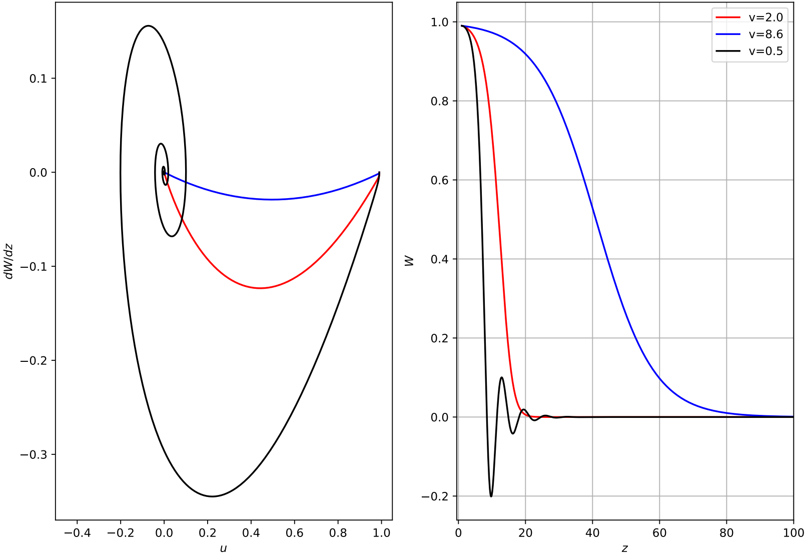


Figure 5: Numerical solution of the travelling wave problem in the phase plane

Lecture 8 Recap

- Two steady states (saddle plus stable node)
- Confined set
- no oscillations

PDE

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u), \qquad x \in \mathbb{R},\ t > 0$$

Travelling wave solution

$$\frac{d^2 W}{dz^2} + v\frac{dW}{dz} + W(1-W) = 0.$$

Recap

Pair of first order ODEs

$$\frac{dW}{dz} = P = F(W,P),$$
$$\frac{dP}{dz} = -vP - W(1-W) = G(W,P).$$

Steady state: (0,0), (1,0)

Linear stability analysis

(0,0) is either a stable node or a stable spiral

(1,0) is a saddle

A heteroclinic trajectory

A minimal wave speed

Existence of a travelling wave solution

Strategy:

- identify a confined set in $\mathfrak{R}^2$
- show no other steady states in confined set
- show no oscillatory solutions

Hence: trajectory that leaves (1,0) via unstable manifold must connect to stable manifold at (0,0)

A confined set

Consider

$$T = \{(W, P) :\ 0 \leq W \leq 1,\ P \leq 0,\ P \geq \mu W\}$$

for some $\mu < 0$.

A confined set - ctd

Lecture 8 Recap

- Two steady states (saddle + stable node)
- Confined set
- No oscillations

Finishing off the confined set

No oscillations

Bendixson's Negative Criterion, Dulac's Negative Criterion

If there exists a function $\varphi(W, P)$, with $\varphi \in C^1(\mathbb{R}^2)$, such that

$$\frac{\partial(\varphi F)}{\partial W} + \frac{\partial(\varphi G)}{\partial P},$$

has the same sign $(\neq 0)$ almost everywhere in a simply connected region (region without holes), then the system

$$\frac{dW}{dz} = F(W, P)$$
$$\frac{dP}{dz} = G(W, P),$$

has no periodic solutions in this region.

Choosing ϕ

For any $v > 2$, there exists a travelling wave solution to Fisher's equation.

