Swansea University
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1. Competition-diffusion models : co-existence and segregation

Elaine Crooks

Swansea

LMS Research School : PDEs in Mathematical Biology

ICMS, 29th April - 3rd May 2019

• Parabolic systems of form

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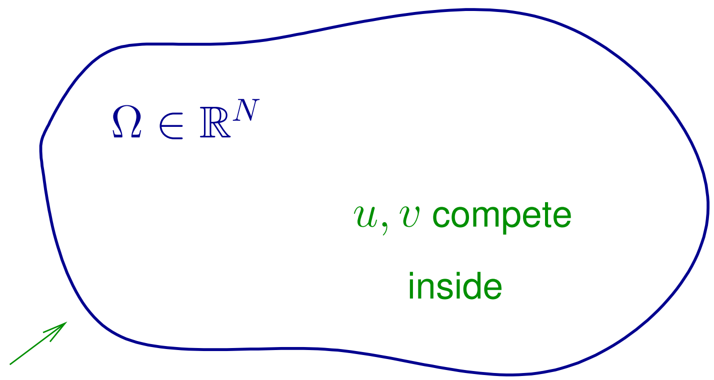
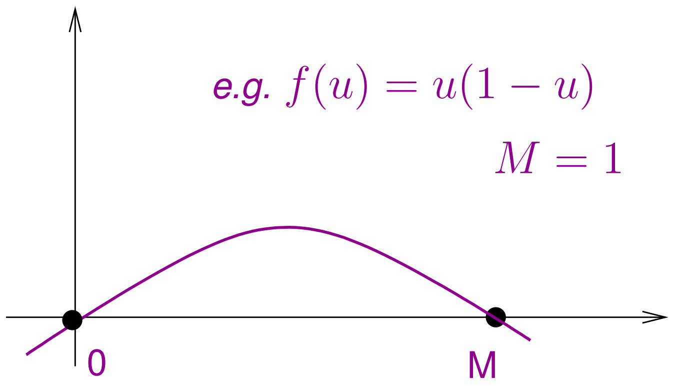
u_t &= d_1 \Delta u + f(u) - kuv, \quad x \in \Omega, \quad t \geq 0, \\
v_t &= d_2 \Delta v + g(v) - \alpha kuv, \quad x \in \Omega \quad t \geq 0
\end{aligned}
$$

model populations of densities u, v that compete in domain $\Omega \in \mathbb{R}^N$



+ boundary conditions

form of self-interaction functions f, g



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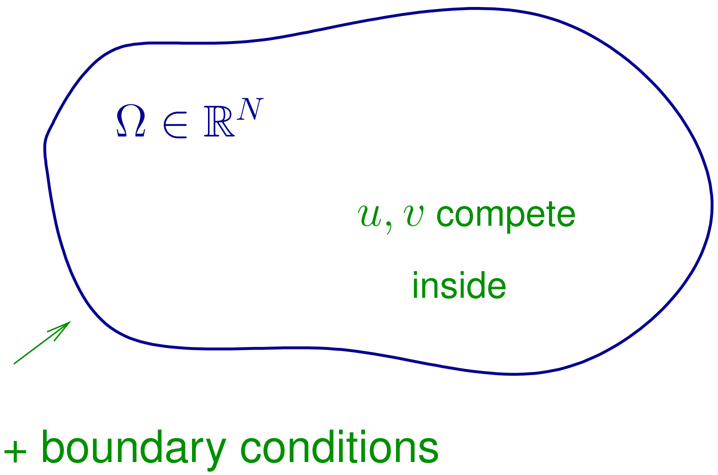

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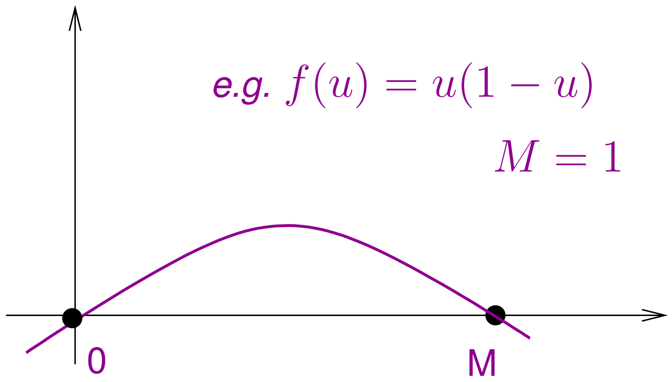

- called competition-diffusion systems or Gause-Lotka-Volterra systems
- arise in, *e.g.*, ecology, population genetics, chemical morphogenesis

- Elliptic systems of form

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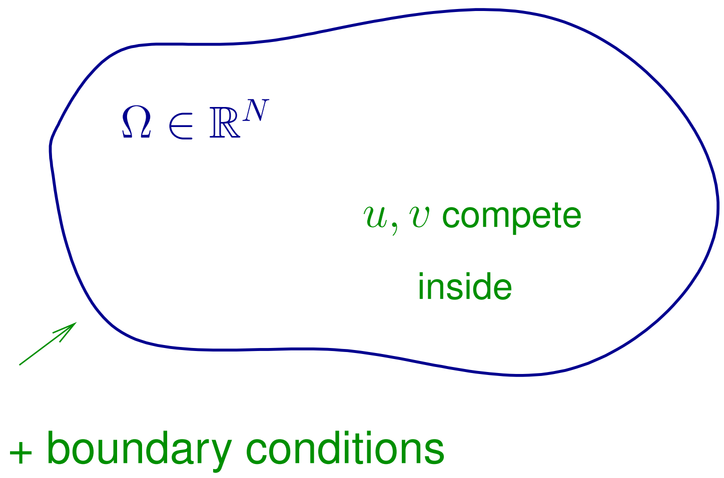

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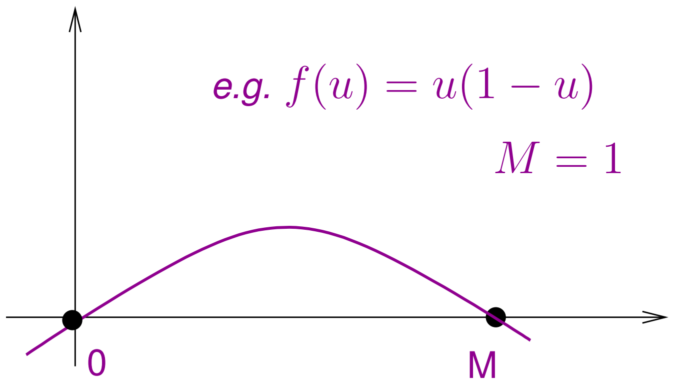

