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

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Homogeneous Environment - Constant Coefficients

Logistic equation (ODE)

\[ u_t = u(a - u) \]

where \( a > 0 \) constant: carrying capacity.

With spatial variables (PDE)

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\begin{align*}
u_t &= d \Delta u + u(a - u) \\
\text{in } &\Omega \times (0, T), \\
\partial_\nu u &= 0 \text{ on } \partial \Omega \times (0, T),
\end{align*}
\]

where \( d > 0 \), \( u = u(x, t) \) and \( \Omega \): bounded smooth domain in \( \mathbb{R}^N \);
\( \Delta = \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2} \); \( \partial_\nu \) is the unit outer normal on \( \partial \Omega \).

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

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

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\end{cases}
\]

Fact: For every $d > 0$, there exists unique positive s.s. denoted by $\theta_d$. Moreover, $\theta_d$ is globally asymptotically stable. Observe that [Lou, 2006] $\int_{\Omega} |\nabla \theta_d|^2 \theta_d^2 d\Omega + \int_{\Omega} m(x) \geq \int_{\Omega} \theta_d^2 d\Omega$ for all $d > 0$, since $\theta_d \neq \text{const}$. 

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\]

**Fact:** For every \( d > 0 \), there exists unique positive s.s. denoted by \( \theta_d \). Moreover, \( \theta_d \) is globally asymptotically stable.

- Observe that [Lou, 2006]

\[
0 = d \int_\Omega \left| \frac{\nabla \theta_d}{\theta_d^2} \right|^2 + \int_\Omega m - \int_\Omega \theta_d \\
\Rightarrow \int_\Omega \theta_d > \int_\Omega m(x) \quad \forall d > 0, \text{ since } \theta_d \neq \text{const}.
\]
i.e. the total population is always greater than the total carrying capacity!
i.e. the total population is **always** greater than the total carrying capacity!

Moreover, \( \int_{\Omega} \theta_d \to \int_{\Omega} m(x) \) as \( d \to 0 \) or \( \infty \), since

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

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\]

**Open:** What is the value \( \max_{d > 0} \int_{\Omega} \theta_d \)?
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**Open:** What is the value
\( \max_{d > 0} \int_{\Omega} \theta_d \)? Where is \( \max_{d > 0} \int_{\Omega} \theta_d \) assumed?
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\textbf{Open:} What is the value \( \max_{d>0} \int_{\Omega} \theta_d \)? Where is \( \max_{d>0} \int_{\Omega} \theta_d \) assumed?
Lotka-Volterra Competition

Lotka-Volterra competition system (ODE):

\[
\begin{align*}
U_t &= U(a_1 - b_1 U - c_1 V) \quad \text{in } (0, T), \\
V_t &= V(a_2 - b_2 U - c_2 V) \quad \text{in } (0, T).
\end{align*}
\]

- \(a_i\): 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!

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\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{align*}
\]

If \(d_1 < d_2\), then \((U, V) \to (\theta d_1, 0)\) as \(t \to \infty\) regardless of \(U_0, V_0\).

"Degenerate" case: \(d_1 = d_2\).

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Theorem (DHMP)

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

(ii) There is no other nonnegative stationary solution than \((0,0)\).

(This step works for general \(n\) species.)
Slower diffuser always prevails!

The proof consists of two steps:

(i) $(\theta_{d_1}, 0)$ is asympt. 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.)

To conclude from theory of monotone flow that $(\theta_{d_1}, 0)$ is globally asympt. stable. (Existence of connecting orbit.)

[This requires $n = 2$ (2 species, $2 \times 2$ system)]
Lotka-Volterra competition-diffusion system in homogeneous environment:

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\begin{cases}
U_t = d_1 \Delta U + U(a_1 - b_1 U - c_1 V) & \text{in } \Omega \times (0, T) \\
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- **Weak competition:**
Lotka-Volterra competition-diffusion system in homogeneous environment:

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- \(a_i\): intrinsic growth rate;
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- **Weak competition**: \(\frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2}\).
Homogeneous Environment - Constant Coefficients

Weak competition: \( \frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2} \).
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Weak competition: \( \frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2} \).