Sign of the wave speed

Consider the travelling wave ODE

$$\frac{d^2W}{dz^2} + vW + W(1 - W) = 0$$

The bistable equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u), \qquad x \in \mathbb{R},\ t > 0, \tag{15}$$

with initial condition

$$u(x,0) = u_0(x), \qquad x \in \mathbb{R}.$$

Let

$$f(0) = f(a) = f(1) = 0, \quad \text{with} \quad 0 < a < 1.$$

There are therefore three spatially uniform steady states $u_1 = 0$, $u_2 = a$, $u_3 = 1$.

$$f'(0) < 0, \quad f'(a) > 0 \quad \text{and} f'(1) < 0$$

$$f = u(u-a)(1-u),$$

which arises in the study of nerve action potentials along nerve fibres and other problems in *excitable media*

Numerical solution

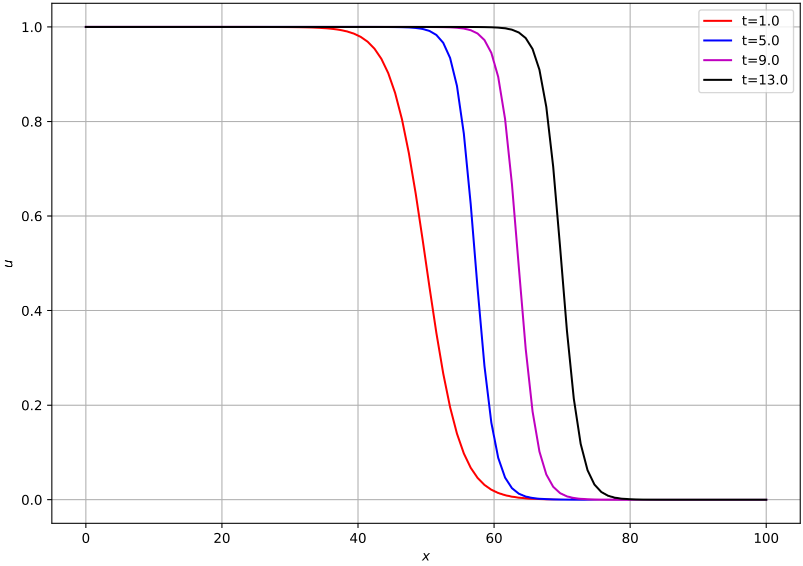


Figure 6: Travelling waves in a numerical solution of bistable PDE.

Lecture 9

- Bistable equation

Travelling wave ansatz

$$\frac{d^2W}{dz^2} + v\frac{dW}{dz} + f(W) = 0,$$

In the phase plane

$$\begin{aligned} \frac{dW}{dz} &= P = F(W,P), \\ \frac{dP}{dz} &= -vP - f(W) = G(W,P), \end{aligned}$$

Steady states and their linear stability

The sign of v

Lecture 10

Recap: travelling wave analysis of bistable equation

$$
\begin{aligned}
\frac{dW}{dz} &= P = F(W,P),\\
\frac{dP}{dz} &= -vP - f(W) = G(W,P),
\end{aligned}
$$

Numerical shooting

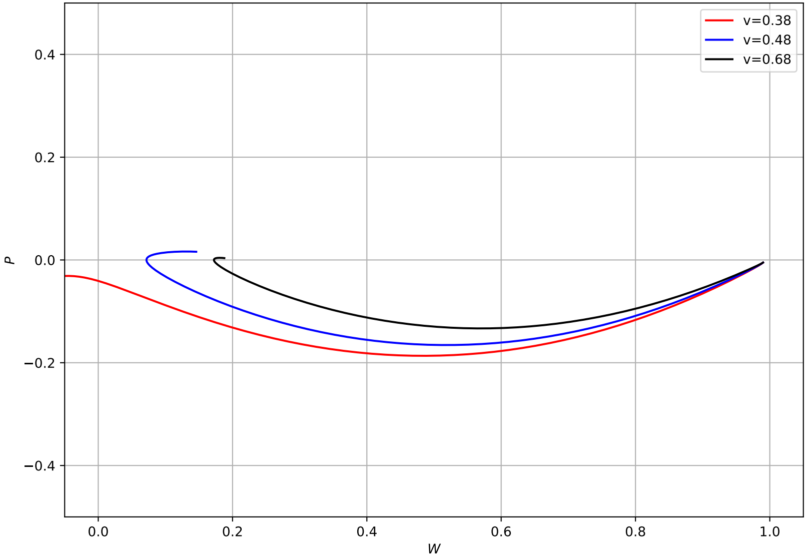


Figure 7: Using a shooting method to investigate travelling wave solutions. Continuity arguments suggest that there exists a travelling

