Reaction-Diffusion Models and Bifurcation Theory
Lecture 4: Numerical methods, chemotaxis, cross-diffusion and nonlocal models

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Advection-reaction-diffusion equations

General initial-boundary value problem:

$$\begin{cases} u_t = D\Delta u - V \cdot \nabla u + f(x,u), & x \in \Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in \Omega, \\ Bu(x,t) = g(x), & x \in \partial\Omega,\ t > 0. \end{cases}$$

1-D problem:

$$\begin{cases} u_t = du_{xx} - au_x + f(x,u), & x \in (0,L),\ t > 0, \\ u(x,0) = u_0(x) \geq 0, & x \in (0,L), \\ du_x(0,t) - au(0,t) = -b, & t > 0, \\ -du_x(L,t) + au(L,t) = cu(L,t), & t > 0. \end{cases}$$

Boundary conditions can be Dirichlet, Neumann, etc.

Most most equations cannot be solved analytically, hence to visualize the solutions, we need to use numerical solutions.

Setup of the finite difference method

A sample problem

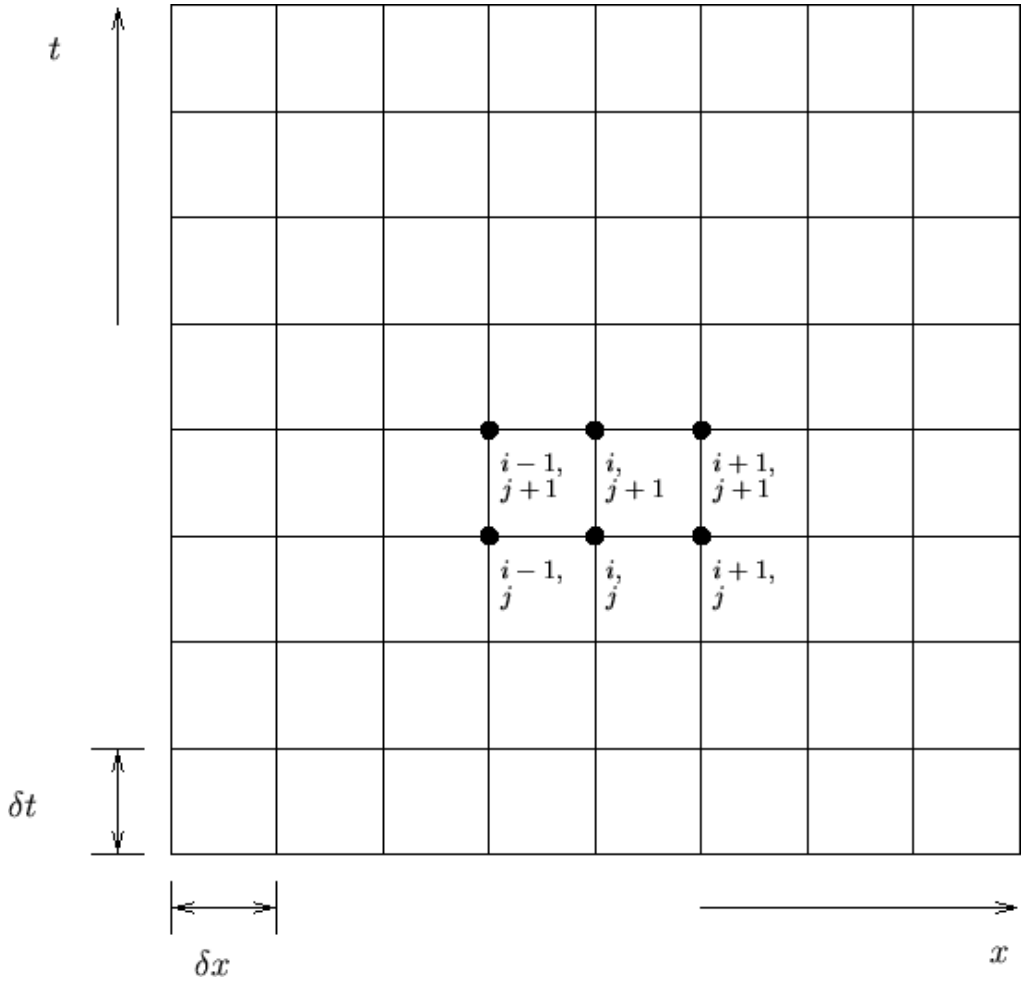
$$\begin{cases} u_t = du_{xx} - au_x + f(u), & x \in (0, L),\ t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in (0, L), \\ u_x(0, t) = u_x(L, t) = 0, & t > 0. \end{cases}$$

We divide the interval $[0, L]$ to n equal subintervals $[x^i, x^{i+1}]$, $i = 1, 2, \cdots, n, n+1$, with $x^i = x^{i-1} + \Delta x$, $x^1 = 0$ and $\Delta x = L/n$ (which we call *grid size*.) We also denote the *step size* (in the time direction) by Δt.

We define
$u_j^i = u(x^i, t_j)$, $t_j = t_{j-1} + \Delta t$, $x^i = x^{i-1} + \Delta x$, $1 \leq j \leq m$, $1 \leq i \leq n+1$.

Basic algorithm:
1. the vector $[u_1^1, u_1^2, \cdots, u_1^{n+1}]$ is known (initial condition);
2. For $j = 1$ to $j = n$, define $[u_{j+1}^1, u_{j+1}^2, \cdots, u_{j+1}^{n+1}]$ from $[u_j^1, u_j^2, \cdots, u_j^{n+1}]$.

The grid



Difference equations

Approximate derivative by difference:

$u_t(x^i, t_j) = \dfrac{u^i_{j+1} - u^i_j}{\Delta t}$ (forward difference), or $u_t(x^i, t_j) = \dfrac{u^i_j - u^i_{j-1}}{\Delta t}$ (backward difference)

$u_x(x^i, t_j) = \dfrac{u^{i+1}_j - u^i_j}{\Delta x}$ (forward difference), or $u_x(x^i, t_j) = \dfrac{u^i_j - u^{i-1}_j}{\Delta x}$ (backward difference)

$u_x(x^i, t_j) = \dfrac{u^{i+1}_j - 2u^i_j + u^{i-1}_j}{(\Delta x)^2}$ (central difference),

We use backward differences. Then $u_t = du_{xx} - au_x + f(u)$ becomes

$$\frac{u^i_j - u^i_{j-1}}{\Delta t} = d\frac{u^{i+1}_j - 2u^i_j + u^{i-1}_j}{(\Delta x)^2} - a\frac{u^i_j - u^{i-1}_j}{\Delta x} + f(u^i_j)$$

$$u^i_{j-1} = -ru^{i+1}_j + (1 + 2r + s)u^i_j - (r + s)u^{i-1}_j - \Delta t \cdot f(u^i_j)$$

where $r = \dfrac{d\Delta t}{(\Delta x)^2}$, $s = \dfrac{a\Delta t}{\Delta x}$.

