Diffusion, persistence and competition

Lecture 1

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CIMPA School in Biomathematics

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Introduction

Let $\Omega \subseteq \mathbb{R}^N$ be a bounded domain with smooth boundary $\partial\Omega$ and outer unit normal vector n.

$$\begin{cases} u_t = d\Delta u + f(x,u)u & \text{in } \Omega \times (0,T), \\ \partial_n u = 0 & \text{in } \partial\Omega \times (0,T), \\ u(x,0) = u_0(x) & \text{in } \Omega. \end{cases} \tag{1}$$

- $u(x,t)$: population density
- $d > 0$: diffusion rate
- $f(x,u)$: per capita growth rate
- More general movement: replace $d\Delta u$ with $a_{ij}\partial^2_{x_i,x_j}u + b_j\partial_{x_j}u$
- Question: Pattern formation, spatial propagation, competition, predation....
  What is the role of diffusion and spatial heterogeneity in these questions?

Diffusion approximation

Let $k(x,y)$ be the rate of movement from y to x, then

$$\frac{d}{dt}u(x,t) = \int k(x,y)u(y,t)\,dy - \left(\int k(y,x)\,dy\right)u(x,t), \tag{2}$$

denoting respectively the rate of change of population due to immigration and emigration. Assume for simplicity $\Omega = (0, L)$ and

$$k(x,y) = \frac{1}{\epsilon}K\left(\frac{x-y}{\epsilon}\right).$$

then

$$\begin{aligned}\frac{d}{dt}u &\approx \int \frac{1}{\epsilon}K\left(\frac{x-y}{\epsilon}\right)\left[u(x,t) + (y-x)u_x(x,t) + \frac{(x-y)^2}{2}u_{xx}(x,t)\right]dy \\ &\quad - \left(\int \frac{1}{\epsilon}K\left(\frac{x-y}{\epsilon}\right)dy\right)u(x,t) \\ &\approx -\epsilon\left(\int zK(z)\,dz\right)u_x(x,t) + \frac{\epsilon^2}{2}\left(\int |z|^2K(z)\,dz\right)u_{xx}(x,t)\end{aligned}$$

This gives a derivation of the movement model

$$u_t = d\Delta u + \vec{b}\cdot\nabla u$$

Review of comparison principles. Parabolic Equations.

Definition 1

We say that $\overline{u}(x,t) \in C^{2,1}(\bar{\Omega} \times [0,T)$ is a supersolution of (1) if

$$\bar{u}_t - d\Delta\bar{u} - \bar{u}f(x,\bar{u}) \geq 0 \quad \text{in } \Omega \times (0,T), \quad \partial_n \bar{u} \geq 0 \quad \text{on } \partial\Omega \times (0,T).$$

Similarly, we say that $\underline{u}(x,t) \in C^{2,1}(\bar{\Omega} \times [0,T)$ is subsolution of (1) if the above inequalities are reversed.

Proposition 1

If $\bar{u}(x,t)$ and $\underline{u}(x,t)$ are a pair of super/subsolutions and such that

$$\underline{u}(x,0) \leq \bar{u}(x,0) \quad \text{in } \Omega.$$

Then

$$\underline{u}(x,t) \leq \bar{u}(x,t) \quad \text{in } \Omega \times (0,T).$$

$$
(1) \quad \begin{cases} u_t = d\Delta u + uf(x,u) & \text{in } \Omega \times (0,T), \\ \partial_n u = 0 & \text{in } \partial\Omega \times (0,T), \\ u(x,0) = u_0(x) & \text{in } \Omega. \end{cases}
$$

Proposition 2

Suppose $f(x,u) \le r(x)$. If the principal eigenvalue (pev) λ_1 of

$$
\begin{cases} d\Delta\psi + r(x)\psi + \lambda\psi = 0 & \text{in } \Omega, \\ \partial_n \psi = 0 & \text{on } \partial\Omega \end{cases} \tag{3}
$$

satisfies $\lambda_1 > 0$, then (1) has no positive steady state and all nonnegative solutions of (1) tends to zero uniformly as $t \to \infty$.