A shooting method to prove the existence of a traveling wave

Outline

Trajectories with small v intersect the P axis with $P < 0$

Assume that

$$\int_0^1 f(u)\,du > 0.$$

Trajectories with large v intersect the W axis with $W > 0$

Continuity there exists a trajectory with intermediate v that passes through the origin

Systems of coupled reaction diffusion equations

Lotka Volterra with diffusion

$$
\begin{aligned}
\frac{\partial u}{\partial t} &= \rho\, u \left(1 - \frac{u}{K}\right) - \alpha\, u\, n + D_u \Delta u, \\
\frac{\partial n}{\partial t} &= \beta\, u\, n - \gamma\, n + D_n \Delta n,
\end{aligned}
\tag{16}
$$

Nondimensional form

$$
\begin{aligned}
\frac{\partial u}{\partial t} = u(1-u-n) + D\frac{\partial^2 u}{\partial x^2} \;&=\; f(u,n) + D\frac{\partial^2 u}{\partial x^2}, \quad x\in\mathbb{R}, t>0\,,\\
\frac{\partial n}{\partial t} = a\,n(u-b) + \frac{\partial^2 n}{\partial x^2} \;&= g(u,n) + \frac{\partial^2 n}{\partial x^2}, \qquad x\in\mathbb{R}, t>0,
\end{aligned}
\tag{17}
$$

Spatially homogeneous steady states

Lecture 11

Recap

$$\frac{\partial u}{\partial t} = u(1-u-n) + D\frac{\partial^2 u}{\partial x^2} \; = \; f(u,n) + D\frac{\partial^2 u}{\partial x^2}, \quad x \in \mathbb{R}, t > 0\,,$$
$$\frac{\partial n}{\partial t} = a\,n(u-b) + \frac{\partial^2 n}{\partial x^2} \; = g(u,n) + \frac{\partial^2 n}{\partial x^2}, \qquad x \in \mathbb{R}, t > 0,$$

Spatially hom. steady states:

- $(0,0)$ - extinction - lin. unstable
- $(1,0)$ - no predator, lin unstable
- $(b, 1-b)$ - coexistence - lin. stable

Question: do travelling wave solutions exist that connect the spatially homogeneous stable steady state to either of the unstable steady states?

A travelling wave that connects $(1, 0)$ and $(b, 1-b)$

$$u(x,t) = W(x+vt) = W(z), \quad v > 0,$$
$$n(x,t) = N(x+vt) = N(z), \quad v > 0.$$

The limit of fast diffusing predator

Three first order ODEs

$$\begin{aligned}
\frac{dW}{dz} &= \frac{1}{v}W(1-W-N) = F(W,N,P),\\
\frac{dN}{dz} &= P = G(W,N,P),\\
\frac{dP}{dz} &= vP - aN(W-b) = R(W,N,P).
\end{aligned} \tag{18}$$

Steady states and their linear stability

Steady states and their linear stability

Lecture 12

- steady states: $(0,0,0)$, $(1,0,0)$, $(b,1-b,0)$
- Heteroclinic trajectory from (1,0,0) to $(b,1-b,0)$
- (1,0,0) has a 2 dim unstable manifold
- Eigenvalues at $(b,1-b,0)$ satisfy

$$\lambda^3 - \lambda^2(v - \frac{b}{v}) - \lambda b - \frac{1}{v}ab(1-b) = p(\lambda) = 0.$$