Four constant steady states: \((0, 0)\), \((\frac{a_1}{b_1}, 0)\), \((0, \frac{a_2}{c_2})\), and \((U^*, V^*) = \left( \frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{b_1 a_2 - b_2 a_1}{b_1 c_2 - b_2 c_1} \right)\).
(\(U^*, V^*\)) is **globally asymptotically stable** in \([U > 0, V > 0]\). (No nontrivial co-existence steady states.)
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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 \(U = U^*, V = V^*\).
Heterogeneous Environment

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

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

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 $d_1 < d_2$. 

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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(1)

**Theorem (Lou (2006))**

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

Here

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

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!
\[ b < b_\ast \Rightarrow (\theta d_1, 0) \text{ unstable (regardless of } d_1, d_2, c) \]
\begin{itemize}
  \item $b < b_* \Rightarrow (\theta_{d_1}, 0)$ unstable (regardless of $d_1, d_2, c$)
  \item $b > b_* \Rightarrow (\theta_{d_1}, 0)$ stable for $d_1 \in (d, \bar{d})$ and $d_2 > 1/\lambda(m - b\theta_{d_1})$
\end{itemize}
\( b < b_* \Rightarrow (\theta d_1, 0) \) unstable (regardless of \( d_1, d_2, c \))

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• $b > b_*, c$ small, for above $d_1, d_2 \Rightarrow$ no co-existence
\( b < b_* \Rightarrow (\theta d_1, 0) \) unstable (regardless of \( d_1, d_2, c \))

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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 \( b, c \))
Consider

\[
\begin{align*}
    d_1 \Delta U + U(m(x) - U - cV) &= 0 \quad \text{in } \Omega \\
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\end{align*}
\]

(1)

Remark: Interesting that \(c\) could be bigger than \(b\) in (I).

(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 \((\tilde{U}, \tilde{V}) \to \frac{1}{1 - bc(1 - c - b)} \theta d\).
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\[
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\]

(I) For any \( \epsilon \), \( \exists \delta(\epsilon) > 0 \) 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 asymptotically stable.
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Recent Progress [Lam and Ni]

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\[
(\tilde{U}, \tilde{V}) \to \frac{1}{1 - bc} \left( \frac{1 - c}{1 - b} \right) \theta_d.
\]
Globally Stable Coexistence S.S.
The region shaded blue represents the $\left( d_1, d_2 \right)$ for which there exists a unique coexistence s.s. which is globally asymptotically stable.

[Diagram showing regions labeled as [Lou], [Lam and Ni], and [Hutson, Lou and Mischaikow] with the condition $b \leq 1$.]
Discussions: Fitness in terms of Diffusion Rate

Return to the single species

\[
\begin{cases}
    u_t = d \Delta u + u(m(x) - u) \quad \text{in } \Omega \times (0, T), \\
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\end{cases}
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We define the "total fitness" of the unique s.s. \( \theta_d \) as follows:

\[ F(d) = \int_{\Omega} |\theta_d - m| \]

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

Recall that \( b^* = \inf_{d > 0} \frac{m}{\theta_d} \).

Question: Is \( b^* \) bounded below by a positive constant independent of \( m \)?
Discussions: Fitness in terms of Diffusion Rate

Return to the single species

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Discussions: Slower diffuser always prevails?

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\begin{aligned}
U_t &= d_1 \Delta U + U(m(x) - U - bV) \quad \text{in } \Omega \times (0, T) \\
V_t &= d_2 \Delta V + V(m(x) - bU - V) \quad \text{in } \Omega \times (0, T) \\
\partial_\nu U &= \partial_\nu V = 0 \quad \text{on } \partial\Omega \times (0, T) \\
U(x, 0) &= U_0(x) \geq 0, \quad V(x, 0) = V_0(x) \geq 0 \quad \text{in } \Omega
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where \( b = 1 - \delta \) close to 1. [Lam-Ni] indicates, \( U \) does not seem to fare better as \( d_1 \) decreases from \( d_2 \) to 0.
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Directed movements

In reality, few species move completely randomly. It is plausible that diffusion combined with directed movement will help the species maximize its chances of survival.
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Strategies?
Directed movements

Consider the following Lotka-Volterra competition system proposed by [Cantrell, Cosner and Lou (2006)] based on an earlier single equation model of [Belgacem and Cosner (1995)].

