Some Recent Progress in Spatially Inhomogeneous Lotka-Volterra Competition-Diffusion Systems

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where $d > 0$, $u = u(x, t)$ and Ω: bounded smooth domain in $\mathbb{R}^N$;

$\Delta = \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$; $\partial_\nu = \frac{\partial}{\partial \nu}$, and ν is the unit outer normal on $\partial\Omega$.

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Fact: The unique steady state (s.s.) $u \equiv a$ is globally asymptotically stable.

Heterogeneous Environment

In a heterogeneous environment $m(x) \geq 0$, *nonconstant*

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

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Fact: For every $d > 0$, there exists unique positive s.s. denoted by θ_d. Moreover, θ_d is globally asymptotically stable.

- Observe that [Lou, 2006]

$$0 = d \int_\Omega \frac{|\nabla \theta_d|^2}{\theta_d^2} + \int_\Omega m - \int_\Omega \theta_d$$

$$\Rightarrow \int_\Omega \theta_d > \int_\Omega m(x) \qquad \forall d > 0, \text{ since } \theta_d \not\equiv const.$$

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Moreover, $\int_\Omega \theta_d \to \int_\Omega m(x)$ as $d \to 0$ or ∞, since

$$\theta_d \to \begin{cases} m & \text{as } d \to 0, \\ \overline{m} := \frac{1}{|\Omega|}\int_\Omega m & \text{as } d \to \infty. \end{cases}$$

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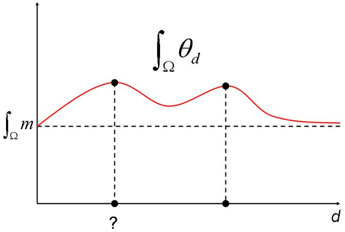

Lotka-Volterra Competition

Lotka-Volterra competition system (ODE):

$$\begin{cases} U_t = U(a_1 - b_1 U - c_1 V) & \text{in } (0, T), \\ V_t = V(a_2 - b_2 U - c_2 V) & \text{in } (0, T). \end{cases}$$

- a_i: carrying capacity / intrinsic growth rate;
- b_1, c_2: intra-specific competition;
- b_2, c_1: inter-specific competition

  are all positive constants.

Slower diffuser always prevails!

Consider the following Lotka-Volterra system

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - V) & \text{in } \Omega \times (0, T) \\ V_t = d_2 \Delta V + V(m(x) - U - V) & \text{in } \Omega \times (0, T) \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0, T) \\ U(x, 0) = U_0(x) \geq 0,\, V(x, 0) = V_0(x) \geq 0 & \text{in } \Omega. \end{cases}$$

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- If $d_1 < d_2$, then $(U, V) \to (\theta_{d_1}, 0)$ as $t \to \infty$ regardless of U_0, V_0. (as long as $U_0 \not\equiv 0$, $V_0 \not\equiv 0$) [Dockery, Hutson, Mischaikow and Pernarowski (1998)]

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- ”Slower diffuser always prevails!”
- ”Degenerate” case: $d_1 = d_2$.

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Theorem (DHMP)

If $d_1 < d_2$, then $(\theta_{d_1}, 0)$ is globally asymp. stable, while $(0, \theta_{d_2})$ is unstable.

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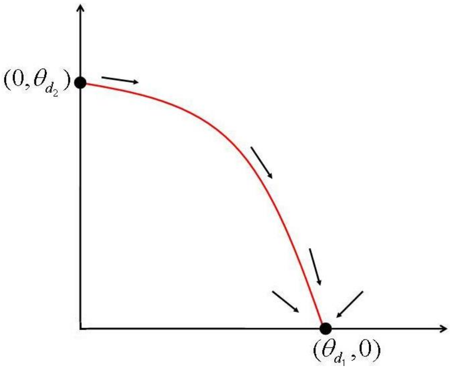

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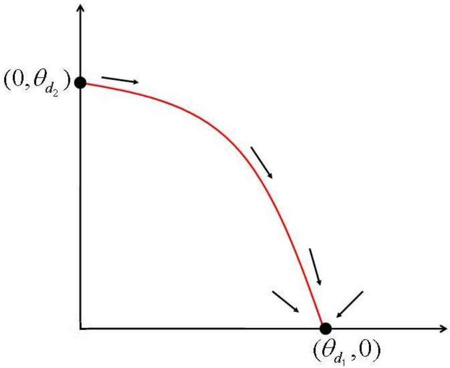

- *Open Problem:* If there are 3 or more competing species involved, it is **NOT KNOWN** if the slowest diffuser would prevail.