TPs are independent of a

p( ) has a real positive root and two roots with negative real part

Plotting the cubic

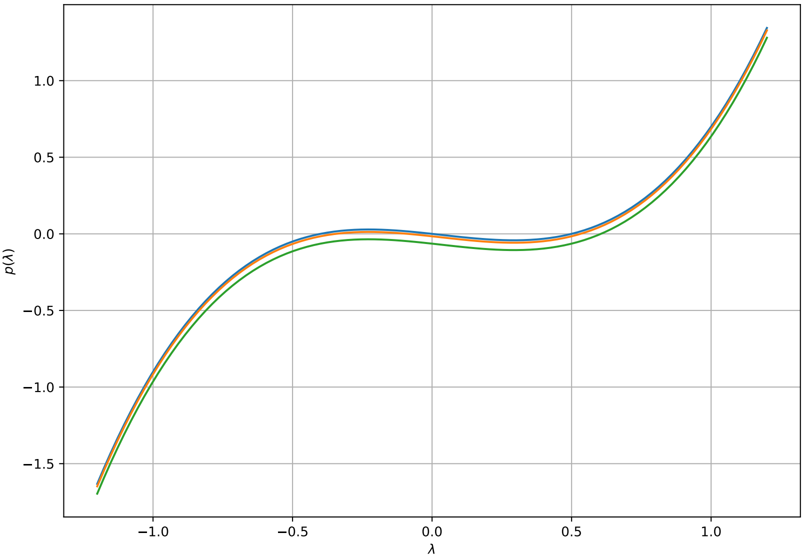


Figure 8: Plot of cubic.

Aggregation via chemotaxis

- *Dictyostelium discoideum* (Dicty) is a slime-mold that is widely studied experimentally as a model organism.
- under nutrient starvation, it exhibits complex collective behaviour
- individual amoebae that constitute a slime-mold exhibit a range of phenomena also observed in mammalian cells e.g. differentiation, proliferation, migration.

Figure 9: Spiral wave patterns underly Dictystelium aggregation.

How do simple rules give rise to complex behaviours?

A chemotactic model

A 1D spatial domain with no-flux boundary conditions

Lecture 13

Domain:

$$x \in [0, L], t > 0$$

PDE:

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - \chi_0 \frac{\partial}{\partial x}\left(n \frac{\partial a}{\partial x}\right),$$

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + \mu n - \delta a, \tag{19}$$

Boundary conditions:

$$\frac{\partial a}{\partial x} = \frac{\partial n}{\partial x} = 0, \quad x = 0, L.$$

ICs:

numerical solution

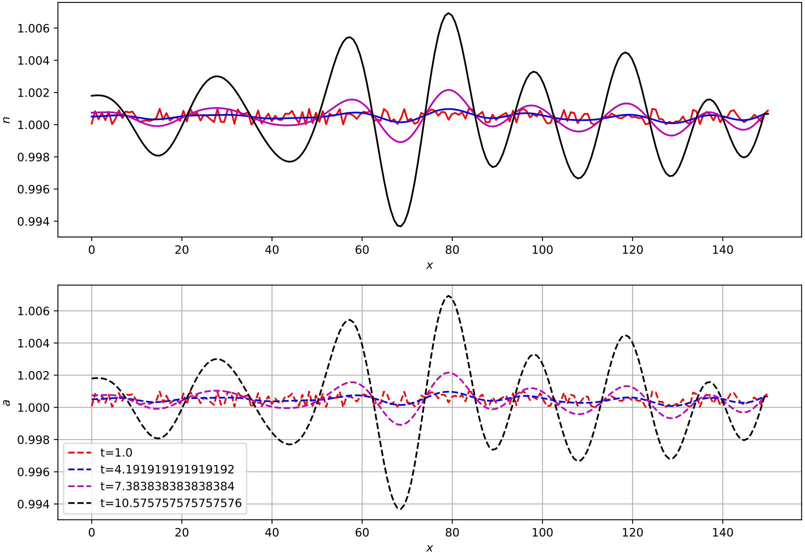


Figure 10: Numerical solution of bacterial chemtaxis model.