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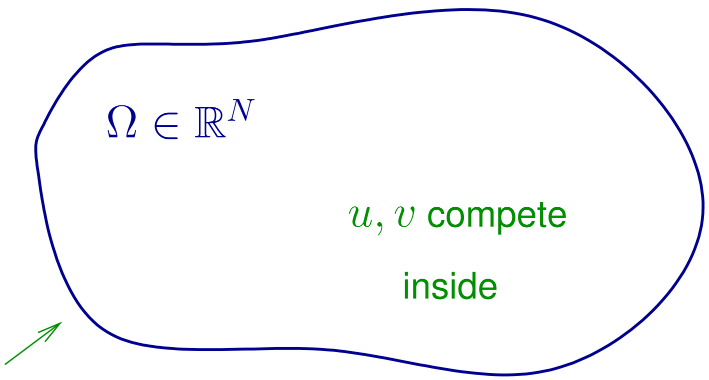

+ boundary conditions

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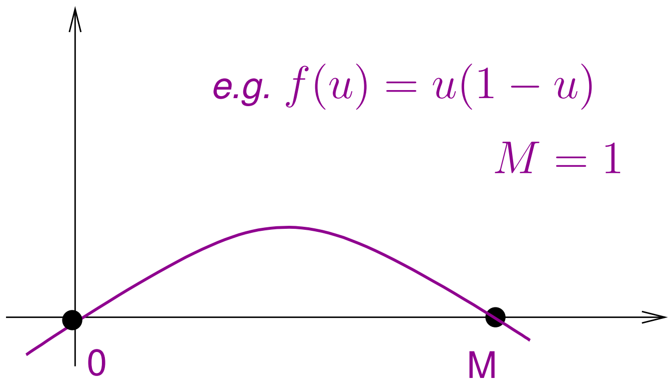

- densities non-negative $\Rightarrow u, v \geq 0$

• Elliptic systems of form

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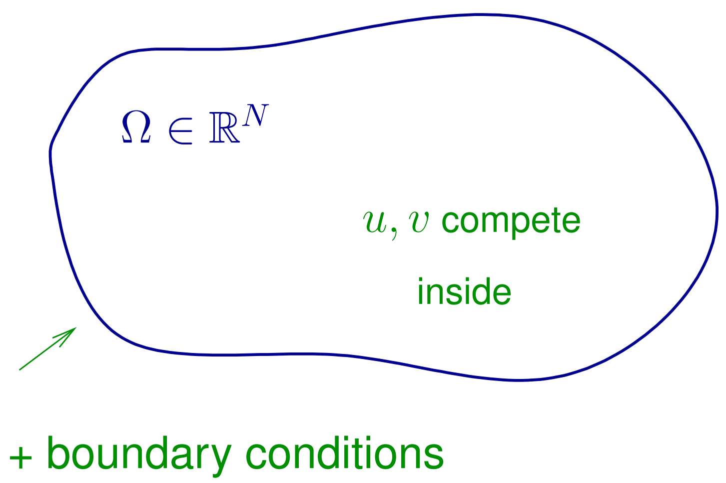

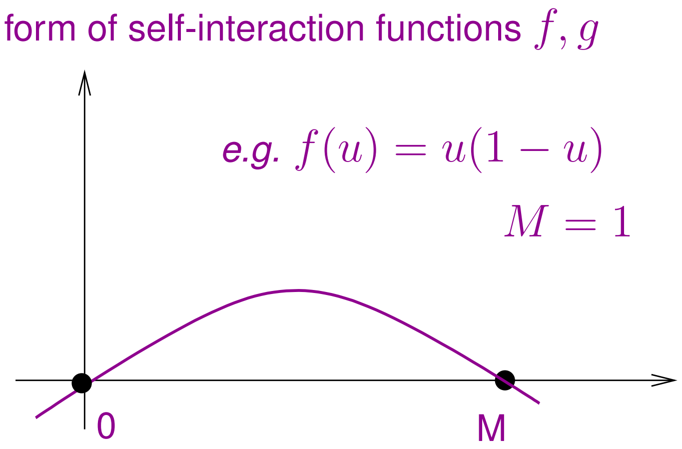

• densities non-negative $\Rightarrow u, v \geq 0$ • competition parameters k, $\alpha > 0$

- Boundary conditions and their ecological interpretation

- zero-flux boundary conditions

$$\frac{\partial u}{\partial \nu}(x,t) = \frac{\partial u}{\partial \nu}(x,t) = 0, \qquad x \in \partial\Omega,$$

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- inhomogeneous Dirchet boundary conditions

$$u(x,t) = m_1(x,t), \quad v(x,t) = m_2(x,t), \qquad x \in \partial\Omega,$$

for some given functions $m_1, m_2 \; \geq 0$ (determined by u, v outside Ω)

A few famous results for the system

$$u_t = d_1 \Delta u + u(r - au) - kuv,$$
$$v_t = d_2 \Delta v + v(s - bv) - \alpha kuv,$$

with zero-flux boundary conditions

$$\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega$$

1. Equilibria play a major rôle in characterising longtime behaviour

For ‘almost all’ initial conditions $u(x,0), v(x,0)$, the solution (u,v) to the initial value problem converges as $t \to \infty$ to the set of all equilibria

- *i.e.* the ω-limit set consists entirely of equilibria

(Hirsch, 1982;   Matano and Mimura, 1983)

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(Hirsch, 1982; Matano and Mimura, 1983)

- in fact, under various additional conditions, can show convergence of all non-negative solutions as $t \to \infty$ to a single equilibrium

e.g. Dancer and Zhang, 2002, assumptions include

k large + non-degeneracy conditions on equilibria of a limit problem

Key ingredient

Under the change of variables $w = 1 - v$, system becomes

$$\begin{aligned} u_t &= d_1 \Delta u + f(u) - ku(1-w) \\ w_t &= d_2 \Delta w - g(1-w) + \alpha ku(1-w) \end{aligned}$$

which is co-operative when $0 \le u, v \le 1$, since

$$\frac{\partial}{\partial w}(f(u) - ku(1-w)) \ge 0, \quad \frac{\partial}{\partial u}(-g(1-w) + \alpha ku(1-w)) \ge 0$$

