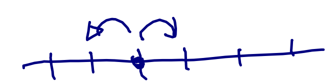
Reaction-Diffusion Models in Ecology and Evolution

Lecture 1 Overview

lam.184@osu.edu Adrian Lam (Ohio State)

Physical diffusion: Random movement of small particles dissolved in fluid that is caused by collisions with other molecules.

Various other movement processes that arise from small random steps can also be described in the same terms.

In ecology, dispersal of organisms can arise from processes similar to diffusion, e.g. small-scale turbulence in aquatic environments, and suitable scaling of unbiased, uncorrelated random walks. 

For a population in one space dimension, where at each time step Δt, each individual moves a distance Δx with probability $\frac{1}{2}$ to go left/right, In the limit $\frac{(\Delta x)^2}{2\Delta t} \to D$ for some $D > 0$, then density satisfies the "heat equation"

$$\partial_t u = D \partial_{xx} u \quad \text{for } x \in \mathbb{R},\ t > 0.$$

In two and three dimensions, the heat equation is given by

$$\partial_t u = D(\partial_{xx} u + \partial_{yy} u)$$

$$\partial_t u = D(\partial_{xy} u + \partial_{yy} u + \partial_{zz} u) \qquad \text{or} \qquad \underline{\partial_t u = D \Delta u}$$

Reaction and Diffusion

Let Ω be a smooth domain in $\mathbb{R}^k$.

For $1 \leq i \leq N$, denote by $u_i(x,t)$ the population densities of N interacting species at location $x \in \Omega$ and time $t > 0$.

Assume that these species move randomly according to Brownian motion with a bias according to a velocity $V_i \in \mathbb{R}^k$, and that they have growth rates $R_i(x,t)$, then the system describing the dynamics is

$$\partial_t u_i - \underbrace{d_i \Delta u_i}_{\substack{\text{random} \\ \text{movement}}} + \underbrace{\operatorname{div}(V_i u_i)}_{\substack{\text{directed} \\ \text{movement}}} = \underbrace{u_i R_i}_{\substack{\text{demography} \\ \text{(birth - death)}}}$$

In the simplest case, $d_i \equiv \text{Const}$ and $V_i \equiv 0$.

The demography term $R_i(x,t) = R_i(x,t, u_1(x,t), \dots, u_N(x,t))$.

e.g. $R_i(x,t) = m_i(x,t) + \sum_{j=1}^{N} c_{ij} u_j(x,t)$. (Lotka-Volterra)

where $m_i(x,t)$: intrinsic growth rate

c_{ij} : intra/interspecific interactions.

(prey-predator) $c_{ij} > 0 > c_{ji}$

(mutualistic) $c_{ij} > 0$, $c_{ji} > 0$

(competitive) $c_{ij} < 0$, $c_{ji} < 0$

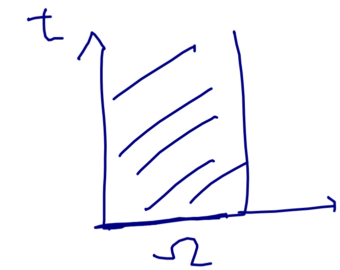
(self-limiting) $c_{ii} \leq 0$ is usually assumed.

The original prey-predator system was used to account for the oscillation in predator (larger fish) and prey (smaller fish) population in an averge fish catch.

$$\begin{cases} \frac{d}{dt} u = u(r_1 + c_{12} v) \\ \frac{d}{dt} v = v(r_2 + c_{21} u) \end{cases}$$

$$\boxed{\begin{array}{c} r_1 > 0 > r_2 \\ c_{12} < 0 < c_{21} \end{array}}$$

Single species model For a bounded spatial domain Ω, consider



$$(0.1)\quad \begin{cases} \partial_t u - d\Delta u = f(x,u)u & \text{in } \Omega\times(0,\infty) \\ n\cdot\nabla_x u = 0 & \text{on } \partial\Omega\times(0,\infty) \\ u(x,0) = \underline{u_0(x)} & \text{in } \Omega \end{cases}$$

- Existence / uniqueness of solution is standard. [D. Henry, Geometric Theory of Semilinear Equations] [A. Lunardi, Analytic Semigroups and optimal regularity in parabolic problems]

- (Persistence) $\boxed{Q}$: Does it holds that $\liminf_{t\to\infty} u(x,t) \geq \varepsilon$ $\exists\, \varepsilon>0$?

  $\boxed{A}$: Stability analysis of the trivial equilibrium, which leads to...

- (Principal eigenvalue)

$$(0.2)\quad \begin{cases} -d\Delta\phi = f(x,0)\phi + \mu\phi & \text{in } \Omega \\ n\cdot\nabla\phi = 0 & \text{on } \partial\Omega \end{cases}$$

We will introduce the Krein-Rutman Theorem and show that (0.2) has a real, simple eigenvalue μ_1, the unique one that has a positive eigenfunction, such that $\mu_1>0 \Rightarrow 0$ is stable / $\mu_1<0 \Rightarrow 0$ is unstable.

(Critical Domain Size) When population can be lost on the boundary, i.e.

$$n \cdot \nabla u + p^0(x) u = 0 \qquad p^0(x) \geq 0, \not\equiv 0,$$

then a closely related question is the minimal domain size for persistence.

(Time-periodicity) In case $u_t - d\Delta u = f(x,t,u)u$ where f is T-periodic in t, one is led to consider the associated periodic-parabolic eigenvalue problem:

$$\begin{cases} \partial_t \phi - d\Delta\phi = f(x,t,0)\phi + \mu\phi & \text{in } \Omega\times\mathbb{R} \\ n\cdot\nabla\phi = 0 & \text{on } \partial\Omega\times\mathbb{R} \\ \phi(x,t) = \phi(x,t+T) & \text{in } \Omega\times\mathbb{R}. \end{cases}$$

The biologically interesting question is how the p.e.v. depends on parameters.