Slower diffuser always prevails!

The proof consists of two steps:

- (i) $(\theta_{d_1}, 0)$ is asymp. stable and $(0, \theta_{d_2})$ is unstable.
  (ii) There is no other nonnegative s.s. than (0,0).

  (This step works for general *n* species.)

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  (This step works for general n species.)
- To conclude from theory of *monotone* flow that $(\theta_{d_1}, 0)$ is *globally asymp. stable*. (Existence of connecting orbit.)

  [This requires $n = 2$ (2 species, 2×2 system)]

Homogeneous Environment - Constant Coefficients

Lotka-Volterra competition-diffusion system in homogeneous environment:

$$\begin{cases} U_t = d_1 \Delta U + U(a_1 - b_1 U - c_1 V) & \text{in } \Omega \times (0, T) \\ V_t = d_2 \Delta V + V(a_2 - b_2 U - c_2 V) & \text{in } \Omega \times (0, T) \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0, T) \end{cases}$$

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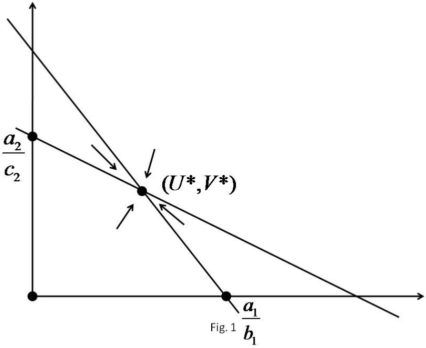

Fig. 1

Homogeneous Environment - Constant Coefficients

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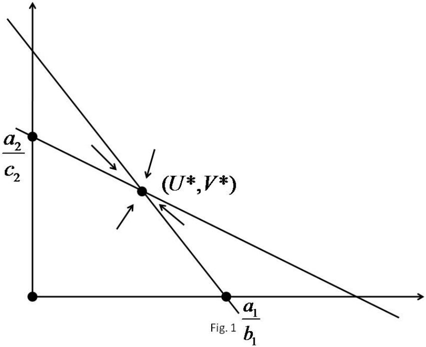

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Four constant steady states: $(0,0), (\frac{a_1}{b_1}, 0), (0, \frac{a_2}{c_2})$, and $(U^*, V^*) = (\frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{b_1 a_2 - b_2 a_1}{b_1 c_2 - b_2 c_1})$

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Proof.

Lyapunov functional [S.-B. Hsu (1977)]

$$E(U,V)(t) =$$
$$\int_\Omega \left[b_2 \left(U - U^* - U^* \log \frac{U}{U^*} \right) + c_1 \left(V - V^* - V^* \log \frac{V}{V^*} \right) \right] dx$$

Then $\frac{d}{dt} E(U,V)(t) \leq 0 \ \forall t \geq 0$ and " $=$ " holds only when $U = U^*, V = V^*$. □

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Consider $0 < b, c < 1$ (weak competition)

$$(1) \quad \begin{cases} d_1 \Delta U + U(m(x) - U - cV) = 0 & \text{in } \Omega \\ d_2 \Delta V + V(m(x) - bU - V) = 0 & \text{in } \Omega \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \end{cases}$$

Theorem (Lou (2006))

There exists $b_* < 1$ such that for all $b > b_*$, there exists $c^* \leq 1$ small such that if $c < c^*$, $(\theta_{d_1}, 0)$ is globally asymp. stable for some $d_1 < d_2$.

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Here

$$b_* = \inf_{d>0} \int_\Omega m \Big/ \int_\Omega \theta_d$$

In particular, for some $0 < b, c < 1$ and d_1, d_2, U will wipe out V, and coexistence is no longer possible even when the competition is weak!