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and hence is order-preserving

if $u, \hat{u} : \Omega \to \mathbb{R}^2$ are bounded and such that

$$u(x,0) \le \hat{u}(x,0) \text{ for all } x \in \Omega, \quad u(x,t) \le \hat{u}(x,t) \text{ if } x \in \partial\Omega,$$

and

$$u_t \le Au_{xx} + f(u), \quad \hat{u}_t \ge A\hat{u}_{xx} + f(\hat{u}) \quad \text{for all } (x,t) \in \Omega \times (0,\infty),$$

then

$$u(x,t) \le \hat{u}(x,t) \quad \text{for all } (x,t) \in \Omega \times [0,\infty)$$

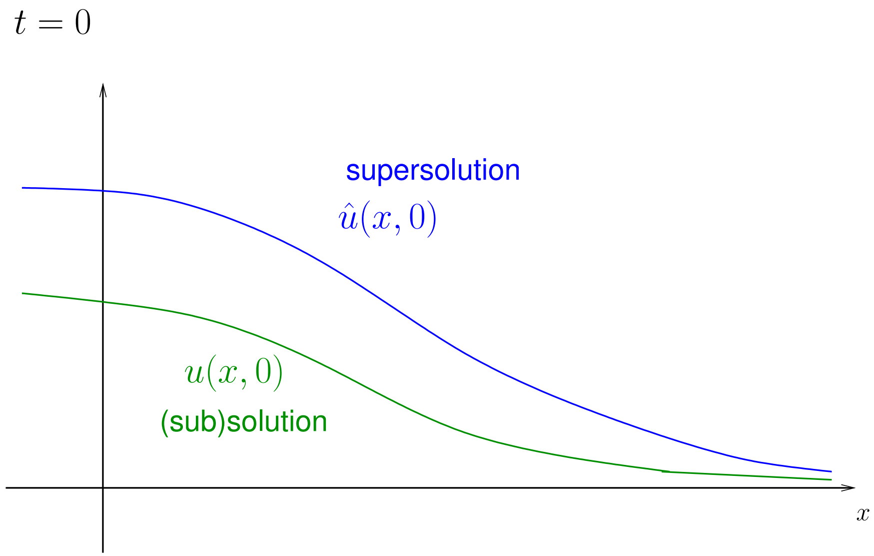
e.g. if $\hat{u}$ is a known/constructed function that satisfies $\hat{u}_t \geq A\hat{u}_{xx} + f(\hat{u})$ (called a supersolution) and u is a solution of $u_t = Au_{xx} + f(u)$ such that

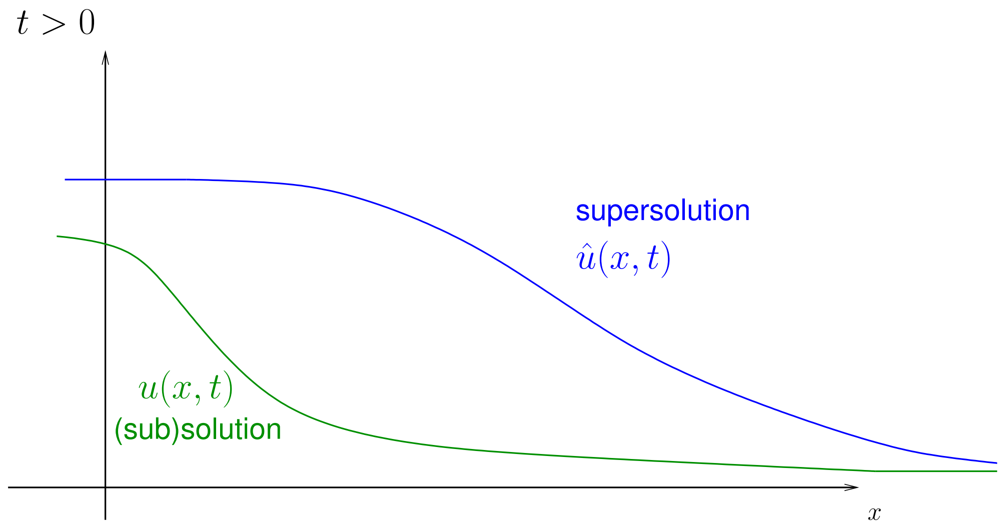
$$u(x,0) \leq \hat{u}(x,0), \; x \in \Omega, \quad \text{and} \quad u(x,t) \leq \hat{u}(x,t), \quad x \in \partial\Omega,$$

then

$$u(x,t) \leq \hat{u}(x,t)$$

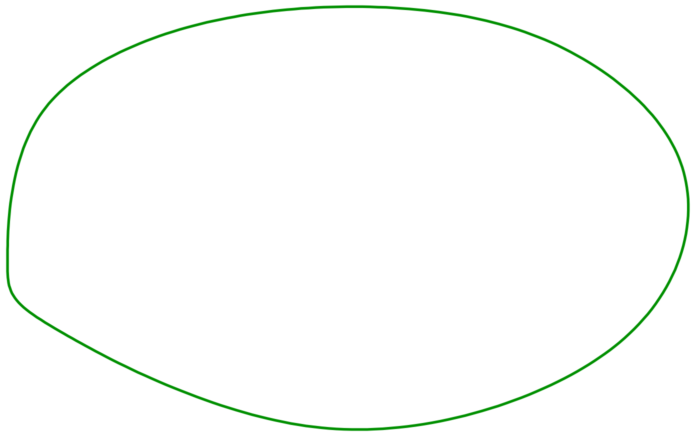
$\therefore$ known function $\hat{u}$ dominates/controls u at later times $t > 0$





2. Any spatially non-constant equilibrium is <u>unstable</u> if Ω is convex

(Kishimoto and Weinberger, 1985)



Ω convex

- builds on earlier results for one equation of Chafee, 1975 ($N = 1$) and Carsten and Holland, 1978, Matano, 1979 ($N > 1$)

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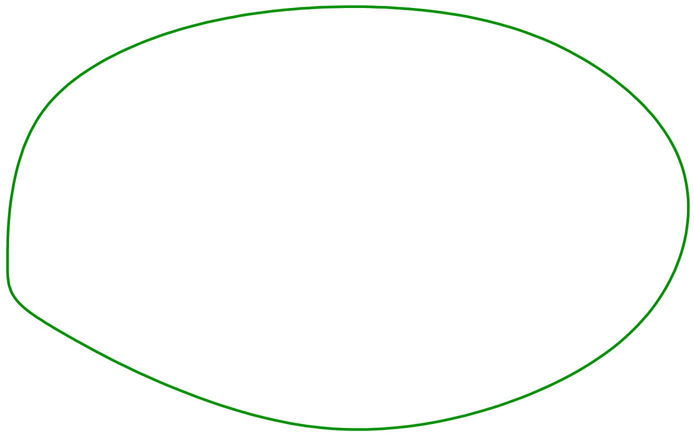