Conservation of cell number

Spatially homogeneous solutions

Linearisation about the spatially homogeneous steady state

$$n(x,t) = n^* + \tilde{n}(x,t), \quad a(x,t) = a^* + \tilde{a}(x,t)$$

Separable solution

$$\tilde{n}(t,x) = u(t)\phi_1(x), \quad \tilde{a}(t,x) = v(t)\phi_2(x)$$

The elliptic problem

$$
\begin{aligned}
\frac{d^2\phi}{dx^2} &= -k^2\phi \qquad \text{in} \ \ (0, L), \\
\frac{d\phi}{dx} &= 0 \qquad\qquad \text{for} \ \ x = 0, \ x = L.
\end{aligned}
$$

$\phi_1 = \phi 2 = \phi$

Linear system solution

$$u(t) = C_1 e^{\lambda t} \quad \text{and} \quad v(t) = C_2 e^{\lambda t}$$

Lecture 13 - Recap

Domain:

$$x \in [0, L], t > 0$$

PDE:

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - \chi_0 \frac{\partial}{\partial x}\left(n\frac{\partial a}{\partial x}\right),$$

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + \mu n - \delta a, \tag{20}$$

Boundary conditions:

$$\frac{\partial a}{\partial x} = \frac{\partial n}{\partial x} = 0, \quad x = 0, L.$$

ICs:

Method

- Linearise about the steady state
- Separation of variables $\tilde{n}(x,t) = u(t)\phi(x)$ $\tilde{a}(x,t) = v(t)\phi(x)$
- Eigenvalues of the Laplacian operator

$$\frac{d^2\phi}{dx^2} = -k^2\phi, \quad k = \frac{\bar{n}\pi}{L}, \bar{n} \in Z$$

- Linear ODEs in $u(t)$ and $v(t)$
- For instability of spatially homogeneous steady state, require $\Re\{\lambda > 0\}$.

Eigenvalue equation

$$\lambda^2 + \left(D_n k^2 + D_a k^2 + \delta\right)\lambda + D_n k^2 \left(D_a k^2 + \delta\right) - \mu \chi_0 n^* k^2 = 0.$$

Conditions for instability of spatially homogeneous pattern

Lecture 16 - Diffusion driven instability

$$\frac{\partial A}{\partial t} = F(A, B) + D_A \nabla^2 A,$$
$$\frac{\partial B}{\partial t} = G(A, B) + D_B \nabla^2 B,$$

Reaction kinetics

Schnackenberg

$$F(A,B) = k_1 - k_2 A + k_3 A^2 B, \quad G(A,B) = k_4 - k_3 A^2 B$$

Gierer Meinhardt:

$$F(A,B) = k_1 - k_2 A + \frac{k_3 A^2}{B}, \quad G(A,B) = k_4 A^2 - k_5 B$$

Thomas:

$$\begin{aligned} F(A,B) &= k_1 - k_2 A - H(A,B), \\ G(A,B) &= k_4 A^2 - k_4 B - H(A,B), \\ H(A,B) &= \frac{k_5 AB}{k_6 + k_7 + k_8 A^2}. \end{aligned}$$

Nondimensionalisation of Schnakenberg model

Using the scaling

$$u = A\left(\frac{k_3}{k_2}\right)^{1/2}, \quad v = B\left(\frac{k_3}{k_2}\right)^{1/2}, \quad t^* = \frac{D_A t}{L^2}, \quad x^* = \frac{x}{L},$$

$$\begin{aligned} \frac{\partial u}{\partial t} &= \gamma(a - u + u^2 v) + \nabla^2 u = \gamma f(u,v) + \nabla^2 u, \\ \frac{\partial v}{\partial t} &= \gamma(b - u^2 v) + d\nabla^2 v = \gamma g(u,w) + d\nabla^2 v, \end{aligned} \tag{21}$$

Interpretation of Schnackenberg model: short range activation/long range inhibition