This formula works for $2 \le i \le n$ but not $i = 1$ and $i = n + 1$ (boundary point)

Boundary points

$$u_{j-1}^{i} = -ru_j^{i+1} + (1+2r+s)u_j^i - (r+s)u_j^{i-1} - \Delta t f(u_j^i), \quad \text{where } r = \frac{d\Delta t}{(\Delta x)^2},$$
$$s = \frac{a\Delta t}{\Delta x}.$$

The definition of u_{j-1}^1 and u_{j-1}^{n+1} would need the values outside of $[0, L]$. So we define u_j^0 to be the value at $x = -\Delta x$ and u_j^{n+2} to be the value at $x = L + \Delta x$.

Neumann boundary: $u_x(0) = 0$: $u_x(0, t_j) = \dfrac{u_j^1 - u_j^0}{\Delta x} = 0$ so $u_j^0 = u_j^1$. Then
$u_{j-1}^1 = -ru_j^2 + (1+2r+s)u_j^1 - (r+s)u_j^0 - \Delta t \cdot f(u_j^1) = -ru_j^2 + (1+r)u_j^1 - \Delta t \cdot f(u_j^1)$
$u_{j-1}^{n+1} = -ru_j^{n+2} + (1+2r+s)u_j^{n+1} - (r+s)u_j^n - \Delta t \cdot f(u_j^{n+1}) =$
$(1+r+s)u_j^{n+1} - (r+s)u_j^n - \Delta t \cdot f(u_j^{n+1})$

So we can put the equations in a matrix form: $[u_{j-1}] = A[u_j] - \Delta t[f(u_j)]$ where A is the $(n+1) \times (n+1)$ conversion matrix (for example $n = 6$)

$$\begin{pmatrix} 1+r & -r & 0 & 0 & 0 & 0 & 0 \\ -r-s & 1+2r+s & -r & 0 & 0 & 0 & 0 \\ 0 & -r-s & 1+2r+s & -r & 0 & 0 & 0 \\ 0 & 0 & -r-s & 1+2r+s & -r & 0 & 0 \\ 0 & 0 & 0 & -r-s & 1+2r+s & -r & 0 \\ 0 & 0 & 0 & 0 & -r-s & 1+2r+s & -r \\ 0 & 0 & 0 & 0 & 0 & -r-s & 1+r+s \end{pmatrix}$$

Implicit finite difference method

Instead of $[u_{j-1}] = A[u_j] - [f(u_j)]$ will use $[u_{j-1}] = A[u_j] - [f(u_{j-1})]$
Then

$$[u_j] = A^{-1}([u_{j-1}] + \Delta t[f(u_{j-1})])$$

Remarks:

1. The key of the above method is to define the $(n+1) \times (n+1)$ matrix A. The rows from $i = 2$ to $i = n$ are same regardless of boundary conditions, and the row $i = 1$ and $i = n+1$ may change with different boundary conditions.

2. It also works for diffusion (no advection) equation with $s = \dfrac{a\Delta t}{\Delta x} = 0$, or advection (no diffusion) equation $r = \dfrac{d\Delta t}{(\Delta x)^2} = 0$.

3. It is more accurate if n is larger. Usually we take $\Delta t = O((\Delta x)^2)$.

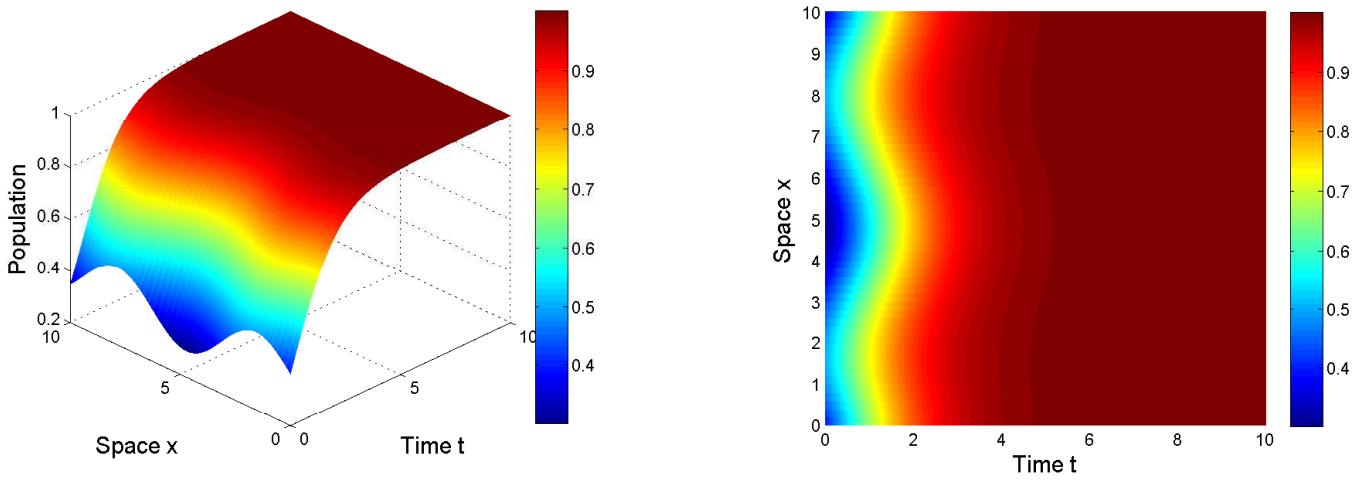
The code: Fisher-KPP equation and Neumann BC

```
% Calculate the solution of Fisher-KPP equation with Neumann BC

xl=0;                %left endpoint
xr=10;               %right endpoint

tfinal=10;               %time to integrate
dx=0.2;              %spatial grid size
dt=0.01;             %time step size

nx=(xr-xl)/dx+1;             %number of spatial subintervals
nt=tfinal/dt+1;              %number of time steps

diff=0.1;            %diffusion coefficient
a=1;             %parameter: growth rate
s=diff*dt/(dx*dx);             %diffusion rate

xmesh=linspace(xl,xr,nx);             %vector in x direction
tmesh=linspace(0,tfinal,nt);             %vector in t direction

U=zeros(nx,nt);              %matrix of solution
U(:,1)=0.4+0.1*sin(xmesh');             %initial condition
```