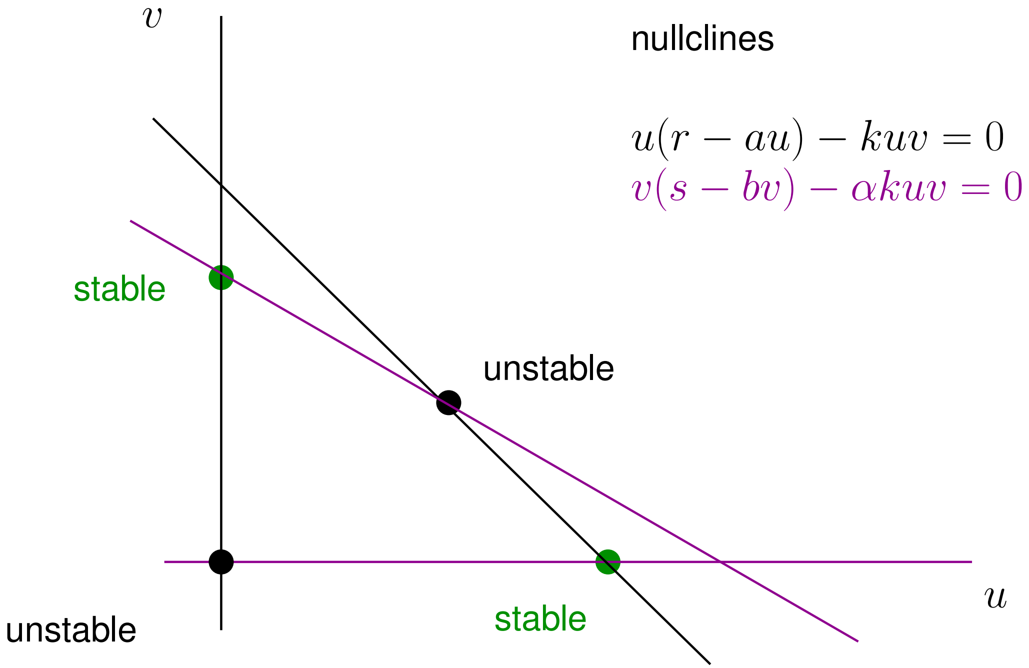
Ω convex

- builds on earlier results for one equation of Chafee, 1975 ($N = 1$) and Carsten and Holland, 1978, Matano, 1979 ($N > 1$)

$\therefore$ do not expect to see non-constant steady states in convex habitats

Special case: when k is large, there are two stable spatially constant equilibria, *i.e.*,

$$(u,v) = \left(\frac{r}{a},\ 0\right), \qquad (u,v) = \left(0,\ \frac{s}{b}\right)$$



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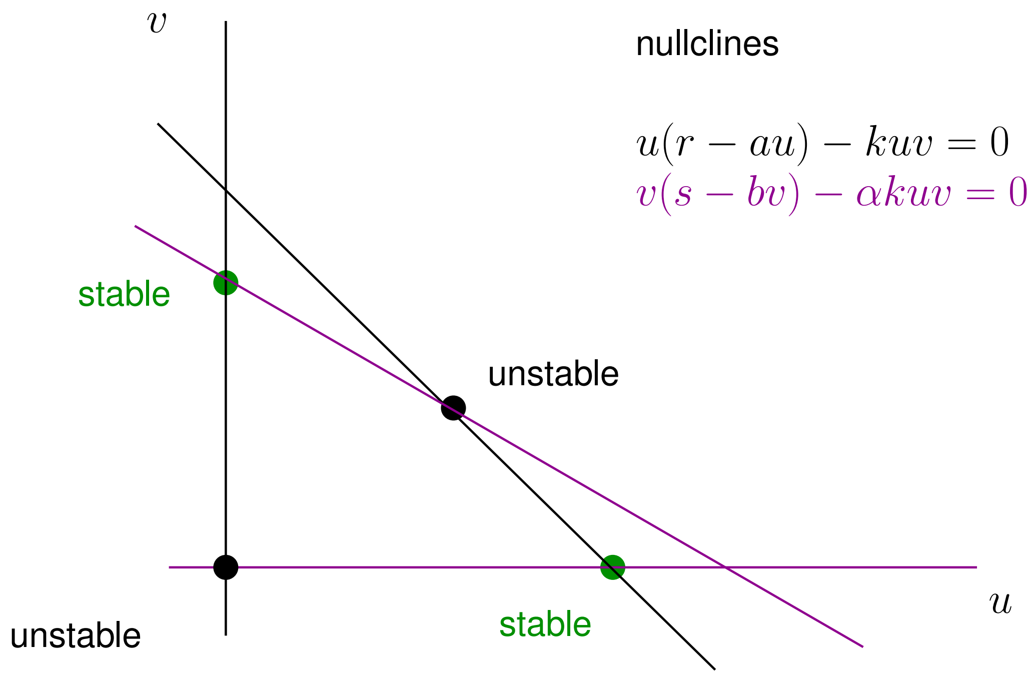