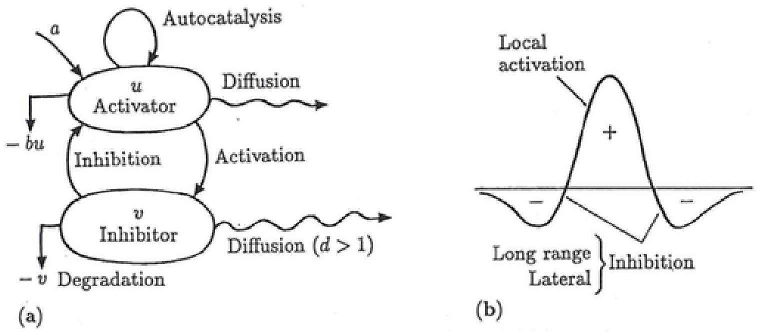
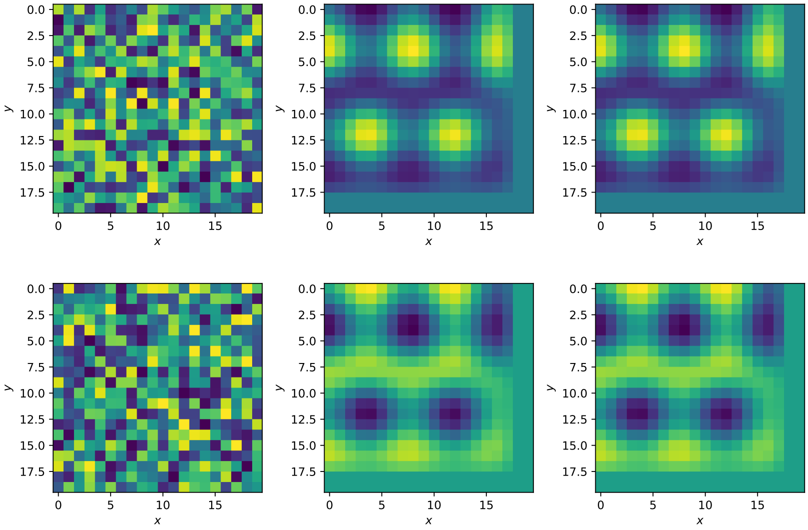


Figure 11

General form for nondimensionalised RD model

$$\frac{\partial u}{\partial t} = \gamma f(u,v) + \nabla^2 u,$$
$$\frac{\partial v}{\partial t} = \gamma g(u,w) + d\nabla^2 v,$$

Numerical solution



Deriving general conditions for diffusion-driven instability

Let $\Omega \subset R^n$ be a domain with smooth (sufficiently regular) boundary $\partial\Omega$, with outward unit normal $\mathbf{n}$.

$$\begin{aligned}
\frac{\partial u}{\partial t} &= \gamma\, f(u,v) + \nabla^2 u, \qquad x \in \Omega, \quad t > 0, \\
\frac{\partial v}{\partial t} &= \gamma\, g(u,v) + d\nabla^2 v, \qquad x \in \Omega, \quad t > 0,
\end{aligned} \tag{22}$$

Boundary and initial conditions

$$\begin{aligned}
&\nabla u \cdot \mathbf{n} = 0, \qquad \nabla v \cdot \mathbf{n} = 0, \qquad x \in \partial\Omega, \quad t > 0, \\
&u(x,0) = u_0(x), \qquad v(x,0) = v_0(x), \qquad x \in \Omega\, .
\end{aligned} \tag{23}$$

Conditions for diffusion driven instability

$$\begin{aligned}
f_u + g_v &< 0, \\
f_u g_v - f_v g_u &> 0, \\
d f_u + g_v &> 0, \\
(d f_u + g_v)^2 - 4d(f_u g_v - f_v g_u)^2 &< 0,
\end{aligned}$$

A spatially homogeneous steady-state

A *spatially homogeneous steady-state* of Equation 22 and Equation 23 satisfies

$$f(u_0, v_0) = g(u_0, v_0) = 0.$$

For linear stability

$$f_u + g_v < 0,$$
$$f_u g_v - f_v g_u > 0$$

Here

$$f_u = \frac{\partial f}{\partial u}_{(u_0, v_0)}$$

etc.