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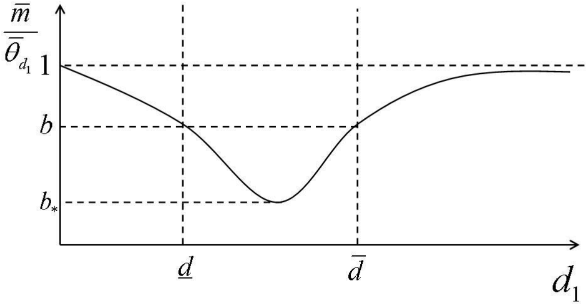

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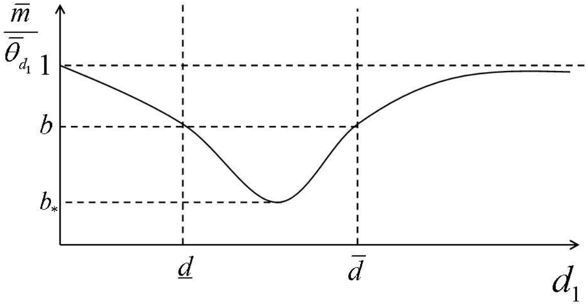

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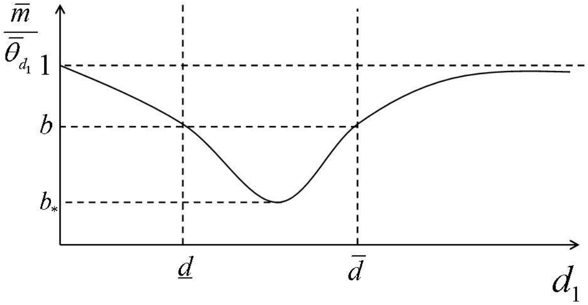

- $b > b_*$, c small, for above $d_1, d_2 \Rightarrow$ no co-existence
- $(0, \theta_{d_2})$ unstable if $d_1 < d_2$ (independent of b, c)

Recent Progress [Lam and Ni]

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(I) *For any* ϵ, $\exists \delta(\epsilon) > 0$ *s.t. for* $1 - \delta < b < 1$, $0 \leq c \leq 1$, $\epsilon < d_1 < 1/\epsilon$ *and* $d_2 \geq d_1 + \epsilon$, $(\theta_{d_1}, 0)$ *is globally asymp. stable.*

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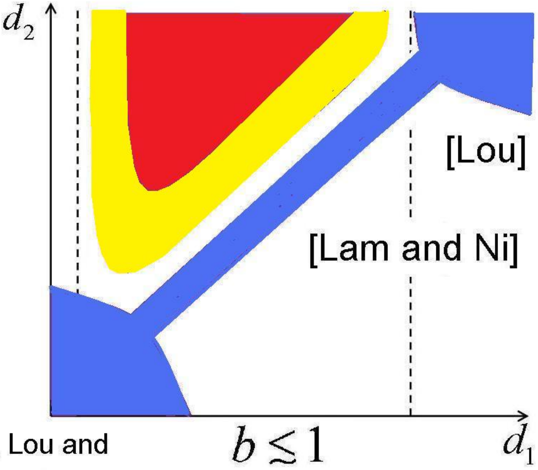
(II) *For* $0 < b, c < 1$, $\exists \epsilon > 0$ s.t. *if* $|d_1 - d_2| < \epsilon$ *then* $\exists$ *unique positive s.s.* $(\tilde{U}, \tilde{V})$. *Moreover,* $(\tilde{U}, \tilde{V})$ *is globally asymp. stable; and if* $d_1, d_2 \to d > 0$, *then*

$$(\tilde{U}, \tilde{V}) \to \frac{1}{1 - bc} \begin{pmatrix} 1 - c \\ 1 - b \end{pmatrix} \theta_d.$$

Globally Stable Coexistence S.S.

The region shaded blue represent the (d_1, d_2) for which there exists a unique coexistence s.s. which is globally asymp. stable.)



[Hutson, Lou and Mischaikow]

Discussions: Fitness in terms of Diffusion Rate

Return to the single species

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- We define the ”total fitness” of the unique s.s. θ_d as follows:

$$F(d) = \int_\Omega |\theta_d - m|$$

Conjecture: F(d) is *monotonically increasing* in $d > 0$.

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  Conjecture: F(d) is *monotonically increasing* in $d > 0$.

- Recall that $b_* = \inf_{d>0} \overline{m}/\overline{\theta_d}$.