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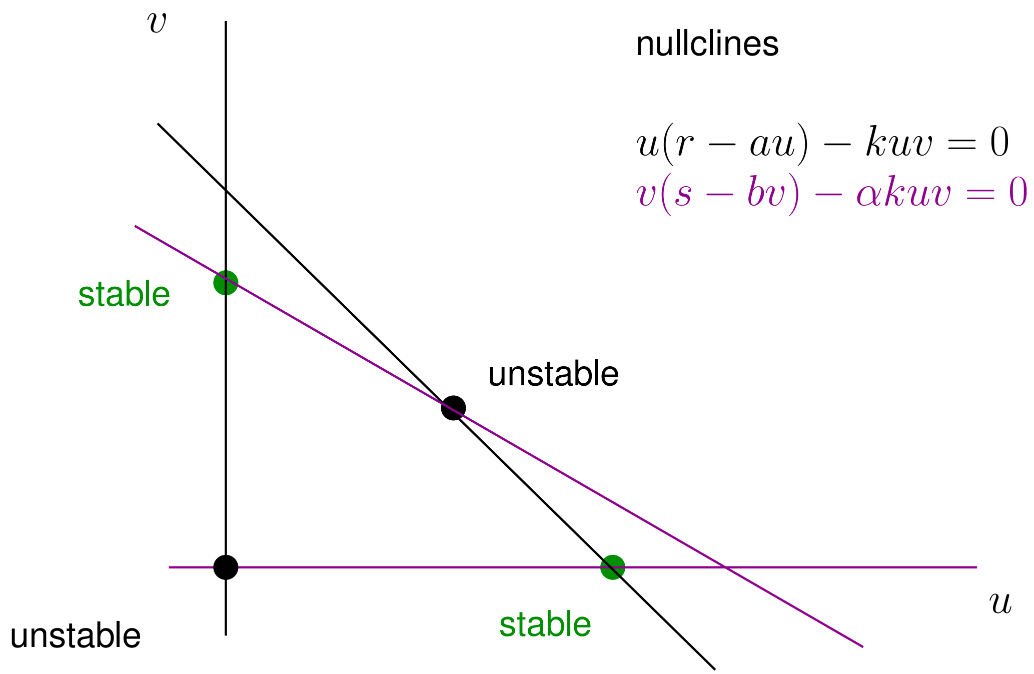

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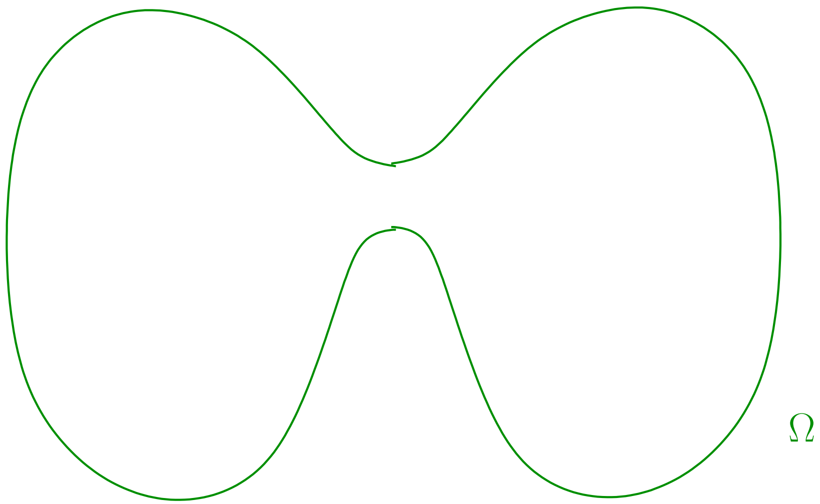
$\therefore$ u and v cannot co-exist in a convex habitat if they are strongly competing

3. Stable non-constant equilibria may exist if Ω is not convex

If Ω has a suitable 'dumb-bell' shape and k is large,



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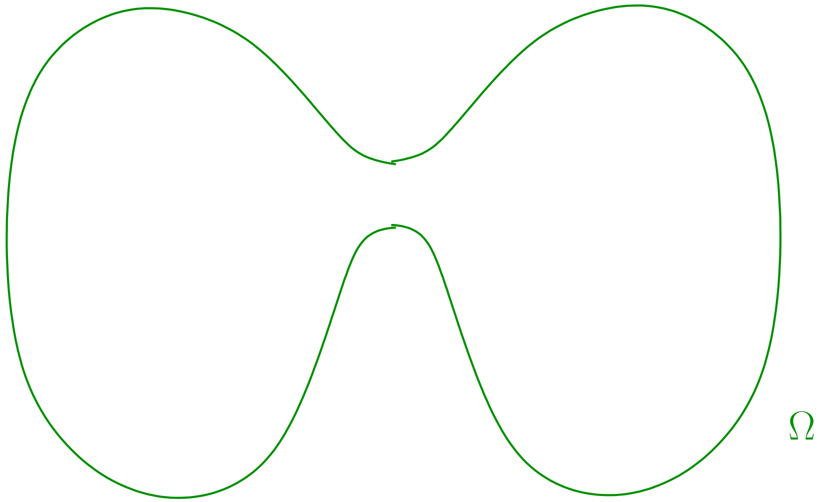


there exist stable non-constant equilibria where the components concentrate in separate parts of the domain

(Matano and Mimura, 1983)

$\therefore$ two strongly competing species may co-exist if the habitat is non-convex

• But the picture can change with different boundary conditions.....

e.g., with in-homogeneous Dirchlet conditions

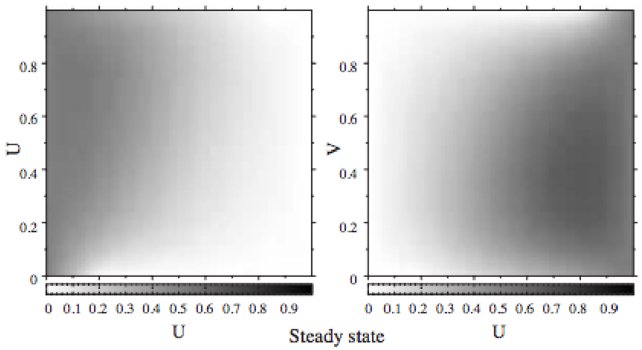
$$u(x,t) = m_1, \quad v(x,t) = m_2, \quad x \in \partial\Omega$$

where $m_1(x), m_2(x) \geq 0$ and $m_1 m_2 = 0$, and

$$\Omega = (0,1) \times (0,1) \qquad \text{(convex)}$$

numerical simulation gives

$k = 10^2$



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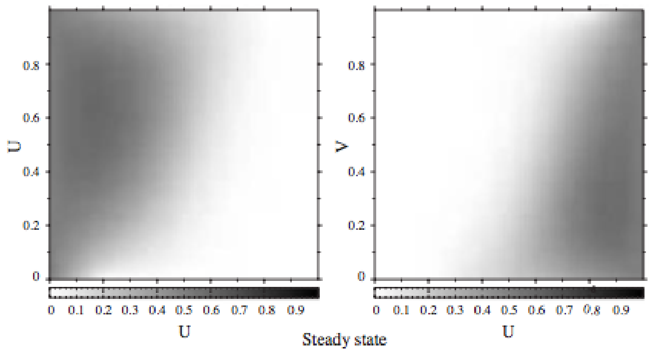