Proof.

By definition of pev, the eigenvalue λ_1 has a positive eigenfunction $\psi(x) > 0$. Assume $\lambda_1 \ge 0$, and set

$$
\overline{u}(x,t) = Ce^{-\lambda_1 t}\psi(x).
$$

Then.... □

Sattinger's monotone iteration

Subequilibrium: $\Delta \underline{U} + f(x, \underline{U})\underline{U} \geq 0$ in Ω and $\partial_n \underline{U} \leq 0$ on $\partial\Omega$.

Proposition 3

Suppose $\bar{U}(x)$ is a superequilibrium, and $\underline{U}$ is a subequilibrium such that $\underline{U} \leq \bar{U}$. Let $\bar{u}$ (resp. $\underline{u}$) be the solution to (1) with initial data $\bar{U}$ (resp. $\underline{U}$). Then $\bar{u}$ is decreasing in t and $\underline{u}$ is increasing in t, i.e.

$$\underline{U}(x) \leq \underline{u}(x,t) \leq \bar{u}(x,t) \leq \overline{U}(x)$$

Moreover,

$$u_M(x) := \lim_{t\to\infty} \bar{u}(x,t) \quad u_m(x) := \lim_{t\to\infty} \underline{u}(x,t)$$

are equilibrium solutions of (1) and for any solution $u(x,t)$ of (1) with initial data satisfying $\underline{U}(x) \leq u(x,0) \leq \bar{U}(x)$, we have

$$u_m(x) \leq \liminf_{t\to\infty} u(x,t) \leq \limsup_{t\to\infty} u(x,t) \leq u_M(x).$$

In particular, if $u_m(x) = u_M(x) = \theta(x)$, then $u(x,t) \to \theta(x)$ uniformly as $t \to \infty$.

Proof:
Let $v = \overline{u}_t$, then $v(x, 0) \leq 0$ and v satisfies a linear parabolic equation, so that $v \leq 0$ for all x, t.
Since it is bounded from below by $\overline{U}(x)$, it follows that $u_M(x) := \lim_{t\to\infty} u(x,t)$ exists. Note also that

$$\int_t^{t+1} \overline{u}(x,\tau)\, d\tau \to u_M(x) \quad \text{uniformly.}$$

We claim that u_M satisfies the stationary problem in the weak sense, i.e.

$$\int_\Omega \left[u_M d\Delta\phi + u_M(m(x) - u_M)\phi\right] dx = 0 \quad \text{for any } \phi \in C^\infty(\bar{\Omega}).$$

Indeed, let $v(x,t) = \int_[t, t+1]u(x,\tau)\, d\tau$, we may integrate the equation of u to obtain

$$u\Big|_t^{t+1} = d\Delta \int_t^{t+1} u(x,\tau)\, d\tau + \int_t^{t+1} u(x,\tau)(m(x) - u(x,\tau))\, d\tau.$$

Then we may conclude the convergence in the distribution sense as $t \to \infty$.

The exponential model: ODE vs PDE

$$\dot{U}(t) = rU(t)$$

then $U(t) = U(0)e^{rt}$, so that the exponential growth rate is r.

$$\begin{cases} u_t = d\Delta u + r(x)u & \text{in } \Omega \times (0, T), \\ \partial_n u = 0 & \text{on } \partial\Omega \times (0, T), \\ u(x, 0) = u_0(x) & \text{in } \Omega. \end{cases} \tag{4}$$

Proposition 4

For any positive solutions $u(x, t)$ of (4), there exists $C > 1$ such that

$$\frac{1}{C} e^{-\lambda_1 t} \le u(x, t) \le Ce^{-\lambda_1 t}$$

Proof: By comparison, we can choose $C > 1$ such that

$$\frac{1}{C} e^{-\lambda_1 t}\psi(x) \le u(x, t) \le Ce^{-\lambda_1 t}\psi(x)$$

then use the fact that ψ is bounded above and below by positive constants.