  Question: Is b_* bounded below by a positive constant indep of m?

Discussions: Slower diffuser always prevails?

Consider a special case

$$(2) \quad \begin{cases} U_t = d_1 \Delta U + U(m(x) - U - bV) & \text{in } \Omega \times (0,T) \\ V_t = d_2 \Delta V + V(m(x) - bU - V) & \text{in } \Omega \times (0,T) \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0,T) \\ U(x,0) = U_0(x) \geq 0, V(x,0) = V_0(x) \geq 0 & \text{in } \Omega \end{cases}$$

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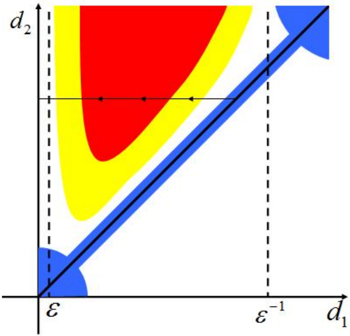

Directed movements

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Strategies?

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- $\nabla \cdot$ - divergence operator, ∇ - gradient operator.
- U is assumed to be "smarter" while V still disperses randomly.
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- No-flux boundary conditions imposed.
- How will U and V compete?

Advection-Mediated Coexistence

- When $d_1 < d_2$, the "slower diffuser" U always wipes out V while it is **not much** smarter than V (when $\alpha > 0$ is small) [Cantrell, Cosner and Lou (2006)].

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Theorem ([Cantrell, Cosner and Lou, (2007)])

Assume

(a) $\{$*critical points of* $m\}$ *has measure 0;*

(b) $\exists x_0 \in \overline{\Omega}$ *s.t.* $m(x_0) = \max_{\overline{\Omega}} m$ *is a strict local max.*

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- Shape of (U_α, V_α)?

A Conjecture

In [Cantrell, Cosner and Lou (2007)], it is shown that whenever the set of critical points of m is of measure zero, then $\forall$ s.s. (U_α, V_α) of (3),

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Conjecture ([Cantrell, Cosner and Lou (2007)])

(3) *has a unique coexistence s.s.* (U_α, V_α) *which is globally asymp. stable, and, as* $\alpha \to \infty$, U_α *concentrates at all local maximum points of* $m(x)$ *in* $\overline{\Omega}$.

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For general m, the profile of U_α in the Conjecture has been determined in the case $N = 1$.

$\Omega = (-1, 1)$, $\Sigma = \{$all *positive* local maximum points of m in $\overline{\Omega}\}$

Theorem ([Lam and Ni (2010)])

Suppose $\Sigma \subseteq (-1, 1)$ *with* $xm'(x) \leq 0$ *at* $x = \pm 1$*, and that all critical points of m are non-degenerate. Let* (U_α, V_α) *be a positive s.s. of* (3)*.*

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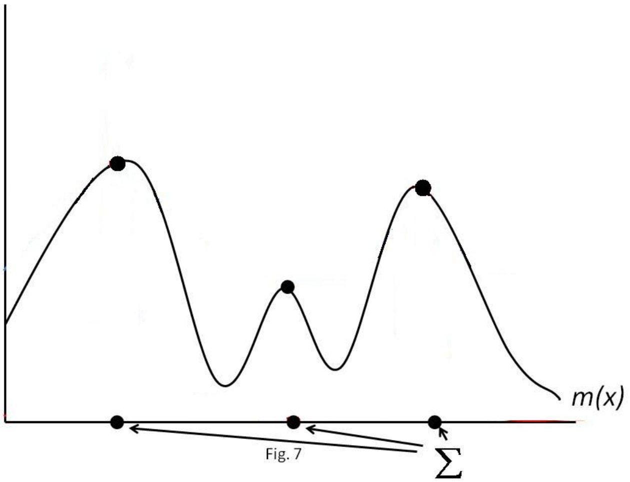
It turns out that the Conjecture needs to be modified slightly.