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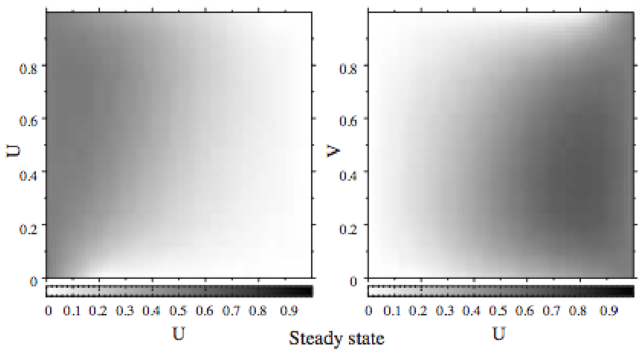

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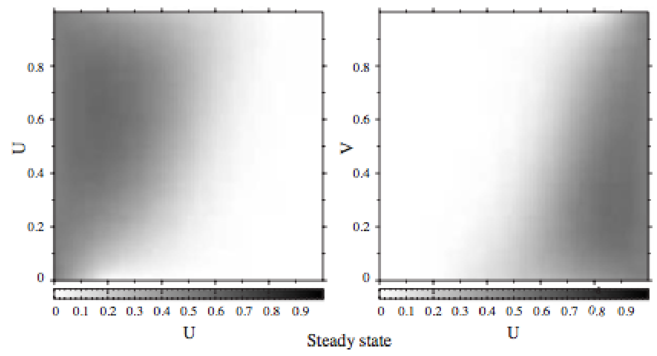

$\therefore$ shows co-existence of strongly competing species in a convex habitat,

in contrast to the zero-flux boundary condition case

(C., Dancer, Hilhorst, Mimura, Ninomiya, 2004; C., Dancer, Hilhorst 2007)

2. Competition-diffusion models : large interaction limits

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2. Competition-diffusion models : $k \to \infty$

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• Focus on elliptic systems

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\end{aligned}
$$

with homogeneous Dirichlet boundary conditions

$$
u(x) = v(x) = 0, \qquad x \in \partial\Omega
$$

• a simplifying rescaling : we have

$$\begin{aligned} 0 &= \Delta u + d_1^{-1} f(u) - k d_1^{-1} uv, && x \in \Omega, \\ 0 &= \Delta v + d_2^{-1} g(v) - \alpha k \alpha d_2^{-1} uv, && x \in \Omega \\ u(x) &= v(x) = 0, && x \in \partial\Omega \end{aligned}$$

so defining

$$\hat{u} := \alpha d_2^{-1} u, \qquad \hat{v} := d_1^{-1} v,$$

and

$$\hat{f}(\hat{u}) := \alpha d_1^{-1} d_2^{-1} f(\alpha^{-1} d_2 \hat{u}), \quad \hat{g} := d_1^{-1} d_2^{-1} g(d_1 \hat{v}),$$

gives

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gives

$$
(P_e^k) \qquad
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0 &= \Delta \hat{u} + \hat{f}(\hat{u}) - k\hat{u}\hat{v}, && x \in \Omega, \\
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\end{aligned}
$$

• note: this uses that (i) system is elliptic (ii) only two components

- Interest in the large-competition ($k \to \infty$) limit comes from

(i) the k-dependent system is difficult to analyse; for example, it is not in general the Euler-Lagrange equations of an energy functional, whereas the limit problem is a scalar equation

(ii) the $k \to \infty$ limit is linked to spatial segregation in population dynamics, or to chemical separation in fast chemical reactions

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- Related problem

$$\begin{aligned} \Delta u + f(u) - kuv^2 &= 0, \quad x \in \Omega, \\ \Delta v + g(v) - ku^2 v &= 0, \quad x \in \Omega \end{aligned}$$

- limit $k \to \infty$ linked to phase separation in Bose-Einstein condensates

- is variational, being the Euler-Lagrange equations of a functional of form

$$J(u,v) = \int_\Omega \frac{1}{2}(|\nabla u|^2 + |\nabla v|^2) - F(u) - G(v) + \frac{1}{2}ku^2v^2 \, dx$$

(references: Conti, Terracini, Verzini; Squassina; Dancer, Wang and Zhang...)

Large-competition limit $k \to \infty$ of solutions (u^k, v^k)

Seminal ref: Dancer and Du, Journal Diff. Eqs. 114 (1994) 434-475

- (u^k, v^k) converge to the positive and negative parts resp. of a limit function w satisfying the scalar equation

$$\begin{aligned} \Delta w + f(w^+) - g(-w^-) &= 0, \quad x \in \Omega, \\ w(x) &= 0, \quad x \in \partial\Omega \end{aligned}$$

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- Key ingredients:

(i) the linear combination $w^k := u^k - v^k$ satisfies

$$\Delta w^k + f(u^k) - g(v^k) = 0, \quad x \in \Omega$$

which does not depend explicitly on k $\Rightarrow$ good bounds for w^k independent of k

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(ii) u^k, v^k converge (in some sense) to limits u, v as $k \to \infty$, by compactness

(iii) u^k and v^k segregate , since $k\, u^k v^k$ bounded $\Rightarrow$ $u^k v^k \to 0$ as $k \to \infty$

and
$$\left.\begin{array}{l} uv = 0 \quad a.e. \\ u, v \geq 0 \\ w = u - v \end{array}\right\} \Rightarrow \begin{array}{l} u = w^+ \quad a.e. \\ v = -w^- \end{array}$$

- Note: there are two aspects to large-interaction limit problem

(i) to show that (u^k, v^k) converges as $k \to \infty$ to a solution of the limit problem

$$\begin{aligned} \Delta w + f(w^+) - g(-w^-) &= 0, \quad x \in \Omega, \\ w(x) &= 0, \quad x \in \partial\Omega \end{aligned}$$

(ii) conversely, to show that given a solution w of the limit problem, there exists a sequence of solutions of the k-dependent system (u^k, v^k) that converge to w as $k \to \infty$