Spatially dependent perturbations

$$u(x,t) = u_0 + \tilde{u}(x,t), \quad v(x,t) = v_0 + \tilde{v}(x,t), \qquad \|\tilde{u}(x,t)\| \ll 1, \quad \|\tilde{v}(x,$$

Separation of variables

$$V(x,t) = \begin{pmatrix} \bar{u}(t)\varphi_1(x) \\ \bar{v}(t)\varphi_2(x) \end{pmatrix},$$

A set of basis functions

Returning to the vectorised form of equations

A modified Jacobian for spatially heterogeneous perturbations

Lecture 18 Recap

For linear instability of spatially homogeneous steady state:

$$\det(\tilde{J}) = h(k^2) = dk^4 - \gamma(d\, f_u + g_v)k^2 + \gamma^2 \det(J) < 0.$$

$$df_u + g_v > 0.$$

$$\frac{(df_u + g_v)^2}{4d} > |J|.$$

Instability for a limited range of wavenumbers

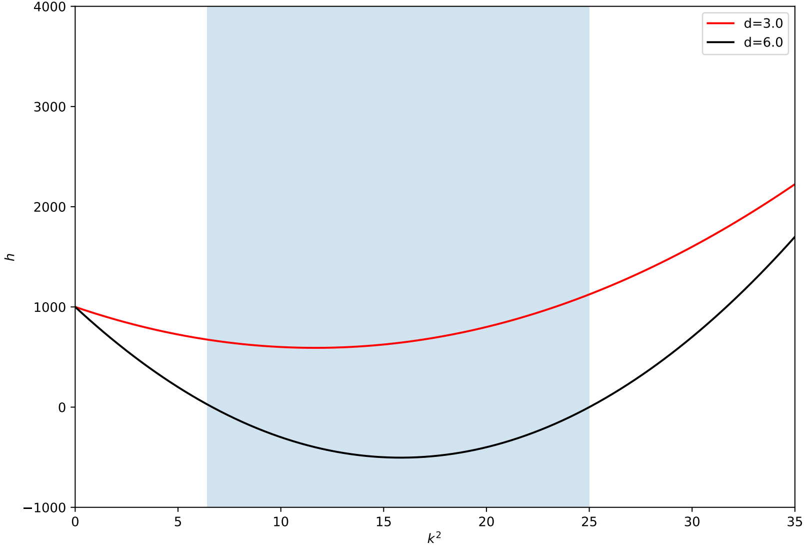


Figure 12: A plot of $h(k^2)$ plotted against k^2. Shaded region denotes unstable wave numbers in case of largets d.

Summary - DDI conditions

$$
\begin{aligned}
f_u + g_v &< 0, \\
f_u g_v - f_v g_u &> 0, \\
d f_u + g_v &> 0, \\
(d f_u + g_v)^2 - 4d(f_u g_v - f_v g_u)^2 &< 0,
\end{aligned}
$$

The SIR model

Assumptions

- Total population is constant: the duration of the epidemic is short compared to the lifetime of its hosts, so we can neglect birth and disease-unrelated death
- Consider a disease which, after recovery, confers immunity (and/or death if lethal)
- Population is well mixed (spatially homogenous)

SIR model - variables

- S – susceptibles - can be infected
- I – infectives - have the disease and can transmit to susceptibles
- R – recovered (removed) - have had the disease and are no longer infective.

Progress through the disease

$$S \longrightarrow I \longrightarrow R$$

SIR model - ODEs

$$
\begin{aligned}
\frac{dS}{dt} &= -rSI, \\
\frac{dI}{dt} &= rSI - aI \\
\frac{dR}{et} &= aI
\end{aligned}
\tag{24}
$$

Epidemic:

$$rS_0 > a \implies R_0 := \frac{rS_0}{a} > 1$$

Spatio-temporal model

$$
\begin{aligned}
\frac{\partial S}{\partial t} &= -rSI + D_S \frac{\partial^2 S}{\partial x^2} \ , \quad x \in \mathbb{R}, t > 0 \ , \\
\frac{\partial I}{\partial t} &= rSI - aI + D_I \frac{\partial^2 I}{\partial x^2} \ , \quad x \in \mathbb{R}, \ t > 0 \ , \\
\frac{\partial R}{\partial t} &= aI + D_R \frac{\partial^2 R}{\partial x^2} \ , \quad x \in \mathbb{R}, \ t > 0 \\
S(0,x) &= S_0(x), \qquad I(0,x) = I_0(x), \quad R(0,x) = R_0(x), \qquad x \in \mathbb{R} \ ,
\end{aligned}
\tag{25}
$$