Directed movements



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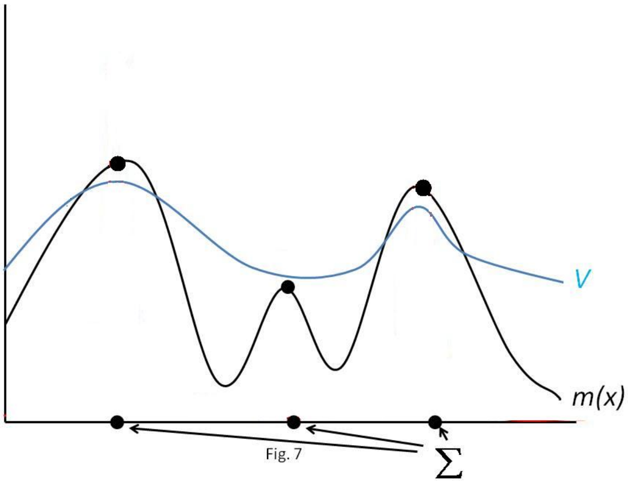

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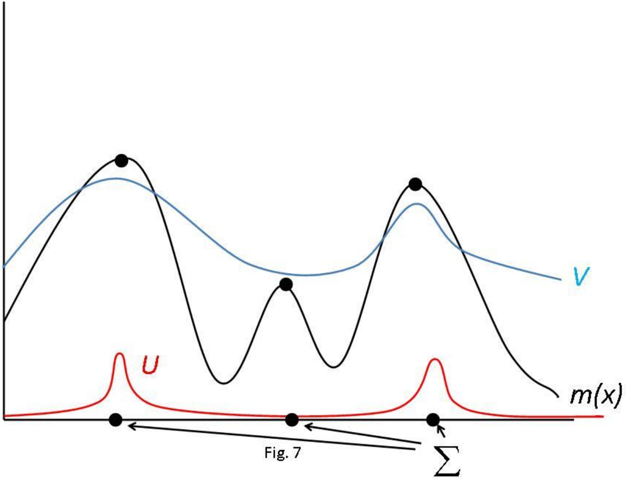

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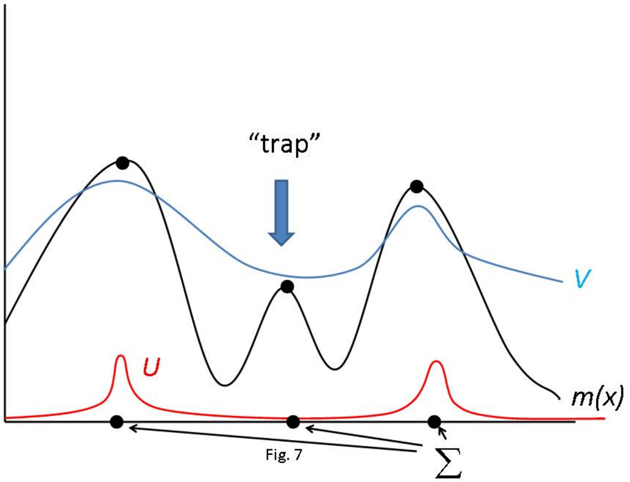

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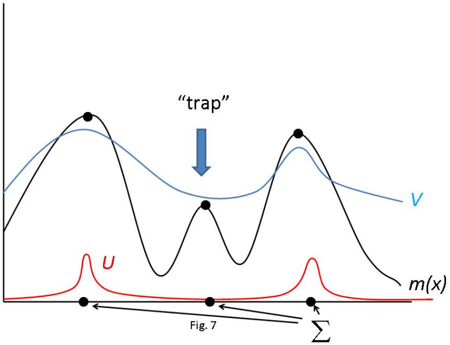

- *U* will **NOT** survive at those local max. pts. of *m* where $m \leq \theta_{d_2}$!
- i.e. local max pts. of *m* could be *traps* for *U* if *m* is less than or equal to θ_{d_2} there!

Higher dimensional case

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- L^{∞} estimate on U_{α} independent of α.
- A Liouville-type theorem concerning the limiting problem near local max of m.