(General time-heterogeneity, the principal Floquet bundle). we will show that there exists a unique positive solution $\phi(x,t) > 0$, $H_1(t) \in \mathbb{R}$ to

$$\begin{cases} \partial_t \phi - d\Delta\phi = f(x,t,0)\phi + H_1(t)\phi & \text{in } \Omega\times\mathbb{R} \\ n\cdot\nabla\phi = 0 & \text{on } \partial\Omega\times\mathbb{R} \\ \int_\Omega \phi(x,t)dx \equiv 1 & \text{in } \mathbb{R} \end{cases}$$

When $f(x,u)=m(x)-u$, then the eqn. (0.1) is called the logistic equation. In such a case, (0.1) has a positive equilibrium $\theta_d(x)$ if and only if 0 is unstable. Moreover, $\theta_d(x)$ is globally asymptotically stable.

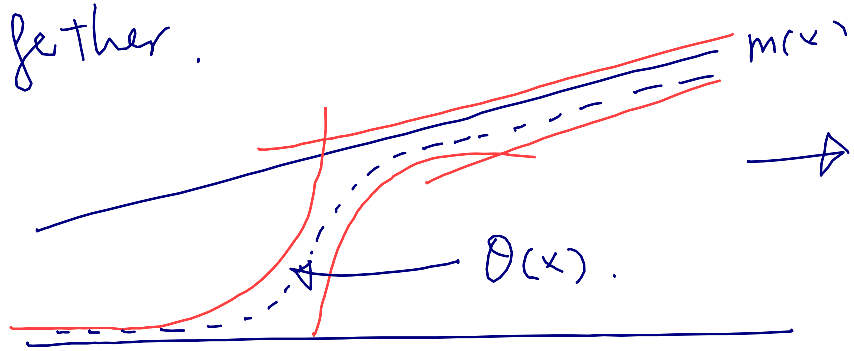
Can we describe the pattern $\theta_d(x)$ when (0.2) is at a dynamic equilibrium?

We will show that

$$\left\{\begin{array}{ll}\theta_d(x)\to\max\{m(x),0\} & \text{as } d\to 0+\\ \theta_d(x)\to \int_\Omega m(x)\,dx & \text{as } d\to\infty.\end{array}\right\}$$

via the method of super-/subsolutions.

For more general situations (e.g. directed movements is involved), it is sometime necessary to construct piecewise super/subsol., and then glue them together.



$\rightarrow$ super/subsol. in the generalized sense.

(Competition of two-species).

- Theory of monotone dynamical systems (Hess, Lazer, Hirsh, Smith, Hsu, Waltman) ....
- Evolutionary questions via invasibility analysis. [Diekmann, A beginner's guide to adaptive dynamics]
  - Evolutionarily stable strategies (ESS).

$w = u+v \quad , d_1 = d_2 = d$

$\partial_t w = d\Delta w + w(m-w)$

e.g.
$$\begin{cases} \partial_t u = d_1 \Delta u + u(m(x) - u - v) & \Omega \times (0,\infty) \\ \partial_t v = d_2 \Delta v + v(m(x) - u - v) & \Omega \times (0,\infty) \\ n\cdot\nabla u = n\cdot\nabla v = 0 & \partial\Omega \times (0,\infty) \end{cases}$$

Thm [Hastings (1983); Dockery et al. (1998)] Let $m(x) \not\equiv$ const., $\int_\Omega m\,dx \geq 0$.
If $0 < d_1 < d_2$, then $(\theta_{d_1}, 0)$ is globally asymptotically stable.

$\rightarrow$ Selection for slow dispersal.

We will review the theory of MDS, which has led to much progress on two-species competition systems.

(Competition for N-species).

(Dockery's conjecture) For $N \geq 3$, $0 < d_1 < d_2 < \cdots d_N$, $(\theta_{d_1}, 0, \ldots, 0)$ is g.a.s.

But the system is no longer MDS!

We will discuss recent progress, which relies on the notion of principal Floquet bundle mentioned earlier.

(The competition for light in phytoplankton populations). $\Omega = [0, L]$

$$\begin{cases} \partial_t u_i - d_i \partial_{xx} u_i = g_i(I(x,t))\, u_i - \mu_i u_i & \text{for } 0 \leq x \leq L,\ t > 0 \\ \partial_x u_i(0,t) = \partial_x u_i(L,t) = 0 & \text{for } t > 0 \end{cases}$$

where the light intensity is given by the Lambert-beer law:

$$I(x,t) = \exp\left(-k_0 x - \sum_{i=1}^{N} k_i \int_0^x u_i(y,t)\,dy\right)$$

single-species - Subhomogeneous MDS

two-species - MDS

Traveling Waves and Spreading Speeds

RD models on unbounded domains support traveling waves. (TW)

E.g. [R.A. Fisher, 1930's] noted for the model $\partial_t u = d\,\partial_{xx} u + ru(1-u)$ in population genetics proves the existence of solution of the form

$$u(x,t) = \phi(x-ct)$$

which moves by translation in space with a fixed shape.

In ecology, TW describes biological invasions,

RD models often predict that a population initially inhabiting a bounded region will have a specific spreading speed even if it does not form and maintain a TW profile.

For a population to have a spreading speed c_* means that an observer moving faster than c_* would outrun the spreading population, but the population would outrun an observer moving slower than c_*.

If time allows, we will also discuss <u>spreading in shifting environment</u>

$$\begin{cases} \partial_t u = \partial_{xx} u + r(x,t)\, u(1-u) & x \in \mathbb{R},\ t>0 \\ u(x,0) = u_0(x) \text{ is compactly supported.} \end{cases}$$

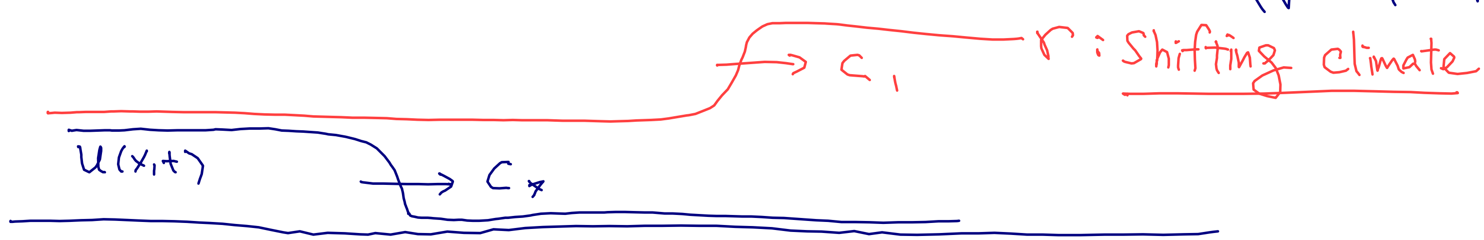
We call c_* the <u>spreading speed</u> (Aronson & Weinberger) if.