In particular, $-\lambda_1$ is the *effective growth rate* for the linear PDE (4).

Existence of Positive Equilibrium

Proposition 5

Suppose that

(i) *there exists* $C_1 > 0$ *such that* $f(x, u) < 0$ *for* $x \in \Omega$ *and* $u \geq C_1$, *and that*

(ii) $\lambda_1 < 0$, *where* λ_1 *is the pev of* (3) *with* $r(x) = f(x, 0)$.

Then (1) *has at least one positive steady state.*

Remark 1

(Persistence result) The arguments in the proof of Proposition 5 demonstrated that, for each initial data u_0 *such that* $u_0 > 0$ *in* $\bar{\Omega}$, *there exists* $\epsilon_0 > 0$ *such that*

$$\liminf_{t \to \infty} \inf_{\Omega} u(x, t) \geq \epsilon_0 \psi(x).$$

Existence of Positive Equilibrium

Proposition 5

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$$\liminf_{t\to\infty} \inf_{\Omega} u(x,t) \geq \epsilon_0 \psi(x).$$

Exercise. Suppose $\lambda_1 < 0$. Modify the arguments in the proof of Proposition 5 to show that there exists $\epsilon_0 > 0$ such that for any positive solutions of (1), we have

$$\liminf_{t\to\infty} \inf_{\Omega} u(x,t) \geq \epsilon_0,$$

where the constant $\epsilon_0 > 0$ can be chosen independent of all positive initial data u_0. (In fact, the constant $\epsilon_0 > 0$ can be chosen uniformly for all nonnegative, nontrivial solutions of (1).) In this case, we say that **the single species is strongly uniformly persistent**.

Exercise. Show that the extinction result holds even if we relax the hyposthesis to $\lambda_1 \geq 0$. Indeed, suppose $\lambda_1 = 0$. [Hint: (1) Show that there is no positive steady states if $\lambda_1 \geq 0$. (2) Show that for any constant $M \gg 1$, $\bar{U}(x) := M\psi(x)$ is a superequilibrium, i.e.

$$d\Delta \bar{U} + \bar{U} f(x, \bar{U}) \leq 0 \quad \text{in } \Omega, \quad \partial_n \bar{U} = 0 \quad \text{on } \partial\Omega.$$

and use the method of monotone iteration we discussed.]

The diffusive logistic model

The logistic ODE is

$$\dot{U} = rU\left(1 - \frac{u}{K}\right)$$

where r is the intrinsic growth rate and K is the carrying capacity. Indeed, we observe that the per capita growth rate satisfies

$$\frac{u_t}{u} = \begin{cases} r & \text{when } u = 0, \\ 0 & \text{when } u = K, \\ r(1 - \frac{u}{K}) & \text{interpolation between 0 and } K. \end{cases} \tag{5}$$

The diffusive logistic model

For the PDE, let's consider the simplified case $r(x) = K(x) := m(x)$

$$\begin{cases} u_t = d\Delta u + u(m(x) - u) & \text{in } \Omega \times (0, T), \\ \partial_n u = 0 & \text{in } \partial\Omega \times (0, T), \\ u(x, 0) = u_0(x) & \text{in } \Omega. \end{cases} \quad (6)$$

i.e.

$$f(x, u) = m(x) - u$$

Another example is the single species with harvesting:

$$f(x, u) = r(x)(1 - \frac{u}{K(x)}) - h(x)$$

where $h(x)$ is the harvesting rate.
Questions: What is the effect of harvesting $h(x)$ on the animal population? What is the optimal $h(x)$ to optimize the output, e.g. $T[h] := \int_\Omega h(x)\theta_h(x)\,dx$, where θ_h is the equilibrium density.