A Liouville-type theorem

Theorem (Lam)

Let B be a symmetric positive-definite $N \times N$ matrix and $0 < \sigma \in L^{\infty}_{loc}(\mathbb{R}^N)$ such that for some $R_0 > 0$,

$$\sigma^2 = e^{-y^T By} \quad \text{for all } y \in R^N \setminus B_{R_0}(0),$$

then every nonnegative weak solution w to

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- In our original problem, at each local maximum point x_0, rescale $x = x_0 + \sqrt{d_1/\alpha}\, y$ and $w = e^{\frac{\alpha}{d_1}[m(x_0) - m(x)]} U_\alpha$, the problem becomes

$$\nabla \cdot (e^{\frac{\alpha}{d_1}[m(x) - m(x_0)]} \nabla w) + U(m - U - V)\frac{d_1}{\alpha} = 0 \to \nabla \cdot (e^{\frac{1}{2} y^T D^2 m(x_0) y} \nabla w) = 0$$

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- No extra conditions on w is imposed except $w \in W^{1,2}_{loc}(\mathbb{R}^N)$
- In general, some kind of asymptotic behavior is needed for this kind of result to hold; e.g. it is proved in [Berestycki, Caffarelli and Nirenberg (1997)] that weak solution of (4) is a constant if $\int_{B_R} \sigma^2 w^2 \leq O(R^2)$.

Concluding Remarks

In fact, the following more general equation is considered

$$\begin{cases} U_t = \nabla \cdot [d_1 \nabla U - \alpha U \nabla p] + U(m - U - V) & \text{in } \Omega \times (0, T), \\ V_t = d_2 \Delta V + V(m - U - V) & \text{in } \Omega \times (0, T), \\ \partial_\nu U - \alpha U \partial_\nu p = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0, T). \end{cases}$$

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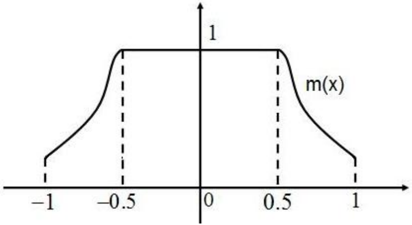

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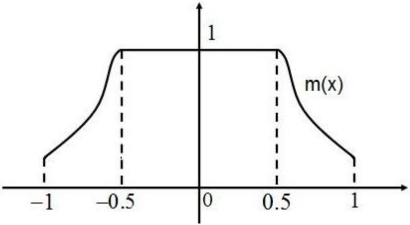

Example [Lam and Ni]: For α large, (3) has at least one stable positive s.s. (U_α, V_α). By passing to a subsequence if necessary, any (U_α, V_α) must converge to (U_0, V_0) which satisfies

$$\begin{cases} d_1 U'' + U(1 - U - V) = 0 & \text{in } (-\frac{1}{2}, \frac{1}{2}), \\ d_2 V'' + V(m(x) - U - V) = 0 & \text{in } (-1, 1), \\ U'(\pm\frac{1}{2}) = 0, V'(\pm 1) = 0. \end{cases}$$

Related results

- The dynamics of the following system has been studied in [Chen, Hambrock and Lou (2009)](m has single interior peak) and [Bezuglyy and Lou (2009)](m has multi-peaks case).

$$\begin{cases} U_t = \nabla \cdot (d_1 \nabla U - \alpha U \nabla m) + (m - U - V)U & \text{in } \Omega \times (0, \infty), \\ V_t = \nabla \cdot (d_2 \nabla V - \beta V \nabla m) + (m - U - V)V & \text{in } \Omega \times (0, \infty), \\ d_1 \partial_\nu U - \alpha U \partial_\nu m = d_2 \partial_\nu V - \beta V \partial_\nu m = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

- In particular, it is proved in some cases that U actually goes extinct when V has a fixed large biased movement.
- Biologically: Selection is against excessive directed-movement.

Related results

- In [Cantrell, Cosner and Lou (2009)], a single equation of u incorporating biased movement and population pressure (or self-diffusion) is considered.

$$\begin{cases} u_t = \nabla \cdot [d\nabla u - \alpha u \nabla(m-u)] + u(m-u) & \text{in } \Omega \times (0,T), \\ d_1 \partial_\nu u - \alpha u \partial_\nu (m-u) = 0 & \text{on } \partial\Omega \times (0,T). \end{cases}$$

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- The dispersal term can also be written as $\Delta(d_1 u + \alpha u^2/2) - \alpha u \nabla m$, representing a nonlinear form of diffusion which avoids crowding.
- It is proved that the unique s.s. approaches m^+ as $\alpha \to \infty$.

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What is the best strategy for survival/competition?

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- Cross-diffusion?– Yaping Wu and her group, Yotsutani and his group