$$\limsup_{t\to\infty} \sup_{x>ct} |u(x,t)| = 0 \quad \forall c > c_* \qquad \text{and} \qquad \liminf_{t\to\infty} \inf_{0<x<ct} u(x,t) > 0 \quad \forall 0<c<c_*$$

- when $r \equiv r_0 \implies c_* = 2\sqrt{r_0}$
- when $r = \tilde{r}(x - c_1 t)$, $\tilde{r}$ is monotone increasing, $0 < \underset{r_1}{\underset{\shortparallel}{\tilde{r}(-\infty)}} < \underset{r_2}{\underset{\shortparallel}{\tilde{r}(+\infty)}}$,

then

$$c_* = \begin{cases} 2\sqrt{r_2} & \text{if } c_1 \le 2\sqrt{r_2} \\ \frac{c_1}{2} - \sqrt{r_2 - r_1} + \dfrac{r_1}{\frac{c_1}{2} - \sqrt{r_2 - r_1}} & \text{if } 2\sqrt{r_2} < c_1 < 2\left(\sqrt{r_2 - r_1} + \sqrt{r_1}\right) \\ 2\sqrt{r_1} & \text{if } c_1 \ge 2\left(\sqrt{r_2 - r_1} + \sqrt{r_1}\right) \end{cases}$$



(Competition of ∞ - species, Selection-Mutation Models).

- $u = u(z,t)$ where $z \in \Omega$ is the phenotype/trait
- $$\partial_t u = \underbrace{M[u]}_{\text{mutation}} + \underbrace{F(z, u(\cdot,t))\,u}_{\text{selection/competition}}$$

e.g. [Magal-Webb (2000)] for bdd domain [Dieckmann et al. (2005), Lorz et al. (2011)] unbdd domain.

$$\begin{cases} \partial_t u = \varepsilon^2 \Delta u + u\left[m(z) - \int_\Omega u(y,t)\,dy\right] & \text{for } z \in \Omega,\ t>0 \\ n \cdot \nabla u = 0 & \text{for } z \in \partial\Omega,\ t>0 \\ u(x,0) = u_0(x) & \text{for } z \in \Omega. \end{cases}$$

<u>Phenomena</u>

Stationary Dirac Concentration $\Leftrightarrow$ selection of trait (ESS)

Moving Dirac concentration $\longleftrightarrow$ Canonical equation in adaptive dynamics.

Main Tools

- Principal eigenvalue & Floquet bundle
- Proof of Krein-Rutman Theorem.
- Elements of Monotone Dynamical Systems
  - Subhomogeneous systems
  - competition systems.
- Super / subsolutions (in the generalized sense)
- Harack Principle
- Hamiton-Jacobi Equations & Viscosity sol.

For (almost) complete proofs, see the draft of my lecturenotes.
Please email me if you find typos!

§ The maximum principle for parabolic equations

Let $\Omega \subseteq \mathbb{R}^k$ is bounded with smooth bdry $\partial\Omega$ and outer unit normal vector $n = (n_i)$.

$$\Omega_T = \Omega \times (0, T], \qquad \bar{\Omega}_T = \bar{\Omega} \times [0, T], \qquad S\Omega_T = \partial\Omega \times (0, T]$$

Consider the linear parabolic equation

(2.1) $$u_t + Lu \equiv u_t - a^{ij} D_{ij} u - b^j D_j u - cu = f \quad \text{in } \Omega_T$$

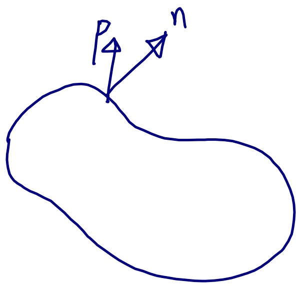
with oblique boundary condition

(2.2) $$Bu \equiv p^i D_i u + p^0 u = g \qquad \text{on } S\Omega_T$$

where $a^{ij}, b^j, c \in C^{\alpha, \alpha/2}(\bar{\Omega}_T)$, $\quad p^i \in C^{1+\alpha, \frac{1+\alpha}{2}}(\bar{\Omega}_T)$

$$\lambda_0 |\xi|^2 \leq a^{ij}(x,t) \xi_i \xi_j \leq \Lambda_0 |\xi|^2 \qquad \forall \xi \in \mathbb{R}^k$$

$$p^i(x,t) n_i(x) > 0 \quad \text{and} \quad p^0 \geq 0 \qquad \text{on } S\Omega_T$$



e.g. (Neumann b.c.) $p^i = n_i$, $\quad p^0 = 0$

(Robin b.c.) $p^i = n_i$, $\quad p^0 \geq 0$.

Def 1. We say that $u \in C^{2,1}(\Omega_T)$ satisfies

(2.4) $\quad u_t + Lu \leq f(x,t,u,Du)$ in Ω_T in the classical sense

if the differential ineq holds everywhere in Ω_T.

In this case, we call u a classical subsol. of $u_t + Lu = f$ in Ω_T.

We similar define classical supersol.

2. We similarly define $Bu \gtreqless g(x,t)$ on $S\Omega_T$ in the classical sense.

3. We say that $u \in C(\overline{\Omega}_T)$ satisfies

$\rightarrow$ $u_t + Lu \leq f(x,t,u,Du)$ in Ω_T and $Bu \leq g$ on $S\Omega_T$

in the generalized sense if, for each $X_0 \in \overline{\Omega} \times (0,T]$,

there exists a neighborhood $\mathcal{U}$ of X_0 in $\overline{\Omega} \times (0,T]$,

and $\hat{u} \in C^{2,1}(\mathcal{U})$ such that $u \geq \hat{u}$ in $\mathcal{U}$, $u(X_0) = \hat{u}(X_0)$, and

$$(2.5) \quad \begin{cases} \hat{u}_t + L\hat{u} \leq f(x,t,\hat{u},D\hat{u}) & \text{at } X_0 \text{ if } X_0 \in \Omega_T \\ B\hat{u} \leq g & \text{at } X_0 \text{ if } X_0 \in S\Omega_T \end{cases}$$

Remark 2.1

- For divergence form equation, there is a notion of weak super/subsol. See, e.g. [Ch.4, monograph of Y. Du].