Exercise: A bistable nonlinearity

Consider

$$\begin{cases} u_t = d\Delta u + u(h(x) - u)(u - g(x)) & \text{in } \Omega \times (0, T), \\ \partial_n u = 0 & \text{in } \partial\Omega \times (0, T), \\ u(x, 0) = u_0(x) & \text{in } \Omega. \end{cases} \tag{7}$$

(a) Assume $h, g \in C^\alpha(\bar{\Omega})$ satisfies $0 < \inf_\Omega g \leq \sup_\Omega g < \inf_\Omega h$. Show that for any $d > 0$, (7) has at least one positive equilibrium solution.

(b) Assume $h, g \in C^\alpha(\bar{\Omega})$ satisfies $0 < g(x) < h(x)$ in $\bar{\Omega}$. Show that for any $d > 0$ sufficiently small, (7) has at least one positive equilibrium solution.

(When $h(x) = 1$ and g is a constant between 0 and 1, (7) is called the Allee model.

The Principal Eigenvalue (pev)

By our discussion, the problem of existence of positive steady state is given by the sign of the pev of

$$\begin{cases} d\Delta\psi + m(x)\psi + \lambda\psi = 0 & \text{in } \Omega, \\ \partial_n \psi = 0 & \text{on } \partial\Omega. \end{cases} \tag{8}$$

Definition 2

We say that λ_1 is the pev of (8) if any one of the following equivalent conditions hold:

(a) $\lambda \in \mathbb{R}$ is the smallest eigenvalue (for non-self-adjoint operators, the eigenvalue with the smallest real part).

(b) $\lambda \in \mathbb{R}$ is an eigenvalue with a positive eigenfunction $\psi(x) > 0$.

Existence: apply Krein-Rutman Theorem to the compact positive operator $T_c\phi = (-\Delta)^{-1}[(m+c)\phi]$ for appropriate values of constant $c > 0$.

Variational Characterization

$$\lambda_1 = \inf_{\substack{\psi \in C^1(\bar{\Omega}) \\ \psi \not\equiv 0}} \frac{\int_\Omega \left[d|\nabla \psi|^2 - m(x)|\psi|^2 \right] \, dx}{\int_\Omega |\psi|^2 \, dx} \tag{9}$$

Exercise: The infimum in (9) is attained by the positive eigenfunction ψ.
Exercise: Show that

$$-\max_{\bar{\Omega}} m \le \lambda_1 \le -⨍_\Omega m \, dx \quad \text{where } ⨍_\Omega m \, dx = \frac{1}{|\Omega|} \int_\Omega m \, dx.$$

Using the variational characterization, we may deduce the following

Proposition 6

Suppose that $m(x)$ is nonconstant. Then

(a) $d \mapsto \lambda_1$ *is strictly increasing.*

(b) $\lim_{d \searrow 0} \lambda_1 = -\max_{\bar{\Omega}} m.$

(c) $\lim_{d \nearrow \infty} \lambda_1 = -⨍_\Omega m \, dx.$

Exercise: Derive assertions (a) and (b) by the variational characterization (9).

Proof of of assertion (c)

Denote the eigenfunction by $\psi_d(x) > 0$ to emphasize its dependence on d. Dividing the equation by d, we have

$$\Delta\psi_d + \frac{m+\lambda_1}{d}\psi_d = 0 \tag{10}$$

Multiply the above by ψ_d and integrating by parts, we have

$$\int |\nabla\psi_d|^2 = \frac{1}{d}\int (m+\lambda)\psi_d^2 \leq \frac{2|m|_\infty|\Omega|}{d}$$

where we normalized by $\int_\Omega \psi_d^2\,dx = |\Omega|$.
In particular, we see that $\sup_{d>0}\|\psi_d\|_{H^1} \leq C$. By passing to a subsequence, we may assume that

$$\begin{cases} \lambda_1(d) \to \bar\lambda \\ \psi_d \to \bar\psi \quad \text{weakly in } H^1(\Omega) \text{ and strongly in } L^2(\Omega). \end{cases}$$

and we also have

$$\fint_\Omega \psi_d \to \fint_\Omega \bar\psi \quad \text{and} \quad \int \bar\psi^2 = \lim_{d\to\infty}\int \psi_d^2 = |\Omega|. \tag{11}$$

It remains to show that $\bar\lambda = -\fint m$.