Nondimensionalise

Defining

$$i = \frac{I}{\bar{S}_0}, s = \frac{S}{\bar{S}_0}, \quad x^* = \left(\frac{r\bar{S}_0}{D_I}\right)^{1/2} x, \tau = r\bar{S}_0 t$$

we obtain (after dropping '$*$')

$$\begin{aligned}
&\frac{\partial s}{\partial t} = -si + d\frac{\partial^2 s}{\partial x^2}\ , && x \in \mathbb{R},\ t > 0\ ,\\
&\frac{\partial i}{\partial \tau} = si - \mu i + \frac{\partial^2 i}{\partial x^2}\ , && x \in \mathbb{R},\ t > 0\ ,\\
&s(x,0) = \frac{S_0(x)}{\bar{S}_0}, \qquad i(x,0) = \frac{I_0(x)}{\bar{S}_0}, && x \in \mathbb{R}\ ,
\end{aligned}$$

where $\bar{S}_0$ is a representative population density and $\mu = a/r\bar{S}_0$.

Aim

- investigate the spatial spread of an epidemic wave of infectives into a uniform susceptibles population $S_0(x) = \bar{S}_0$.
- determine conditions for existence of an epidemic wave and propagation speed.

Travelling wave analysis

$$s(x,t) = \bar{s}(z), \quad i(x,t) = \bar{i}(z), \quad z = x - vt, \quad v > 0$$

Boundary conditions

$$\begin{aligned}
\bar{s}(z) &\to 1 \qquad z \to +\infty, \qquad & \bar{i}(z) &\to 0 \qquad z \to +\infty\ , \\
\bar{s}(z) &\to \sigma \qquad z \to -\infty, \qquad & \bar{i}(z) &\to 0 \qquad z \to -\infty\ , \\
\bar{s}'(z) &\to 0 \qquad z \to \pm\infty, \qquad & \bar{i}'(z) &\to 0 \qquad z \to \pm\infty\ ,
\end{aligned} \tag{26}$$

where $0 \leq \sigma < 1$.

Steady states of the travelling wave problem

$$(s^*, i^*) = (1, 0), \qquad (s^*, i^*) = (\sigma, 0)$$

A heteroclinic connection

Writing as a system of first order ODEs

Linearistation and a minimum wavespeed

The solution profile at the leading edge of the epidemic front

Spatial spread of rabies among foxes

$$
\begin{aligned}
&\frac{\partial S}{\partial t} = -SI \ , && x \in \mathbb{R},\ t > 0 \ , \\
&\frac{\partial I}{\partial t} = SI - \mu I + \frac{\partial^2 I}{\partial x^2} \ , && x \in \mathbb{R},\ t > 0 \ , \\
&S(0,x) = 1, \qquad I(0,x) = \frac{I_0}{\bar{S}_0}, && x \in \mathbb{R} \ ,
\end{aligned}
\tag{27}
$$

Travelling wave equations

Considering

$$S(t,x) = s(z), \quad I(t,x) = i(z), \quad z = x - vt, \quad v > 0$$

$$\begin{aligned} & vs' = is \ , \\ & i'' + vi' + is - \mu i = 0 \end{aligned} \tag{28}$$

Travelling wave equations + boundary conditions

$$
\begin{aligned}
s(z) &\to 1 \qquad z \to +\infty, \qquad & i(z) &\to 0 \qquad z \to +\infty\ , \\
s(z) &\to \sigma \qquad z \to -\infty, \qquad & i(z) &\to 0 \qquad z \to -\infty\ , \\
s'(z) &\to 0 \qquad z \to \pm\infty, \qquad & i'(z) &\to 0 \qquad z \to \pm\infty\ ,
\end{aligned}
\tag{29}
$$

where $0 \leq \sigma < 1$.

Steady states and a minimal wave speed

The susceptible density behind the wavefront