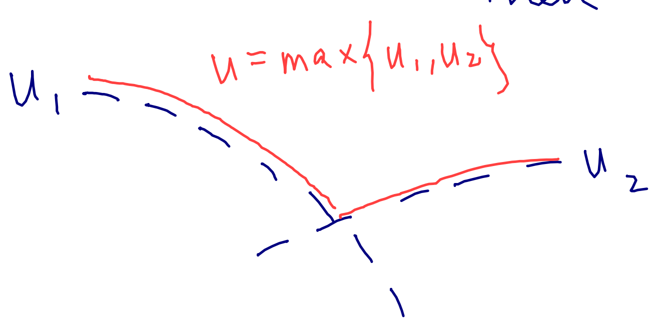
- For non-divergence form equations,

$$\{\text{classical super/subsol}\} \subseteq \{\text{generalized super/subsol}\} \subseteq \{\text{viscosity super/subsol}\}$$

- If u_1, u_2 are generalized subsol. $\Rightarrow \max\{u_1, u_2\}$ is generalized subsol

- If $\begin{cases} V_1, V_2 \text{ are relative open in } \overline{\Omega}, \\ V_1 \cup V_2 = \overline{\Omega} \\ \text{For } i=1,2, \ u_i \text{ is generalized subsol in } V_i \end{cases}$

then $u(x,t) = \begin{cases} u_1 & V_1 \setminus V_2 \\ u_2 & V_2 \setminus V_1 \\ \max\{u_1, u_2\} & V_1 \cap V_2 \end{cases}$ is generalized subsol.



Theorem 2.1 (The weak max. prin.) Suppose $u \in C(\overline{\Omega_T})$ satisfies

$u_t + Lu \le 0$ in Ω_T in the generalized sense.

1. If $c \le 0$ in Ω_T, then

$$\max_{\overline{\Omega_T}} u \le \max_{P\Omega_T} u^+ , \quad \text{where } \Omega_T = \Omega \times (0, T], \quad P\Omega_T = \overline{\Omega_T} \setminus \Omega_T . \tag{2.7}$$

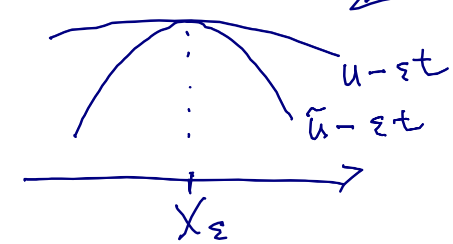
2. If $\max_{P\Omega_T} u \le 0$, then $\max_{\overline{\Omega_T}} u \le 0$.

Proof Assume for the moment that $u_t + Lu \le 0$ in Ω_T in the generalized sense.

We claim that (2.7) holds for $u_\varepsilon(x,t) = u(x,t) - \varepsilon t$.

Otherwise, $u - \varepsilon t$ has a positive local max at some $X_\varepsilon \in \Omega_T$

By def of gen. subsol., $\exists\, U$ and $\tilde{u} \in C^{2,1}(U)$ s.t.



$$\left\{ \begin{array}{l} \tilde{u} \le u \text{ in } U \text{ and } \tilde{u}(X_\varepsilon) = u(X_\varepsilon) \Rightarrow \tilde{u} - \varepsilon t \text{ has local max at } X_\varepsilon \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \Downarrow \\ \underline{\tilde{u}_t + L\tilde{u} \le 0 \text{ at } X_\varepsilon} \longrightarrow \longleftarrow \tilde{u}_t + L\tilde{u} \ge (\varepsilon t)_t = \varepsilon \text{ at } X_\varepsilon \end{array} \right.$$

$$\Longrightarrow \boxed{\max_{\overline{\Omega_T}} u_\varepsilon \le \max_{P\Omega_T} u_\varepsilon^+}.$$ Let $\varepsilon \to 0^+$ to conclude 1.

For 2, let $u \le 0$ in $P\Omega_T$, we apply 1 to $e^{\|c\| t} u(x,t)$. #

Thm 2.2 (The Boundary Point Lemma) Given $R>0$ and $Y=(y,s)\in\mathbb{R}^{k+1}$, consider the lower paraboloid,

$$P_R = P_R(Y) = \{ X=(x,t) : |x-y|^2+(s-t) < R^2 \text{ and } t<s \}.$$

Suppose $u\in C(\Omega_T)$ satisfies $u_t+Lu\geq 0$ in P_R in the generalized sense, and that there is $X_1=(x_1,s)$ with $|x_1-y|=R$ such that

$$u(X_1)>u(X) \quad \text{and} \quad c(X)u(X_1)\leq 0 \qquad \forall X\in P_R.$$

Then $\beta\cdot Du(X_1)>0$ for any β such that $\beta\cdot(x_1-y)>0$, in the sense

$$\liminf_{h\to 0+} \frac{u(x_1,s)-u(x_1-\beta h,s)}{h} > 0$$

Pf Observe that the proof in [Lieberman, Ch II, Lemma 2.8], which is based on weak maximum principle. Specifically, $u(X_1)-u$ and $\sigma_R(r)=e^{-\alpha r^2}-e^{-\alpha R^2}$ form a pair of super/subsol.