Proof of of assertion (c) By Poincaré's inequality,

$$\int \left| \psi_d - \fint \psi_d \right|^2 \leq C \int |\nabla \psi_d|^2 \leq \frac{C'}{d}$$

We can then take $d \to \infty$ to deduce that

$$\int \left| \bar{\psi} - \fint \bar{\psi} \right|^2 = 0.$$

Hence $\bar{\psi}$ is a constant, and that constant must be 1 due to $\int \bar{\psi}^2 = |\Omega|$. i.e. $\psi_d \to 1$ strongly in $L^2(\Omega)$.
Now, we integrate (10), we have

$$\int (m + \lambda_1(d))\psi_d = 0$$

Letting $d \to \infty$, we have

$$\int (m + \bar{\lambda}) = 0.$$

This completes the proof.

Application to Diffusive Logistic Equation

Theorem 3

Let Ω and a nonconstant function $m(x)$ be given. Consider the diffusive logistic equation (6)*.*

(a) *If* $\max_{\bar{\Omega}} m \le 0$*, then* $u(\cdot, t) \to 0$ *uniformly as* $t \to \infty$*.*

(b) *If* $-\max_{\bar{\Omega}} m < 0$*, then there exists* $d_* \in (0, \infty]$ *such that*

- *for any* $d \in [d_*, \infty)$, $u(\cdot, t) \to 0$ *for any nonnegative, nontrivial solutions* $u(t, x)$ *of* (6)*;*
- *for* $d \in (0, d_*)$*, there exists a unique positive equiliubrium solution* $\theta_d(x)$ *which is globally asymptotically stable.*

Proof: Case A: if $\max m \le 0$ then observe that

$$\lambda_1(d) > \lim_{d \to 0} \lambda_1(d) = -\max m \ge 0$$

This proves extinction, i.e. $u \to 0$.

Case B: if $-\max m \le -\fint m \le 0$. Then

$$\lambda_1(d) < \lim_{d \to \infty} \lambda_1(d) = -\fint m \, dx \le 0.$$

Case C: $-\max m < 0 < -\fint m$. Then $\lambda_1(d) < 0$ for small d and is positive for $d \gg 1$. We conclude that there exists $0 < d_* < \infty$ such that

$$\lambda_1(d) < 0 \quad \text{for } 0 < d < d_* \quad \text{and } \lambda_1(d) > 0 \quad \text{for } d > d_*.$$

Then the persistence vs extinction can be treated as in previous cases.
Finally, we show that $u_m = u_M$ in case $\lambda_1(d) < 0$. Multiply u_m to the stationary equation satisfied by u_M, we have

$$u_m \left[d\Delta u_M + u_M(m(x) - u_M) \right]$$

Integrate by parts, we have

$$-d \int \nabla u_m \cdot \nabla u_M + \int u_m u_M (m - u_M) = 0.$$

Exchanging the roles of u_m and u_M, we have

$$-d \int \nabla u_M \cdot \nabla u_m + \int u_m u_M (m - u_m) = 0.$$

Subtracting the former from the latter, we have

$$\int u_m u_M (u_M - u_m) = 0$$

This proves that $u_M = u_m$ in Ω, and concludes the proof.