The code: Fisher-KPP equation and Neumann BC

```
A=zeros(nx,nx);                %diffusion matrix
A(1,1)=1+s;    A(1,2)=-s;                %first row
A(nx,nx-1)=-s; A(nx,nx)=1+s;                %last row

for i=2:nx-1                %other rows
A(i,i)=1+2*s;    A(i,i-1)=-s;    A(i,i+1)=-s;
end

AA=inv(A);                %take the inverse matrix

for i=1:nt-1                %for time t
for j=1:nx                %for space x
F(j)=U(j,i)+dt*(a*U(j,i)-U(j,i)*U(j,i));                % logistic nonlinearity
end
U(:,i+1)=AA*(F');                %multiply the inverse matrix
end

surf(tmesh,xmesh,U,'EdgeColor','none');                %graph in 3D
```

Numerical results: Neumann boundary



Left: 3D view of the solution; Right: 2D view of the solution

No flux boundary condition

No flux boundary: $du_x(0) - au(0) = 0$: $du_x(0, t_j) = d\dfrac{u_j^1 - u_j^0}{\Delta x} = au_j^1$ so
$u_j^0 = \left(1 - \frac{a\Delta x}{d}\right) u_j^1 = \left(1 - \frac{s}{r}\right) u_j^1$. Then
$u_{j-1}^1 = -ru_j^2 + (1 + 2r + s)u_j^1 - (r + s)u_j^0 - \Delta t \cdot f(u_j^1) =$
$-ru_j^2 + (1 + r + s + s^2/r)u_j^1 - \Delta t \cdot f(u_j^1)$

$$\begin{pmatrix} 1+r+s+s^2/r & -r & 0 & 0 & 0 & 0 & 0 \\ -r-s & 1+2r+s & -r & 0 & 0 & 0 & 0 \\ 0 & -r-s & 1+2r+s & -r & 0 & 0 & 0 \\ 0 & 0 & -r-s & 1+2r+s & -r & 0 & 0 \\ 0 & 0 & 0 & -r-s & 1+2r+s & -r & 0 \\ 0 & 0 & 0 & 0 & -r-s & 1+2r+s & - \\ 0 & 0 & 0 & 0 & 0 & -r-s & 1+r \end{pmatrix}$$

Periodic boundary condition

$$\begin{cases} u_t = du_{xx} - au_x + f(u), & x \in (0, L),\ t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in (0, L), \\ u(0, t) = u(L, t),\ u_x(0, t) = u_x(L, t), & t > 0. \end{cases}$$

In this case: we think $u_j^1 = u_j^{n+1}$, and we use $n \times n$ matrix instead of $(n+1) \times (n+1)$ matrix

$$\begin{pmatrix} 1+2r+s & -r & 0 & 0 & 0 & 0 & -r-s \\ -r-s & 1+2r+s & -r & 0 & 0 & 0 & 0 \\ 0 & -r-s & 1+2r+s & -r & 0 & 0 & 0 \\ 0 & 0 & -r-s & 1+2r+s & -r & 0 & 0 \\ 0 & 0 & 0 & -r-s & 1+2r+s & -r & 0 \\ 0 & 0 & 0 & 0 & -r-s & 1+2r+s & -r \\ -r & 0 & 0 & 0 & 0 & -r-s & 1+2r+s \end{pmatrix}$$

So periodic boundary condition corresponds to a cyclic matrix!

Dirichlet Boundary condition

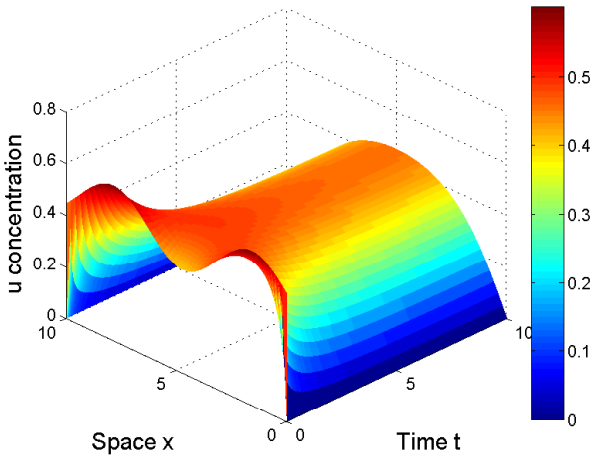
In this case, u_j^1 and u_j^{n+1} are always 0, so we use an $(n-1)\times(n-1)$ matrix

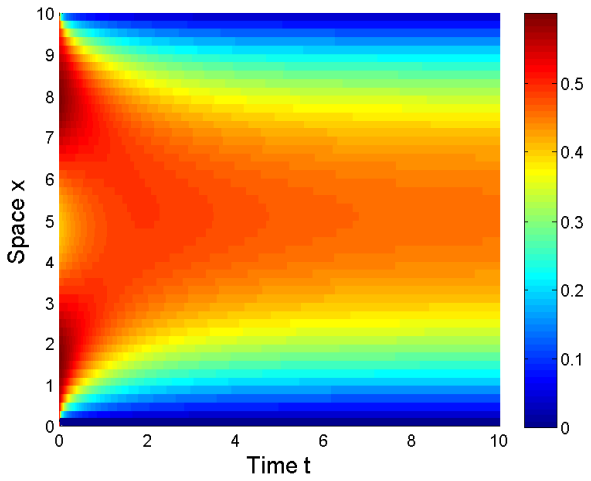
$$\begin{pmatrix} 1+2r+s & -r & 0 & 0 & 0 & 0 & 0 \\ -r-s & 1+2r+s & -r & 0 & 0 & 0 & 0 \\ 0 & -r-s & 1+2r+s & -r & 0 & 0 & 0 \\ 0 & 0 & -r-s & 1+2r+s & -r & 0 & 0 \\ 0 & 0 & 0 & -r-s & 1+2r+s & -r & 0 \\ 0 & 0 & 0 & 0 & -r-s & 1+2r+s & -r \\ 0 & 0 & 0 & 0 & 0 & -r-s & 1+2r+s \end{pmatrix}$$