Choose $\varepsilon>0$ s.t. $u(x_1,s)-u(x,t)\geq \varepsilon\,\sigma_R(r)$ holds on $\partial(P_R\setminus \overline{P_{R/2}})$

Thm 2.1 $\Longrightarrow$ $u(x_1,s)-u(x,t)\geq\varepsilon\,\sigma_R(r)$ in $P_R\setminus\overline{P_{R/2}}$. #

Thm 2.1 (Growth Lemma due to Krylov \ Safonov)

Let $R>0$ and $\alpha>0$ be positive constants and set

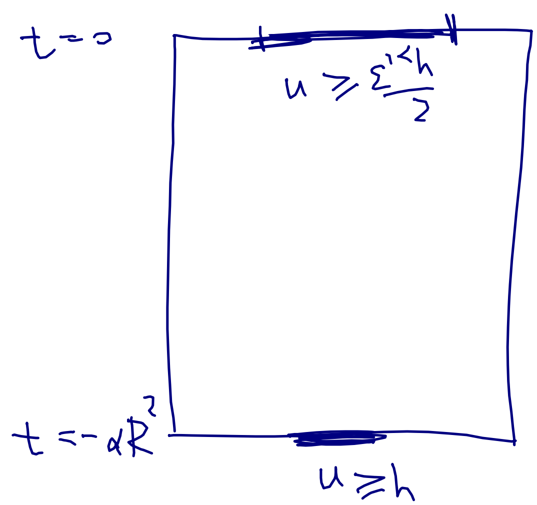
$$Q=\{(x,t):|x|<R,\ -\alpha R^2<t<0\}.$$

Then there exists a positive constant K such that for any $u\in(\bar{\Omega}_T)$ such that $u\geq 0$ in Q and $u_t+Lu\geq 0$ in Q in the generalized sense,

if $\quad u\geq h$ in $\{|x|<\varepsilon R,\ t=-\alpha R^2\}$ for some $h>0$, $0<\varepsilon<1$,

then $\quad u\geq \frac{\varepsilon^{K}h}{2}$ in $\{|x|<\frac{R}{2},\ t=0\}$.

Pf. Also follows from weak max. prin. See [Lieberman, Lemma 2.6].



$$Q=B_R(0)\times(-\alpha R^2,0)$$

Thm 2.3 (The strong max. prin.) Assume $u \in C(\overline{\Omega_T})$ satisfies

$u_t + Lu \lesssim 0$ in Ω_T and $Bu \le 0$ in $S\Omega_T$ in the generalized sense.

1. If $u(y,0) \lesssim 0$ in Ω, then $u \lesssim 0$ in Ω_T.
2. If, in addition, $u(x_0,t_0) = 0$ for some $(x_0,t_0) \in \overline{\Omega} \times (0,T]$, then $u \equiv 0$ in $\overline{\Omega} \times [0,t_0]$.

Pf. Follows from Thms 2.1 and 2.2, and Lem 2.1. See lecture notes for detail.

Cor (For $u = u(x,t)$)

$$\begin{cases} u_t + Lu = 0 & \Omega_T \\ Bu = 0 & S\Omega_T \\ u \lesssim 0 & \Omega_T \end{cases} \Rightarrow \begin{cases} u \equiv 0 & \Omega_T \\ \text{or } u < 0 & \Omega_T \end{cases}$$

Cor (For $u = u(x)$)

$$\begin{cases} Lu \lesssim 0 \text{ in } \Omega, \; Bu \lesssim 0 \text{ on } \partial\Omega \text{ in gen. sense} \\ u \lesssim 0 \text{ in } \Omega \end{cases} \Rightarrow \begin{cases} u \equiv 0 & \overline{\Omega} \\ \text{or} & \\ u < 0 & \overline{\Omega} \end{cases}$$

§ The comparison principle for semilinear equations.

Corollary 2.1 Suppose f is C^1, and $u, v \in C(\bar{\Omega}_T)$ satisfies

$$(2.13)\quad \begin{cases} u_t + Lu \le f(x,t,u,Du) \quad \text{and} \quad v_t + Lv \ge f(x,t,v,Dv) & \text{in } \Omega_T \\ B(u-v) \le 0 & \text{on } S\Omega_T \end{cases}$$

in the generalized sense. If $u(x,0) \le v(x,0)$ in Ω, then $u \le v$ in Ω_T.

Pf. Suppose (2.13) is satisfied in the classical sense, then

$w = u - v$ satisfies

$$w_t + Lw \le b \cdot Dw + cw \quad \text{in } \Omega_T, \quad Bw \le 0 \quad \text{on } S\Omega_T$$

where

$$b(x,t) = \int_0^1 D_4 f(x,t,u(x,t), \xi Du(x,t) + (1-\xi) Dv(x,t))\, d\xi.$$

$$c(x,t) = \int_0^1 D_3 f(x,t, \xi u(x,t) + (1-\xi) v(x,t), Dv(x,t))\, d\xi.$$

We leave the general case as an exercise.

Corollary 2.2 (Monotone Method due to [Sattinger, (1971/72)])

Suppose $f=f(x,u)$ is independent of t, and $u \in C^{2,1}(\Omega_T) \cap C^{1,0}(\overline{\Omega_T})$ is classical solution of $u_t + Lu = f(x,u,Du)$ Ω_T, $Bu=0$ $S\Omega_T$.

If $u(x,0) =: u_0(x)$ satisfies

$$Lu_0 \le f(x,u_0,Du_0) \text{ in } \Omega \qquad Bu_0 \le 0 \text{ on } \partial\Omega$$

in the generalized sense, then $t \longmapsto u(x,t)$ is non-decreasing.

Moreover, if $T=+\infty$, and

$$\sup_{t\ge 0} \|u(\cdot,t)\|_{C(\overline{\Omega})} < +\infty, \quad \limsup_{t\to\infty} \|f(\cdot,u(\cdot,t),Du(\cdot,t))\|_{C(\overline{\Omega})} < +\infty,$$

then $u_\infty(x) := \lim_{t\to\infty} u(x,t)$ exists in $C(\overline{\Omega})$, such that

$u_\infty \in W^{2,p}(\Omega)$ satisfies $\begin{cases} Lu_\infty = f(x,u_\infty,Du_\infty) & \text{in strong sense} \\ Bu_\infty = 0 & \text{in classical sense.} \end{cases}$

(If $f(x,u_\infty,Du_\infty) \in C^\alpha$, then u_∞ is classical sol. by Schauder estimate.)

Pf By <u>Cor 2.1</u>, $u(x,\tau) \geq u_0(x)$ $\forall x \in \Omega$, $\tau \geq 0$.