The next model considers a population in river. [Lutscher & Lou JMB 14'; Lou & Zhou JDE 15']

$$\begin{cases} u_t = \mu u_{xx} - u_x + u(1-u) & 0 < x < \ell, \ t > 0, \\ \mu u_x(0,t) - u(0,t) = \mu u_x(\ell,t) + (b-1)u(\ell,t) = 0 \end{cases} \tag{12}$$

- Parameter b is the **rate of population loss** at $x = \ell$.
  - The case $b = 0$ means no net loss of population.
  - The case $b = +\infty$ means lethal boundary.

Question: How does the environment parameters (b, ℓ) affect the persistence?

Critical Domain Size ℓ^*

- (Kierstead-Slobodkin 1953) *The domain size required to independently sustain a population.*
- When there is population loss at boundary (i.e. $b > 0$), the number ℓ^* signifies the minimal size of domain that can enable the persistence of the species. [Ludwig et al 79'; Okubo & Levin 01'; Shigesada & Kawasaki 97']
- It is known that ℓ^* is stictly increasing in the advection rate. [Potapov & Lewis 04'].
- We will analyze the effect of diffusion μ and boundary loss b in detail.

Exercise: For the diffusive logistic model with diffusion,

$$u_t = \mu u_{xx} + u(1-u) \quad \text{for } (0,\ell), \qquad u(0,t) = u(\ell,t) = 0,$$

show that the trivial solution is unstable if and only if $d < \frac{\ell^2}{\pi^2}$.

$$i.e. \qquad \ell^* = \pi\sqrt{\mu} \qquad \text{is increasing in } \mu.$$

i.e. **faster diffusion is detrimental to persistence.**

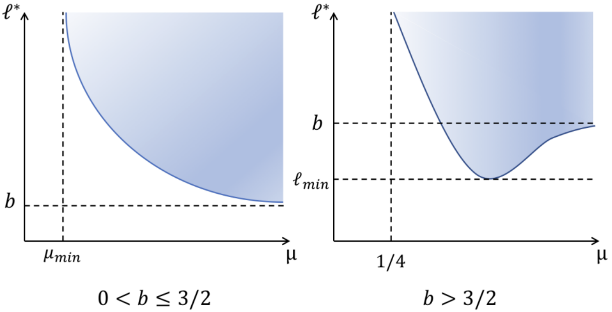
Critical Domain Size ℓ^* for $u_t = \mu u_{xx} - u_x + u(1-u)$

In the following, we write $\ell^* = \ell^*(\mu, b) \in (0, \infty]$. Then the population persists if and only if $\ell > \ell^*$.

Theorem [Hao-L.-Lou, DCDS-B, 2021]

Suppose $0 < b \leq \frac{3}{2}$, then $\mu \mapsto \ell^*(\mu, b)$ is **strictly decreasing** in μ.

Suppose $b > \frac{3}{2}$, then $\mu \mapsto \ell^*(\mu, b)$ first decreases, and then increases.



For $b > \frac{3}{2}$, it is sometimes optimal to persist by intermediate diffusion.

Critical Domain Size ℓ^* for $u_t = \mu u_{xx} - u_x + u(1-u)$

Theorem [Hao-L.-Lou, DCDS-B, 2021]

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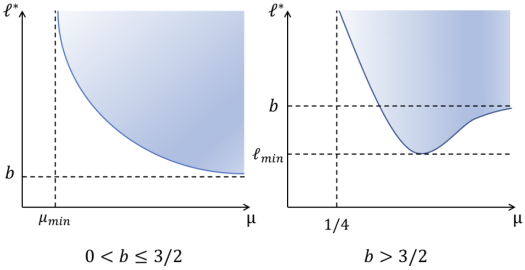

In case Dirichlet boundary conditions are imposed on both up and downstream boundary, the change in monotonicity was shown in [Berestycki et al. JMB 09] in connection with a shifting climate. This result is generalized when population loss is introduced at both upstream and downstream end [L.-Lee-Lou CAMC 24'].