The code: Fisher-KPP equation and Dirichlet BC

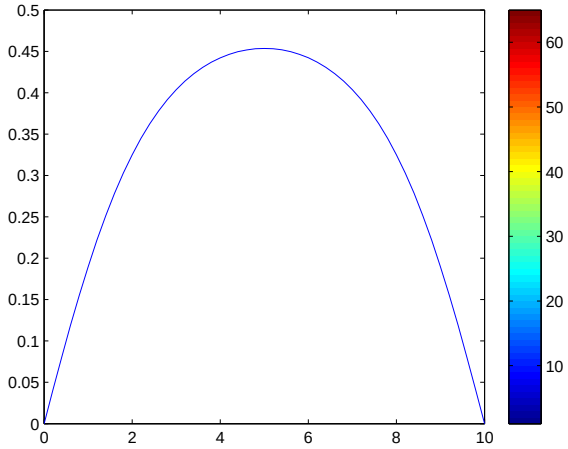
```
A=zeros(nx-2,nx-2);
A(1,1)=1+2*s;  A(1,2)=-s;
A(nx-2,nx-3)=-s;  A(nx-2,nx-2)=1+2*s;
for i=2:nx-3
A(i,i)=1+2*s;   A(i,i-1)=-s;   A(i,i+1)=-s;
end

AA=inv(A);

for i=1:nt-1
for j=2:nx-1
F(j-1)=U(j,i)+dt*a*U(j,i)-dt*U(j,i)*U(j,i);
end
Utemp=AA*(F');
U(1,i+1)=0;  U(nx,i+1)=0;
for j=2:nx-1
U(j,i+1)=Utemp(j-1);
end
end
```

Numerical results: Dirichlet Boundary

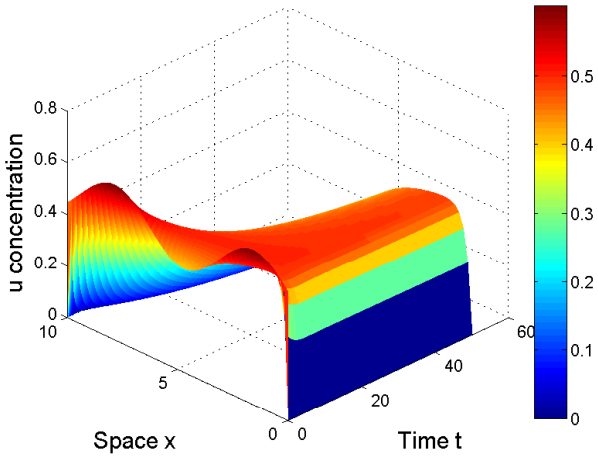


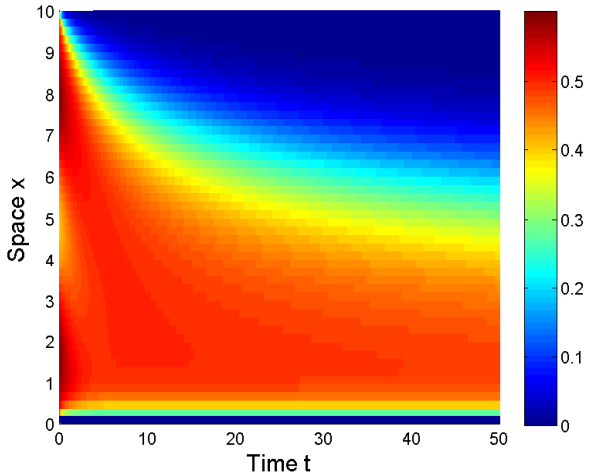


Left: 3D view of the solution; Right: 2D view of the solution;
Below: when $t = t_{final}$ (close to a steady state)



Numerical results: KPP-Fisher with advection and Dirichlet Boundary





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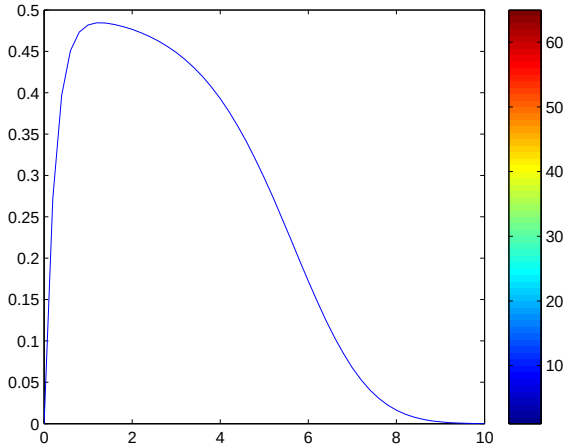

Numerical methods for systems of equations

$$\begin{cases} u_t = d_1 u_{xx} - a_1 u_x + f(u,v), & x \in (0,L),\ t > 0, \\ v_t = d_2 v_{xx} - a_2 v_x + g(u,v), & x \in (0,L),\ t > 0, \\ u(x,0) = u_0(x),\ v(x,0) = v_0(x), & x \in (0,L), \\ u_x(0,t) = u_x(L,t) = 0, & t > 0, \\ v_x(0,t) = v_x(L,t) = 0, & t > 0. \end{cases}$$

$[u_j] = A_1^{-1}([u_{j-1}] + \Delta t[f(u_{j-1}, v_{j-1})])$, $[v_j] = A_2^{-1}([v_{j-1}] + \Delta t[g(u_{j-1}, v_{j-1})])$. Here A_1 and A_2 are the diffusion-advection matrices for u and v respectively.