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\begin{align*}
U_t &= \nabla \cdot (d_1 \nabla U - \alpha U \nabla m) + U(m(x) - U - V) \quad \text{in } \Omega \times (0, T) \\
V_t &= d_2 \Delta V + V(m(x) - U - V) \quad \text{in } \Omega \times (0, T) \\
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where

\(\nabla\cdot\) divergence operator,

\(\nabla\) gradient operator.

\(U\) is assumed to be "smarter" while \(V\) still disperses randomly.

\(\alpha \geq 0\) measures the strength of "directed" movement of \(U\).

No-flux boundary conditions imposed.

How will \(U\) and \(V\) compete?
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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) $\{\text{critical points of } m\}$ has measure 0;
- (b) $\exists x_0 \in \Omega$ s.t. $m(x_0) = \max_{\Omega} m$ is a strict local max.

$\Rightarrow \forall d_1, d_2, (3)$ has a stable coexistence s.s. $(U_\alpha, V_\alpha)$, $U_\alpha > 0$, $V_\alpha > 0$ for every $\alpha$ large.

Shape of $(U_\alpha, V_\alpha)$?
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- Shape of \( (U_\alpha, V_\alpha) \)?
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. $(U_\alpha, V_\alpha)$ of (3),

$$U_\alpha \to 0 \text{ in } L^2 \text{ and } V_\alpha \to \theta_{d_2} \text{ in } C^{1+\beta} \text{ as } \alpha \to \infty.$$
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Conjecture ([Cantrell, Cosner and Lou (2007)])

(3) has a unique coexistence s.s. \((U_\alpha, V_\alpha)\) which is globally asymp. stable, and, as \( \alpha \to \infty \), \( U_\alpha \) concentrates at all local maximum points of \( m(x) \) in \( \bar{\Omega} \).
In [X. Chen and Lou (2008)], important progress on the conjecture was made when \( m \) has a unique non-degenerate global maximum point.

**Theorem (X. Chen and Lou (2008))**

Suppose that \( m \) has a unique critical point \( x_0 \) on \( \overline{\Omega} \) which is a non-degenerate global max point, \( x_0 \in \Omega \) and \( \partial_\nu m \leq 0 \) on \( \partial \Omega \). Then, as \( \alpha \to \infty \),
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(i) $V_\alpha \to \theta_{d_2}$ in $C^{1+\beta}(\overline{\Omega})$ and

(ii) $\|U_\alpha e^{\alpha \frac{\alpha}{2d_1} (x-x_0)^T D^2 m(x_0)(x-x_0) - 2^{N/2} [m(x_0) - \theta_{d_2}(x_0)]\|_{L^\infty(\Omega)} \to 0$. 

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(i) \( V_{\alpha} \to \theta_{d_2} \) in \( C^{1+\beta}(\bar{\Omega}) \) and

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- the integral constraint \( \int_\Omega U_\alpha(m - U_\alpha - V_\alpha) = 0. \)
For general $m$, the profile of $U_\alpha$ in the Conjecture has been determined in the case $\mathcal{N} = 1$.

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

**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 $(U_\alpha, V_\alpha)$ be a positive s.s. of (3). Then as $\alpha \to \infty$,
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(i) $V_\alpha \to \theta_{d_2}$ in $C^{1+\beta}(\bar{\Omega})$,

(ii) for any $x_0 \in \Sigma$ and any $r > 0$ small

$$\left\| U_\alpha - \max\{\sqrt{2}(m - \theta_{d_2})(x_0), 0\} e^{\frac{\alpha}{2\sigma_1} m''(x_0)(x-x_0)^2} \right\|_{L^\infty(B_r(x_0))} \to 0;$$

(iii) for any compact subset $K$ of $[-1, 1] \setminus \Sigma$, $U_\alpha \to 0$ in $K$ uniformly and exponentially.