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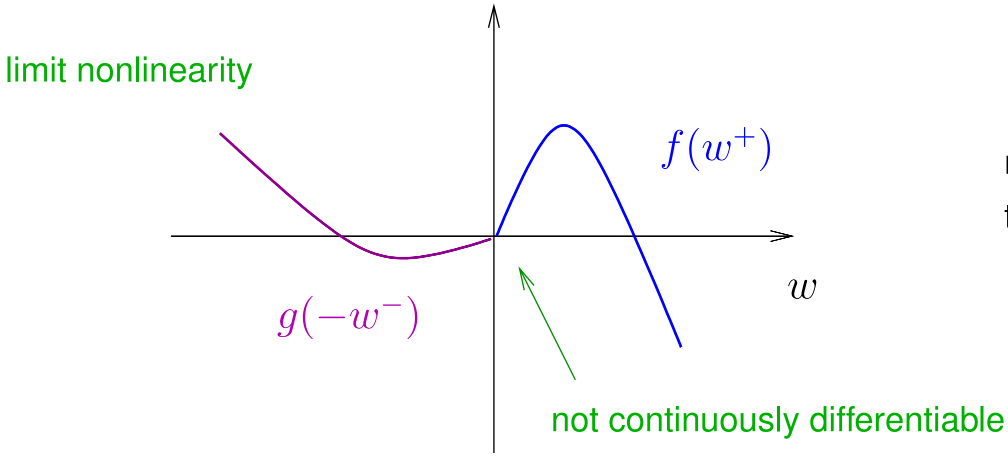

methods: *e.g.* degree theory in cones

- Note: there are two aspects to large-interaction limit problem

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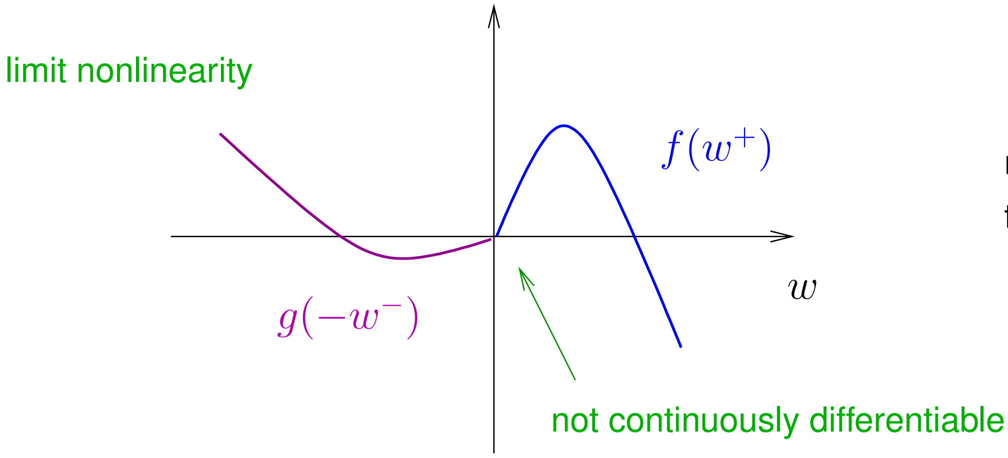

methods: *e.g.* degree theory in cones

Mainly focus on (i) here

Theorem Given a sequence of non-negative solutions (u^k, v^k) of k-dependent elliptic system (P_e^k), there exist subsequences $\{u^{k_n}\}$, $\{v^{k_n}\}$ and non-negative functions $u, v \in L^\infty(\Omega) \cap W_0^{1,2}(\Omega)$ such that

- $u^{k_n} \to u, \quad v^{k_n} \to v$ in $W_0^{1,2}(\Omega)$ as $k_n \to \infty$;
- $uv = 0 \;\; a.e.$ in Ω,

and the function $w := u - v$ is such that $w^+ = u$, $w^- = -v$, w is a weak solution of the equation

$$\begin{aligned} \Delta w + f(w^+) - g(-w^-) &= 0 \quad \text{in } \Omega, \\ w &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

in the sense that for all $\phi \in W_0^{1,2}(\Omega)$,

$$-\int_\Omega \nabla w \cdot \nabla \phi \, dx + \int_\Omega [f(w^+) - g(-w^-)]\phi \, dx = 0,$$

and satisfies

$$w \in W^{2,p}(\Omega) \cap C^{1,\eta}(\Omega)$$

for all $p \in [1, \infty)$ and $\eta \in (0, 1)$

Basic estimates on solutions (u^k, v^k) of (P_e^k)

(i) L^∞-bound:

$$0 \le u^k, v^k \le M \ \ \text{for all } x \in \Omega, k > 0$$

by maximum principle, since $f(u), g(v) < 0$ when $u, v > M$ and so if, say, u^k attains a maximum value $u^k(x_0) > M$, then

$$-\Delta u^k(x_0) \le f(u^k(x_0)) < 0,$$

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(ii) L^2-gradient bound: there exists $K_1 > 0$ such that

$$\int_\Omega |\nabla u^k(x)|^2 \, dx, \ \int_\Omega |\nabla v^k(x)|^2 \, dx \le K_1 \ \text{ for all } \ k > 0$$

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(i) + (ii) $\Rightarrow u^k, v^k$ bounded in $W_0^{1,2}(\Omega) \Rightarrow u^{k_n} \rightharpoonup u$ in $W_0^{1,2}(\Omega)$, etc

(iii) L^1-“segregation” bound: there exists $K_2 > 0$ such that

$$\int_\Omega k u^k v^k \, dx \leq K_2$$

because

$$\begin{aligned} 0 \leq \int_\Omega k u^k v^k \, dx &= \int_\Omega \Delta u^k + f(u^k) \, dx \\ &= \int_{\partial\Omega} \frac{\partial u^k}{\partial \nu} \, dx + \int_\Omega f(u^k) \, dx \\ &\leq C \end{aligned}$$

since

$$\frac{\partial u^k}{\partial \nu} \leq 0 \quad \text{and} \quad 0 \leq u^k \leq M$$

Identification of the $k \to \infty$ limit of (P_e^k)

- if $w^{k_n} := u^{k_n} - v^{k_n}$, then

$$\Delta w^{k_n} + f(u^{k_n}) - g(v^{k_n}) = 0,$$

so for each $\phi \in W_0^{1,2}(\Omega)$,

$$(*) \qquad \int_\Omega \nabla w^{k_n} \cdot \nabla \phi \, dx = \int_\Omega [f(u^{k_n}) - g(v^{k_n})] \phi \, dx,$$

- let $k_n \to \infty$ in $(*)$ using

$$u^{k_n} \rightharpoonup u, \quad v^{k_n} \rightharpoonup v \ \text{ in } \ W_0^{1,2}(\Omega),$$

$$u^{k_n} \to u, \quad v^{k_n} \to v \quad a.e. \ \text{ in } \ \Omega$$

Better convergence properties for solutions (u^k, v^k) of (P_e^k)