Example: Brusellator model

$$\begin{cases} u_t = d_1 u_{xx} + u^2 v - (b+1)u + a, & x \in (0,L),\ t > 0, \\ v_t = d_2 v_{xx} - u^2 v + bu, & x \in (0,L),\ t > 0, \\ u(x,0) = u_0(x),\ v(x,0) = v_0(x), & x \in (0,L), \\ u_x(0,t) = u_x(L,t) = 0, & t > 0, \\ v_x(0,t) = v_x(L,t) = 0, & t > 0. \end{cases}$$

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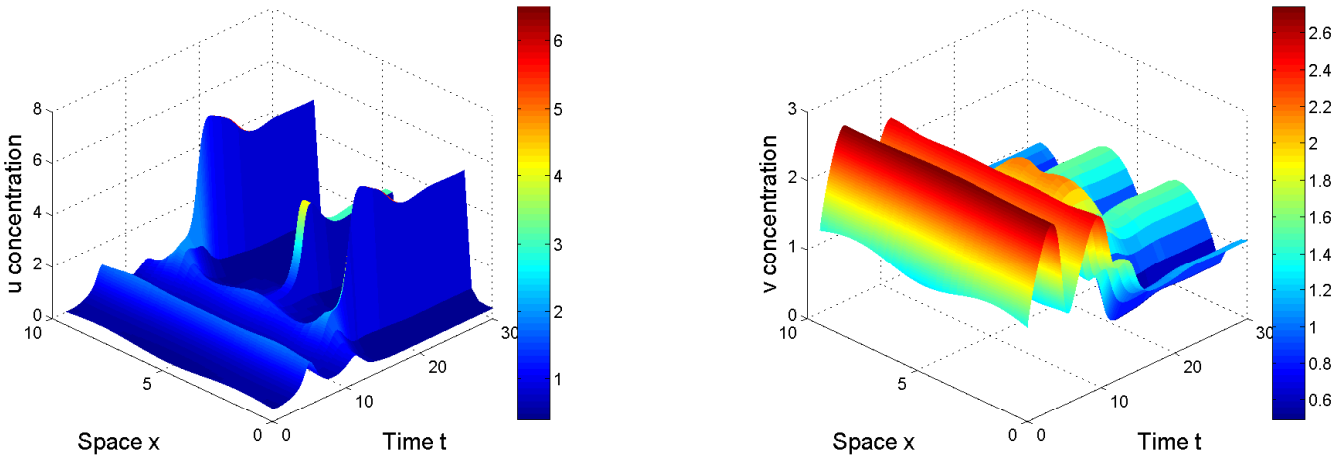
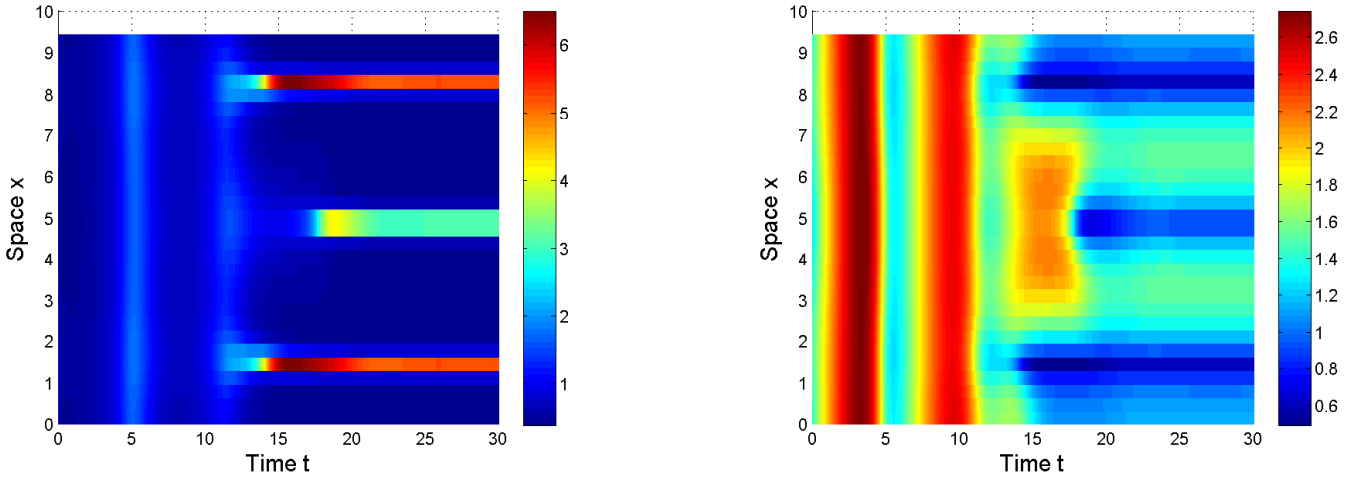


Upper left: 3D view of $u(x,t)$; Upper right: 3D view of $v(x,t)$;
Lower left: 2D view of $u(x,t)$; Lower right: 2D view of $v(x,t)$.



Comparison of different numerical schemes

Explicit method: (based on forward difference)

$$\frac{u_{j+1}^i - u_j^i}{\Delta t} = d\frac{u_j^{i+1} - 2u_j^i + u_j^{i-1}}{(\Delta x)^2} - a\frac{u_j^i - u_j^{i-1}}{\Delta x} + f(u_j^i)$$

Implicit method: (based on backward difference)

$$\frac{u_j^i - u_{j-1}^i}{\Delta t} = d\frac{u_j^{i+1} - 2u_j^i + u_j^{i-1}}{(\Delta x)^2} - a\frac{u_j^i - u_j^{i-1}}{\Delta x} + f(u_{j-1}^i)$$

1. For linear diffusion equation, the explicit method is stable when $\frac{\Delta t}{(\Delta x)^2} < \frac{1}{2}$. But the implicit method is always stable.
2. The implicit method needs more computation as it requires to solve an inverse matrix.

CrankVNicolson method:

$$\frac{u_j^{i+1} - u_j^i}{\Delta t} = \frac{1}{2}\left(\frac{u_{j+1}^{i+1} - 2u_j^{i+1} + u_{j-1}^{i+1}}{(\Delta x)^2} + \frac{u_{j+1}^i - 2u_j^i + u_{j-1}^i}{(\Delta x)^2}\right).$$

also stable and more accurate.

Finite element method: based on Fourier decomposition.