By weak max prin, $u(x,\tau+t) \geq u(x,t)$ $\forall x \in \Omega$, $\tau, t \geq 0$.

$\Rightarrow$ $t \mapsto u(x,t)$ is non-decreasing.

For the second part, observe that $u_\infty(x) = \lim_{t\to\infty} u(x,t)$ exists.

By boundedness in L^∞, we apply the parabolic L^p estimates to deduce that $\sup_{t\geq 1} \|u\|_{W^{2,1,p}(\Omega\times[t,t+1])} < \infty$.

$$\Rightarrow V_k(x,t) = u(x,t+k) - u_\infty(x) \xrightarrow{k\to\infty} 0 \quad \begin{array}{l} \text{weakly in } W^{2,1,p}(\Omega\times[0,1]) \\ \text{strongly in } C^{1+\alpha, 1+\frac{\alpha}{2}}(\overline{\Omega}\times[0,1]) \end{array}$$

$\Rightarrow$ $u_\infty(x)$ is a strong sol.

#

Thm 2.5 (Harnack Principle) Let $c \in L^\infty(\Omega_T)$, $T \geq \delta_0$ and $u \in W^{2,1,p}(\Omega_T)$ for some $p > k+2$, so that $u \geq 0$ in Ω_T, $u_t + Lu = 0$ in Ω_T is strong sense. $Bu = 0$ in classical sense.

$u(x,t) \leq C u(y,t)$ $\forall x, y \in \Omega$ $\forall t \geq \delta_0$

Then there exists C,

$$\sup_{x \in \Omega} u(x,t) \leq C \inf_{x \in \Omega} u(x,t), \quad \text{for each } t \in [\delta_0, T].$$

Here C is independent of T and $u(x,t)$.

Pf. It is well-known that $\sup_{x \in \Omega} u(x, t-\delta_0) \leq C \inf_{x \in \Omega} u(x,t)$

Next, observe that $\bar{u}(x,t) = Ce^{\|c\|t}$ is supersolution.

If $u \leq \bar{u}$ at time $t - \delta_0 \Rightarrow \sup_{x \in \Omega} u(x,t) \leq e^{\|c\|\delta_0} \sup_{x \in \Omega} u(x, t-\delta_0)$

[J. Húska, J. Differential Equations (2006)] [Húska - Poláčik - Safonov (2007)]

[Húska - Poláčik - Safonov (2007)]

§ The Logistic Equation

Consider

$$(3.12)\quad \begin{cases} \partial_t u - d\Delta u = u(m(x)-u) & \Omega\times(0,\infty) \\ n\cdot\nabla u = 0 & \partial\Omega\times(0,\infty) \\ u(x,0) = u_0(x) & \Omega \end{cases}$$

Proposition 3.5 (3.12) has a nonnegative, nontrivial equilibrium iff $\mu_1 < 0$,

where $\mu_1 \in \mathbb{R}$ is the eigenvalue of $\begin{cases} -d\Delta\phi = m(x)\phi + \mu_1\phi & \text{in } \Omega \\ n\cdot\nabla\phi = 0 & \text{on } \partial\Omega \end{cases}$

with a positive eigenfunction.

Pf. Suppose (3.12) has a non-trivial equilibrium $\theta(x)$. $\boxed{\begin{cases} -d\Delta\theta = \theta(m-\theta) & \text{in } \Omega \\ n\cdot\nabla\theta = 0 & \text{on } \partial\Omega. \end{cases}}$

Then $\theta(x) > 0$ in $\bar{\Omega}$. be the strong maximum principle.

Multiply by ϕ, and integrate by parts, we have

$$\int_\Omega \theta^2\phi_1 = \int_\Omega \phi_1(d\Delta\theta + m\theta) = \int_\Omega \theta(d\Delta\phi_1 + m\phi_1) = -\mu_1\int_\Omega \theta\phi_1 .$$

Since LHS > 0, we have $\mu_1 < 0$.

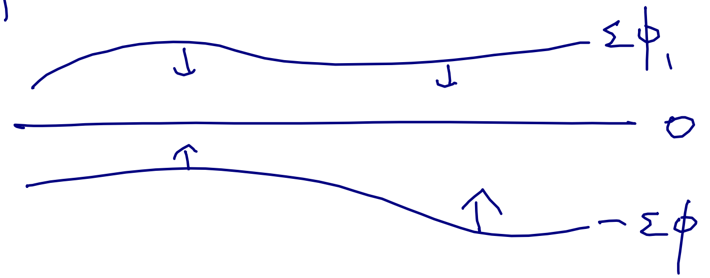
This proves sufficiency.

Now, suppose $\mu_1 < 0$, then one may verify that, for $0 < \varepsilon \ll 1$, $M \gg 1$. $\varepsilon \phi_1$ and M forms a pair of sub/supersol. in classical sense.

By Sattinger's method, we obtain the existence of the maximal and minimal equilibrium θ_M and θ_m. #

supersol.
$$\begin{cases} -d\Delta M - M(m-M) \geq 0 \quad \text{if } M \geq \sup_{\Omega} m \\ BM = p^i D_i(M) + p^0 M = p^0 M \geq 0 \quad \text{since } p^0 \geq 0 \text{ on } S\Omega_T \end{cases}$$

subsol.
$$\begin{cases} -d\Delta(\varepsilon\phi) - \varepsilon\phi(m - \varepsilon\phi) = \varepsilon\phi(\overset{<0}{\mu_1} - \varepsilon\phi) \leq 0 \quad \text{for } \varepsilon > 0 \text{ small} \\ B\phi = 0 \quad \text{on } S\Omega_T \end{cases}$$



Theorem 3.2

1. If $\mu_1 \geq 0$, then $u(x,t) \xrightarrow{t\to\infty} 0$ for every nonneg. sol u. of (3.12)
2. If $\mu_1 < 0$, then (3.12) has a unique positive equilibrium $\theta(x)$ such that $u(x,t) \xrightarrow{t\to\infty} \theta(x)$ for every nonneg, nontrivial sol. u. of (3.12).

Pf 1. For any $M \gg 1$, the solution u_M with initial data M decreases monotonically in t to some equilibrium.