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

Fig. 7

\[ m(x) \]
Directed movements
Directed movements

Fig. 7
Directed movements

"trap"

$m(x)$

$U$

$V$

Fig. 7

$\sum$
Directed movements

- \( U \) 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 \( \theta_{d_2} \) there!
Higher dimensional case

Recently, a new argument that works for higher dimensions is found. Recall $\Sigma = \{\text{positive local max. pts. of } m(x) \text{ in } \overline{\Omega}\}$
Higher dimensional case

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**Theorem ([Lam (2011b)])**

Assume $\Sigma \subseteq \Omega$ with $\partial_{\nu} m \leq 0$ on $\partial\Omega$, and that all critical points of $m$ are non-degenerate. Moreover, assume $\Delta m(x_0) > 0$ whenever $x_0$ is a saddle point of $m$. Let $(U_\alpha, V_\alpha)$ be a positive s.s. of (3).

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$$\left\| U_\alpha - \max\{2^{N/2}(m - \theta_{d_2})(x_0), 0\} e^{\frac{\alpha}{2d_1} (x - x_0)^T D^2 m(x_0)(x - x_0)} \right\|_{L^\infty(B_r(x_0))} \to 0;$$

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- $L^\infty$ estimate on $U_\alpha$ independent of $\alpha$. 
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The proof has two main ingredients.

- $L^\infty$ estimate on $U_\alpha$ independent of $\alpha$.
- 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 $0 < \sigma \in L_{\text{loc}}^\infty(\mathbb{R}^N)$ such that for some $R_0 > 0$,

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

then every nonnegative weak solution $w$ to

$$(4) \quad \nabla \cdot (\sigma^2 \nabla w) = 0 \text{ in } \mathbb{R}^N,$$

is a constant.
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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

$$\nabla \cdot (e^{\frac{\alpha}{d_1} [m(x) - m(x_0)]} \nabla w) + U(m - U - V) \frac{d_1}{\alpha} = 0 \rightarrow \nabla \cdot (e^{\frac{1}{2} y^T D^2 m(x_0) y} \nabla w) = 0.$$
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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 $R_0 > 0$,

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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

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

where \( p(x) = \chi(m(x)) \) for some increasing function \( \chi \).
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where \( p(x) = \chi(m(x)) \) for some increasing function \( \chi \).

- In particular, the different roles played by \( p \) and \( m \) are understood more clearly.
In fact, the following more general equation is considered

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- Roughly speaking, \( p \) is responsible for the shape of the concentrated peaks, while the values of \( m \) on \( \Sigma \) determines the height of those peaks.
Concluding Remarks

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- General \( m \)?
Dropping the Hypothesis on \( m \)

**Question:** What if we drop the assumption that \( \text{the set of critical points of } m \text{ is of measure } 0 \)?
Dropping the Hypothesis on $m$

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

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

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\begin{align*}
    u_t &= \nabla \cdot [d \nabla u - \alpha u \nabla (m - u)] + u(m - u) \quad \text{in } \Omega \times (0, T), \\
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- Apart from random diffusion, $u$ moves up the gradient of "fitness" $(m - u)$, and tends to match the carrying capacity $m(x)$ perfectly.
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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.
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representing a nonlinear form of diffusion which avoids crowding.

- It is proved that the unique s.s. approaches $m^+$ as $\alpha \to \infty$. 
Future directions

What is the best strategy for survival/competition?

\[ \begin{align*}
U_t &= \nabla \cdot \left( d_1 \nabla U - \alpha U \nabla F(x, U, V) \right) + UF(x, U, V) \quad \text{in} \quad \Omega \times (0, T) \\
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\end{align*} \]

with no-flux boundary conditions.

\( U \) tends to optimize the fitness/available resources.

Question: Will \( U \) wipe \( V \) out if \( \alpha \) is large?

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

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Question: Will \( U \) wipe out \( V \) if \( \alpha \) is large? Cross-diffusion? – Yaping Wu and her group, Yotsutani and his group

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