Chemotaxis

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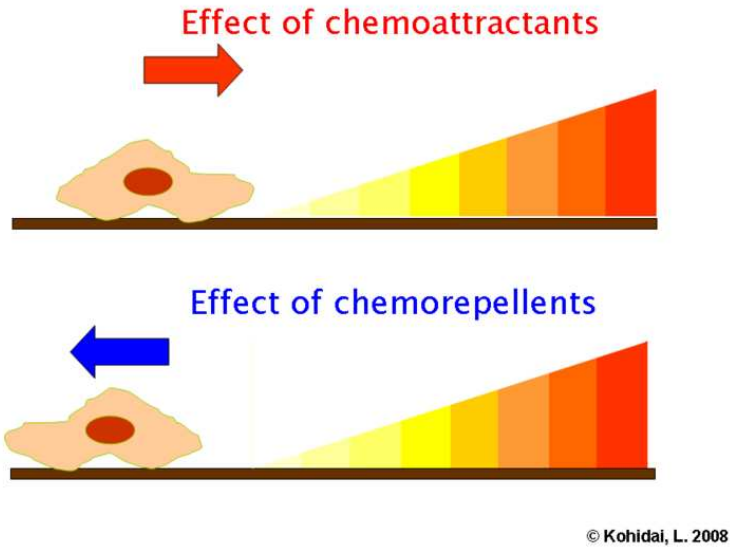
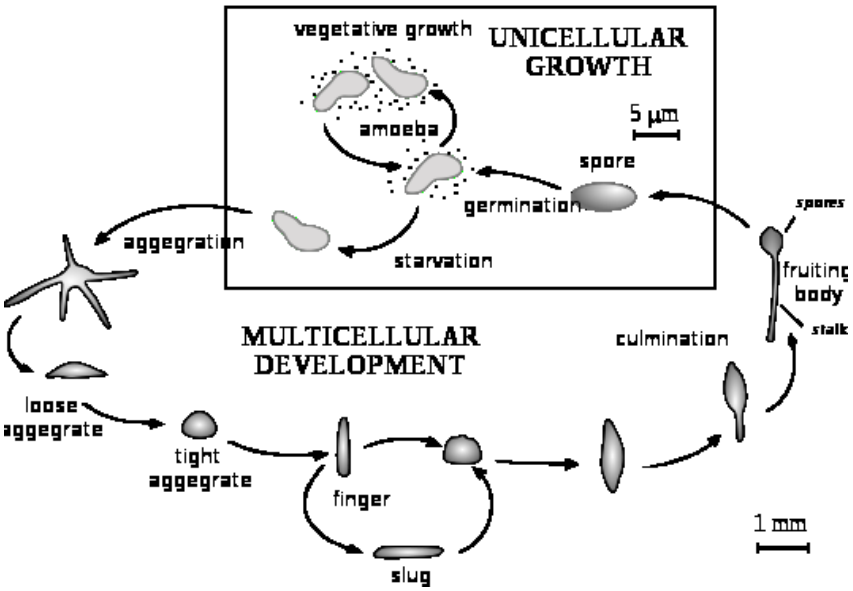


Dictyostelium discoideum (Dicky)

Dictyostelium discoideum is a species of soil-living amoeba belonging to the phylum Mycetozoa, commonly referred to as slime mold.

1. In its native state a slime mold population consists of hundreds or thousands of unicellular amoeboid cells, and each one moves independently and feeds on bacteria.
2. When food becomes scarce, the amoebae enter a phase of starvation. An initially uniform cell distribution develops a multicellular mass. Cells are attracted to these loci called aggregate and move towards them. Eventually they become a sluglike multicellular mass.
3. The sluglike collection of cells undertakes a sequence of shapes including that of a dome. And at the end, the result is a slender, beautifully sculptured stalk bearing acapsule at its top. (It is called a *sporangiophore*.)

Life cycle of slime mold



Keller-Segel model

Question: What cause cells to aggregate, and how do cells know where an aggregation center should form?

[Keller-Segel, JTB, 1970,1971]
The starved slime mold amoebae secrete a chemical that attracts other cells. It is called cyclic AMP (cAMP), whose role is that of an intracellular messenger. To model the aggregation of slime mold, the following assumptions are made:

1. Individual cells undergo a combination of random and chemotactic motions towards cAMP.
2. Cells neither die nor divide during aggregation.
3. cAMP is produced in a constant rate by each cell.
4. The rate of degradation of cAMP depends linearly on its concentration.
5. cAMP diffuses passively over the aggregation field.

Keller-Segel Model

Law of mass conservation, Fick's law and chemotaxis flux
$J = -D_a \nabla a + ha\nabla c$.

$$\begin{cases} a_t = D_a a_{xx} - h(ac_x)_x, & x \in (0, L),\ t > 0, \\ c_t = D_c c_{xx} + fa - kc, & x \in (0, L),\ t > 0, \\ a(x, 0) = a_0(x),\ c(x, 0) = c_0(x), & x \in (0, L), \\ a_x(0, t) = a_x(L, t) = 0, & t > 0, \\ c_x(0, t) = c_x(L, t) = 0, & t > 0. \end{cases}$$

$a(x, t)$ is the concentration of amoebae (slime mold)
$c(x, t)$ is the concentration of cAMP.
D_a, D_c: diffusion coefficients
h: chemotactic coefficient
f: rate of cAMP secreation per unit density of amoebae
k: rate of degradation of cAMP

Higher dimensional:

$$\begin{cases} a_t = D_a \Delta a - h \cdot div(a\nabla c), & x \in \Omega,\ t > 0, \\ c_t = D_c \Delta c + fa - kc, & x \in \Omega,\ t > 0, \\ a(x, 0) = a_0(x),\ c(x, 0) = c_0(x), & x \in \Omega, \\ \nabla a \cdot n = \nabla c \cdot n = 0, & t > 0. \end{cases}$$

$div(a\nabla c) = \nabla a \cdot \nabla c + a\Delta c$

Original Keller-Segel model

[Keller-Segel, 1970, JTB]
$a(x,t)$: The density of myxamoebae
$\rho(x,t)$: The concentration of the chemical attractant acrasin (cAMP)
$\eta(x,t)$: The concentration of acrasinase, an enzyme that degrades acrasin
$c(x,t)$: The concentration of a complex that forms when acrasin and acrasinase react.