Since $\mu_1 \geq 0$, $u_M \longrightarrow 0$ as $t \to \infty$.

so for any $u(x,t)$, with initial data u_0,

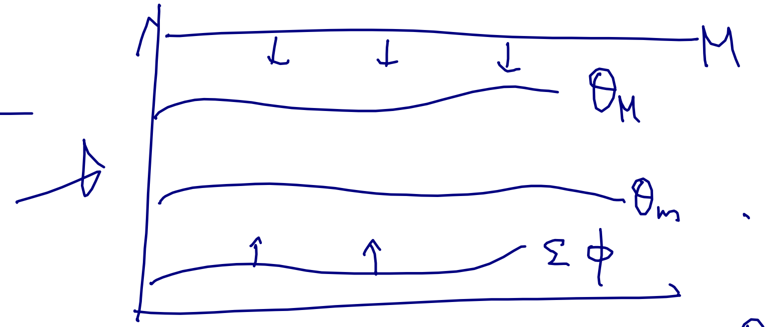
choose $M \gg 1$ such that $\underline{0} \leq u_0 \leq \underline{M}$ in Ω,

By comparison,

$$0 \leq u(x,t) \leq \underline{u_M(x,t)} \xrightarrow{\text{as } t\to\infty} 0 .$$

This proves 1.

Pf of 2.



Observe that any equilibrium θ satisfies $\theta_m \le \theta \le \theta_M$ in Ω.

It suffices to show that $\theta_M \equiv \theta_m$.

$-d\Delta\theta_M = \theta_M(m-\theta_M)$

Multiply the eqn of θ_M by θ_m and integrat by parts,

$$d\int \nabla\theta_M\cdot\nabla\theta_m = -d\int \theta_m \Delta\theta_M = \int \theta_m\theta_M(m-\theta_M).$$

Similarly, $d\int \nabla\theta_m\cdot\nabla\theta_M = \int \theta_M\theta_m(m-\theta_m)$.

subtracting, $0 = \int \theta_M\theta_m(\theta_M-\theta_m)$.

Using $\theta_M \ge \theta_m$, we deduce that $\theta_M \equiv \theta_m$. #

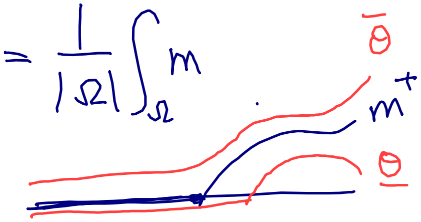
Remark The same holds for $\begin{cases} u_t + Lu = f(x,u)u & \text{in } \Omega\times(0,\infty) \\ Bu = 0 & \text{on } \partial\Omega\times(0,\infty) \end{cases}$

with f strictly decreasing in u.

Qualitative properties of θ_d

Proposition (a) Suppose $\max_{\Omega} m > 0$, then θ_d exists $\forall\, 0<d\ll 1$ and $\boxed{\lim_{d\to 0}\theta_d = m^+.}$

(b) Suppose $\int_\Omega m > 0$, then θ_d exists $\forall\, d>0$ and $\lim_{d\to\infty}\theta_d = \frac{1}{|\Omega|}\int_\Omega m$



Proof of (a) Take homog. C^2 functions $\bar\theta$, $\underline{\theta}$ s.t.

$$\chi_{\{\underline{\theta}>0\}}\underline{\theta}(x) < \max\{m(x),0\} < \bar\theta \quad \text{in } \bar\Omega \quad \text{and} \quad n\cdot\nabla\bar\theta \geq 0 \geq n\cdot\nabla\underline{\theta} \text{ on } \partial\Omega$$

then it is easy to check that $\bar\theta$ and $\underline{\theta}$ form a pair of classical super/subsol. Indeed,

$$-d\Delta\bar\theta - \bar\theta(m(x)-\bar\theta) \geq O(d) + (\inf\bar\theta)\left[\inf(\bar\theta - m)\right] > 0 \text{ for } d \text{ small.}$$

One can similarly check that $\underline{\theta}$ is a generalized subsol.

$$\Longrightarrow \qquad \underline{\theta} \leq \theta_d \leq \bar\theta \quad \text{in } \bar\Omega \text{ for } d \text{ small.}$$

Since $\bar\theta$ and $\underline{\theta}$ are arbitrary, this proves $\theta_d \to m^+$.

<u>Proof of (b)</u> Divide $-d\Delta\theta_d = \theta_d(m-\theta_d)$ by θ_d, and integrate by parts,

$$(*) \qquad \int m-\theta_d = -d\int\frac{\Delta\theta_d}{\theta_d} = -d\int\frac{|\nabla\theta_d|^2}{\theta_d^2} \le 0 \Rightarrow \boxed{\int_\Omega \theta_d \ge \int_\Omega m > 0}. \quad (3.19)$$

Multiply $(*)$ by θ_d, and integrate by parts,

$$d\int|\nabla\theta_d|^2 \le C \quad \text{where } C \text{ is indep. of } d>0.$$

By Poincaré's ineq.,

$$\int_\Omega |\theta_d - \textstyle\fint\theta_d|^2 = O(1/d). \quad (3.21)$$

Integrate $(*)$ $\Rightarrow$ $0 = \int_\Omega \theta_d(m-\theta_d)$

$$\Rightarrow -\fint_\Omega\left(\theta_d - \fint_\Omega\theta_d\right)(m-\theta_d) = \left[\fint_\Omega\theta_d\right]\left[\fint_\Omega(m-\theta_d)\right] = \left[\fint_\Omega\theta_d\right]\left[\fint_\Omega m - \fint_\Omega\theta_d\right].$$

By (3.19) and (3.21), we deduce $\fint_\Omega\theta_d \to \fint_\Omega m > 0$ as $d\to\infty$.

By (3.21), $\theta_d \longrightarrow \fint_\Omega m$ in $L^2(\Omega)$.

By L^p estimate, $\|\theta_d\|_{W^{2,p}(\Omega)} \le C$, so one may improve the convergence to $C(\bar\Omega)$.