Assumptions:
1. Acrasin and acrasinase react to form a complex that dissociates into a free enzyme (acrasinase) and a degraded product $\eta + \rho \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} c \xrightarrow{k_1} \eta +$ degraded product
2. Acrasin is produced by the amoebae at a rate of $f(\rho)$ per amoebae.
3. Acrasinase is produced by the amoebae at a rate of $g(\rho,\eta)$ per amoebae.
4. ρ, η, and c diffuse by Fick's Law.
5. The amoebae a move in the direction of increasing gradient of ρ and by diffusion.

$$\begin{cases} a_t = div[D_2(\rho,a)\nabla a - D_1(\rho,a)\rho], & x\in\Omega,\ t>0,\\ \rho_t = D_\rho\Delta\rho + af(\rho) - k_1\rho\eta + k_{-1}c, & x\in\Omega,\ t>0,\\ \eta_t = D_\eta\Delta\eta + ag(\rho,\eta) - k_1\rho\eta + (k_{-1}+k_2)c, & x\in\Omega,\ t>0,\\ c_t = D_c\Delta c + k_1\rho\eta - (k_{-1}+k_2)c, & x\in\Omega,\ t>0. \end{cases}$$

$D_1(\rho,a) = \delta a/\rho,$

Reduced Original Keller-Segel model

By using quasi-steady-state assumption, we get

$$\begin{cases} a_t = div[D_1(\rho, a)\nabla a - D_2(\rho, a)\rho], & x \in \Omega,\ t > 0, \\ \rho_t = D_\rho \Delta \rho + af(\rho) - \rho k(\rho), & x \in \Omega,\ t > 0, \end{cases}$$

where $k(\rho) = \dfrac{\eta_0 k_2 K}{1 + K\rho}$, and $K = \dfrac{k_1}{k_{-1} + k_2}$.

In [Keller-Segel, 1971, JTB], the following equations were sued:

$$\begin{cases} b_t = div[\mu(s)\nabla b - b\chi(s)\nabla s], & x \in \Omega,\ t > 0, \\ s_t = D\Delta s - k(s)b, & x \in \Omega,\ t > 0, \\ \nabla b \cdot n = \nabla s \cdot n = 0, & t > 0. \end{cases}$$

$b(x, t)$: the concentration of bacteria; $s(x, t)$: the concentration of substrate.
$\mu(s)$: the motility of the bacteria;
$\chi(s)$: the chemotactic sensitivity coefficient function. Examples: $\chi(s) = \dfrac{\delta}{s - s_T}$, or $\chi(s) = \dfrac{\delta}{s}$.

References on chemotaxis models

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4. D. Horstmann, From 1970 Until Present: The Keller-Segel Model in Chemotaxis and its Consequences. I. Jahresber. Deutsch. Math.-Verein. (2003), 105:103-165.
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Movement of individuals

[Shigesada-Kawasaki-Teramoto, 1979, JTB
Fick's law: $J = -d\nabla u$

(SKT model) the movement of an individual searching its residence is under influence of the following forces:
1. the dispersive force which is associated with random movement of individuals;
2. the population pressure due to mutual interferences between individuals;
3. the attractive force which induces directed movements of individuals toward favorable places.

1. random dispersal: $J_1 = -\alpha\nabla u$,
2. dispersal due to population pressure: $J_2 = -\beta u\nabla u$,
3. dispersal toward favorable environment: $J_3 = -u\nabla U$, where $-U(x)$ is a potential function representing the value or "favorableness" of habitat at the position x.

$$u_t = div(\alpha\nabla u + \beta u\nabla u + u\nabla U) = \alpha\Delta u + \beta div(u\nabla u) + div(u\nabla U).$$

Steady state matching with environment

$$\begin{cases} u_t = (\alpha u_x + \beta u u_x + u U_x)_x, & x \in (0, L),\ t > 0, \\ u(x, 0) = u_0(x), & x \in (0, L), \\ \alpha u_x + \beta u u_x + u U_x = 0, & x = 0, L,\ t > 0. \end{cases}$$

Steady state solution: $\alpha \ln u + \beta u + U = C$

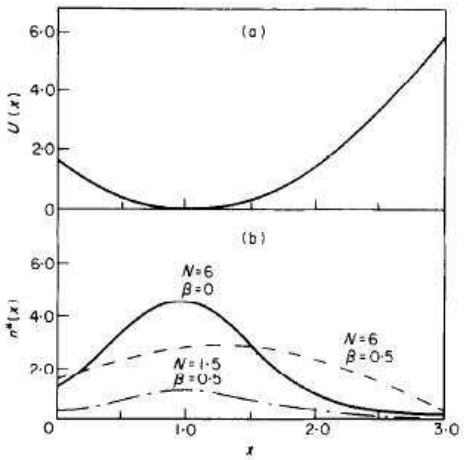

FIG. 1. (a) Environmental potential function $U(x) = 1{\cdot}5(x-1)^2$. (b) Stational population densities. N is the total number of individuals.

Competition model with diffusion, self-diffusion and cross-diffusion

[Shigesada-Kawasaki-Teramoto, 1979, JTB]

$$\begin{cases} u_t = div(\alpha_1 \nabla u + \beta_{11} u \nabla u + \beta_{12} u \nabla v + \gamma_1 U_1) + (\varepsilon_1 - \mu_{11} u - \mu_{12} v)u, & x \in \Omega,\ t > 0, \\ v_t = div(\alpha_2 \nabla v + \beta_{21} v \nabla u + \beta_{22} v \nabla v + \Gamma_2 U_2) + (\varepsilon_2 - \mu_{21} u - \mu_{22} v)v, & x \in \Omega,\ t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

[Mimura-Kawasaki, JMB, 1980] [Yagi, NA, 1993] [Lou-Ni, JDE, 1996, 1999]
[Ni, Notices AMS, 1998] [Lou-Ni-Wu, DCDS-A, 1998]
[Choi-Lui-Yamada, DCDS-A, 2003, 2004] [Kuto, JDE, 2004]
[Kuto-Yamada, JDE, 2004] [Lou-Ni-Yotsutani, DCDS-A, 2004] [Wu, JDE, 2005]
and so many others

Heterogeneous landscapes and ideal free distribution

[Fretwell-Lucas, Acta Biotheoretica, 1970]
In ecology, an ideal free distribution is a way in which animals distribute themselves among several patches of resources. The theory states that the number of individual animals that will aggregate in various patches is proportional to the amount of resources available in each. For example, if patch A contains twice as many resources as patch B, there will be twice as many individuals foraging in patch A as in patch B. The ideal free distribution (IFD) theory predicts that the distribution of animals among patches will minimize resource competition and maximize fitness.

$$\begin{cases} u_t = d\Delta u + (m(x) - u)u, & x \in \Omega,\ t > 0, \\ \nabla u \cdot n = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

It is known that this equation has a unique positive steady state $u_d^*(x)$ which is globally asymptotically stable. In an IFD, $u_*(x) \equiv Cm(x)$. But this is not possible for this reaction-diffusion Fisher equation, so diffusion is not a dispersal strategy which produces an IFD.

[Lou, JDE, 2006] $\lim_{d \to 0} \frac{u_d^*(x)}{m(x)} = 1.$
(the distribution of the species is closer to an IFD for smaller dispersal rate)

What are the best dispersal strategy for IFD?

[Cantrell-Cosner-Lou, MBE, 2010] [Averill-Munther-Lou, JBD, 2012]

$$\begin{cases} u_t = d\ div(\nabla u + u\nabla U) + (m(x) - u)u, & x \in \Omega,\ t > 0, \\ (\nabla u + u\nabla U) \cdot n = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

$U(x) = -\ln m(x)$ can produce an ideal free distribution so that $u_d^*(x) \equiv m(x)$.
In equilibrium, there is no movement: $\nabla u + u\nabla U = \nabla m - m\nabla \ln(m) \equiv 0$.

Another strategy: [Lewis]

$$\begin{cases} u_t = d\Delta\left(\dfrac{u}{m(x)}\right) + (m(x) - u)u, & x \in \Omega,\ t > 0, \\ (\nabla u + u\nabla U) \cdot n = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

Nonlocal dispersal

[Hutson-Martinez-Mischaikow-Vickers, JMB, 2003]
[Bates-Fife-Ren-Wang, ARMA, 1997] [Bates-Chmaj, JSP, 1999]
Divide $\mathbb{R}$ (the habitat) into contiguous sites, each of length Δx. Discretize time into steps of size Δt. Let $u(i,t)$ be the density of individuals in site n at time t. Assume that the probability of individuals leaving site i and going to site j is $\alpha(j,i)$. Then the number of individuals leaving site i during the interval $[t, t+\Delta t]$ is $\sum_{j=-\infty}^{\infty} \alpha(j,i)u(i,t)(\Delta x)^2\Delta t$. During this same time interval, the number of arrivals to site i from elsewhere is $\sum_{j=-\infty}^{\infty} \alpha(i,j)u(j,t)(\Delta x)^2\Delta t$. Finally let $f(u(i,t),i)$ denote the per capita net reproduction rate at site i at the given population density.

$$u(i,t+\Delta t) = u(i,t) + \left(\sum_{j=-\infty}^{\infty} \alpha(i,j)u(j,t) - \sum_{j=-\infty}^{\infty} \alpha(j,i)u(i,t) \right) \Delta x \Delta t + f(u(i,t),i)u(i,t)\Delta t$$

Limit as $\Delta x, \Delta t \to 0$:
$$u_t(x,t) = \int_{\mathbb{R}} [\alpha(x,y)u(y,t) - \alpha(y,x)u(x,t)]dy + f(u(x,t),x)u(x,t).$$

Relation to diffusion model

If $\int_{\mathbb{R}} \alpha(y,x)dy = 1$ (probability), then

$$u_t(x,t) = \int_{\mathbb{R}} \alpha(x,y)u(y,t)dy - u(x,t) + f(u(x,t),x)u(x,t).$$

If $\alpha(x,y) = k(x-y)$ (only depends on distance between x and y), then

$$u_t(x,t) = \int_{\mathbb{R}} k(x-y)u(y,t)dy - u(x,t) + f(u(x,t),x)u(x,t)$$

$$\int_{\mathbb{R}} k(x-y)u(y,t)dy = \int_{\mathbb{R}} k(y)u(x-y,t)dy = \int_{\mathbb{R}} k(y)\sum_{j=0}^{\infty} \frac{u_x^{(j)}(x,t)}{j!}(-y)^j dy$$

$$= \sum_{j=0}^{\infty} \frac{u_x^{(j)}(x,t)}{j!} \int_{\mathbb{R}} k(y)(-y)^j dy = u(x,t) + \frac{1}{2}u_{xx}(x,t)\int_{\mathbb{R}} k(y)(-y)^j dy + \cdots.$$

So by using Taylor expansion, we can see the diffusion equation is the first approximation of the nonlocal dispersal model.

[Lutscher-Pachepsky-Lewis, SIAM-AM, SIAM-Rev, 2005]
[Corta'zar-Coville-Elgueta-Marti'nez, JDE, 2007], [Bates-Zhao, JMAA, 2007]
[Coville-Da'vila-Marti'nez, JDE, 2008], [Coville-Da'vila-Marti'nez, SIAM-MA, 2008]
and many others

Nonlocal growth

Fisher-KPP equation: $u_t = Du_{xx} + au(1-u)$

Nonlocal Fisher-KPP equation: $u_t = Du_{xx} + au\left(1 - \int_{\mathbb{R}} k(x-y)u(y,t)dy\right)$

[Britton, JTB, 1989], [Britton, SIAM-AM, 1990], [Gourley, JMB, 2000]
[Fuentes-Kuperman-Kenkre, PRL, 2003; JPC, 2004]

The nonlocal term represents intra-specific competition for resources and having this particular form implies that individuals are competing not only with others at their own point in space but also with individuals at other points in the domain.

[Sun-Shi-Wang, ZAMP, 2013 to appear]

$$\begin{cases} u_t = u_{xx} + \lambda u - \lambda u \int_{-1}^{1} f(x,y)u(y,t)\mathrm{d}y, & x \in (-1,1),\ t > 0, \\ u(-1,t) = u(1,t) = 0, & t > 0, \\ u(x,0) = g(x), & x \in (-1,1), \end{cases}$$

1. When $\lambda < \pi^2/4$, there is no positive steady state solution.
2. When $\lambda > \pi^2/4$, there is a positive steady state solution.

Summary

1. Movement of individuals in a population can be modeled by partial differential equations or integral-differential equations (nonlocal models). These models can be derived from (i) law of mass conservation and Fick's law (or other similar movement patterns); or (ii) Brownian motion or random walk.
2. These models are capable to describe the phenomena of diffusion, advection, chemotaxis, cross-diffusion, nonlocal movement.
3. Combining the movements with the reaction dynamics, more complicated models are obtained and usually we look for these properties of the models:
    1. Traveling wave propagation.
    2. Persistence and extinction; or, competition exclusion and coexistence.
    3. Pattern formation, existence and multiplicity of non-constant steady state solutions.
    4. Time-periodic solutions, oscillatory patterns.