#

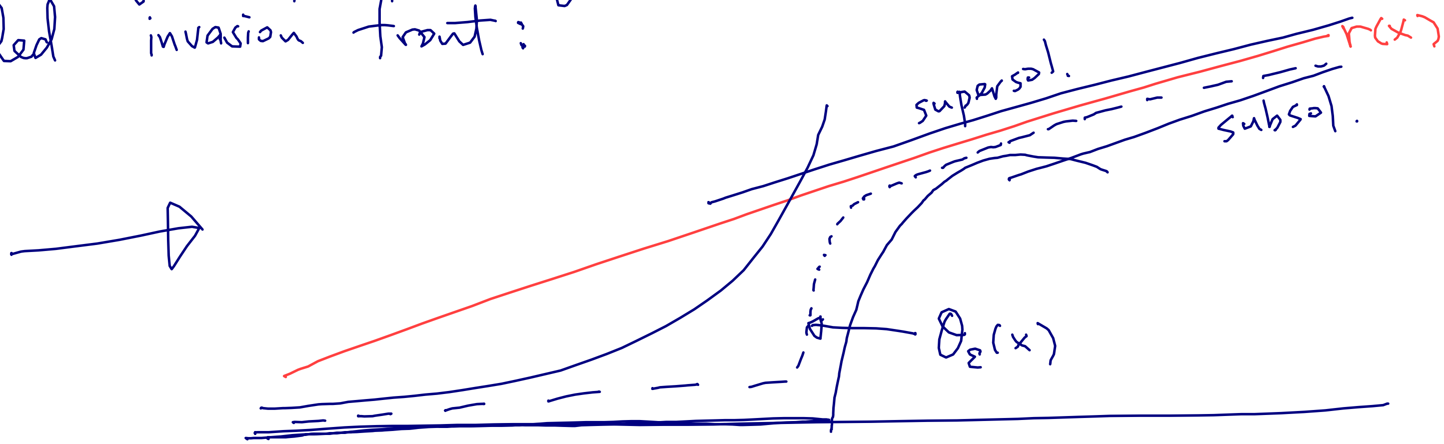
We close by stating a few applications of generalized super/subsol:

In [L.-Lou-Lutscher (2016)], we considered a river population model:

$$\begin{cases} u_t - \varepsilon^2 d u_{xx} + \varepsilon q u_x = u(r(x) - u) & \text{in } [0,L] \times (0,\infty) \\ \varepsilon u_x - q u = 0 & \text{on } \{0, L\} \times (0,\infty). \\ u(x,0) = u_0(x) \end{cases}$$

When ε is small, the length of the river is of order $1/\varepsilon$.

The unique positive equilibrium θ_ε is of the form of a stalled invasion front:



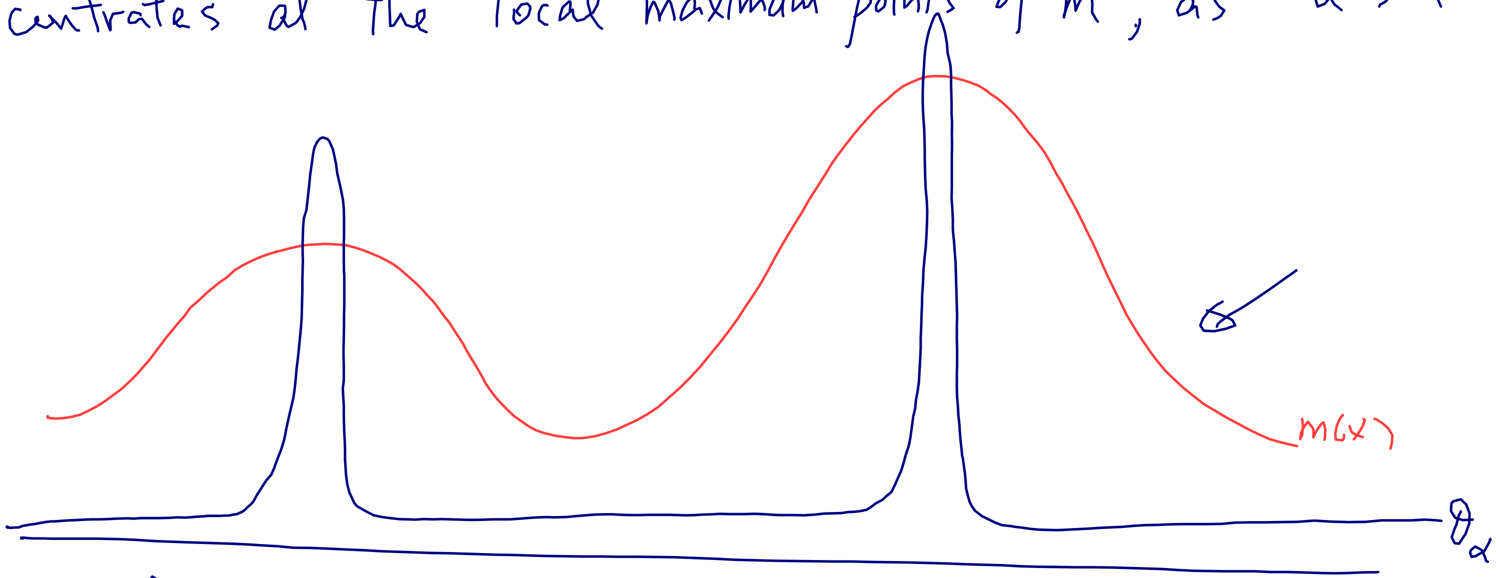
where the invasion front is stalled at $x^* \in [0,L]$ such that

$$2\sqrt{d r(x^*)} = q$$

In [Chen-L.-Lou, (2012)], we consider the case when the single species combines random motion with a directed movemt up the gradient of resource ∇m.

$$\begin{cases} u_t - \mu \Delta u + \alpha \,\mathrm{div}(u \nabla m) = u(m(x) - u) & \text{in } \Omega \times (0,\infty) \\ n \cdot (\mu \nabla u - \alpha u \nabla m) = 0 & \text{on } \partial\Omega \times (0,\infty) \\ u(x,0) = u_0(x) & \text{in } \Omega \end{cases}$$

It can be shown that the unique equilibrium θ_α concentrates at the local maximum points of m, as $\alpha \to +\infty$.



[Cantrell et. al. 2007] A species with large α can coexist with a species with $\alpha = 0$.