(i) Convergence of $w^{k_n} := u^{k_n} - v^{k_n}$ in $C^{1,\lambda}(\overline{\Omega})$ for each $\lambda \in (0,1)$

- since $0 \leq u^k, v^k \leq M$ and

$$\Delta w^{k_n} + f(u^{k_n}) - g(v^{k_n}) = 0,$$

we have

$$\Delta w^k \text{ is bounded in } L^\infty(\Omega), \quad \text{and } \; w^k = 0 \text{ on } \partial\Omega$$

- $\Rightarrow$ w^k is bounded independently of k in

$$W^{2,p}(\Omega) \text{ for each } \; p \in [1, \infty),$$

and hence in

$$C^{1,\lambda}(\overline{\Omega}) \text{ for each } \; \lambda \in (0,1)$$

- so

$$w^{k_n} \to w = u - v \text{ in } \; C^{1,\lambda}(\overline{\Omega}) \text{ for each } \; \lambda \in (0,1)$$

Better convergence properties for solutions (u^k, v^k) of (P_e^k)

(ii) Improved segregation by blow-up argument Given $\varepsilon > 0$, there exists $k_0 \in \mathbb{N}$ such that if $k \geq k_0$ and (u^k, v^k) is a solution of (P_e^k), then for each $x \in \Omega$,

$$0 \leq u^k(x) \leq \varepsilon_0 \quad \text{or} \quad 0 \leq v^k(x) \leq \varepsilon_0$$

Idea of proof :

• If not, there exist $\varepsilon_0 > 0$ and sequences $k_j \to \infty$ and $x_j \in \Omega$ such that

$$u^{k_j}(x_j) \geq \varepsilon_0 \;\text{ and }\; v^{k_j}(x_j) \geq \varepsilon_0.$$

• rescaled variables centered on x_j

$$(U^{k_j}, V^{k_j})(\sqrt{k_j}(x - x_j)) = (u^{k_j}, v^{k_j})(x), \quad x \in \Omega$$

• compactness arguments give bounded solution of limit system

$$\begin{aligned} \Delta U &= UV \\ \Delta V &= UV \qquad \text{on } \mathbb{R}^N \end{aligned}$$

with $U(0), V(0) \geq \epsilon_0 > 0$ ....which is impossible

(iii) consequence of (i)+(ii) for uniform convergence of u^{k_n}, v^{k_n}

pointwise spatial segregation $\Rightarrow$

$$\begin{aligned} (w^{k_n})^+ - u^{k_n} &\to 0 \\ (w^{k_n})^- + v^{k_n} &\to 0 \end{aligned} \qquad \text{uniformly in } \Omega$$

where $w^{k_n} = u^{k_n} - v^{k_n}$, so since

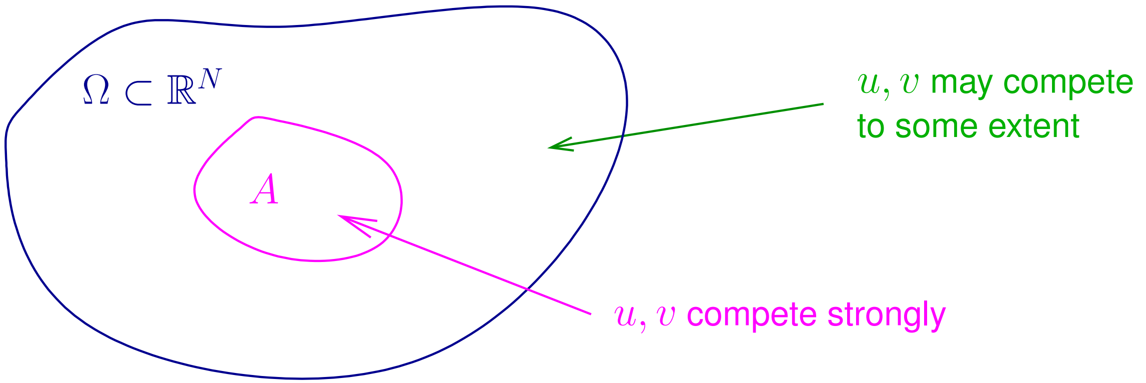
$$w^{k_n} \to w \qquad \text{uniformly in } \Omega,$$

it follows that

$$\begin{aligned} u^{k_n} &\to w^+ \\ v^{k_n} &\to -w^- \end{aligned} \qquad \text{uniformly in } \Omega$$

Related problem (C.-Dancer): what happens as $k \to \infty$ if u and v may compete to some extent on the whole of Ω but compete strongly only on a subdomain A?

$$
\begin{aligned}
0 &= \Delta u + f(u) - ruv - k\chi_A uv, \quad x \in \Omega, \\
0 &= \Delta v + g(v) - suv - \alpha k\chi_A uv, \quad x \in \Omega, \\
u(x) &= v(x) = 0, \qquad x \in \partial\Omega,
\end{aligned}
$$



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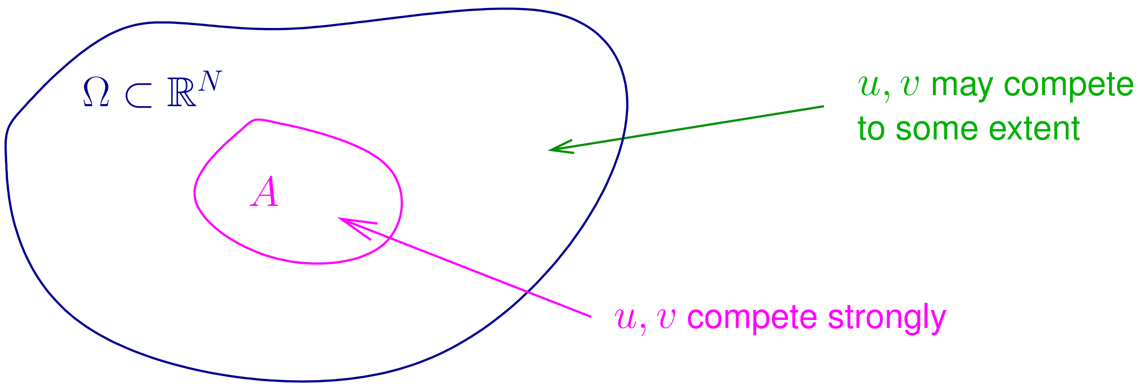

- Related earlier work ....

  - problems with refuge/protection zone : López-Gómez, Cano-Casanova, Du, Liang, ...
  - localised strong interaction with non-competitive coupling: Igbida, Karami, ...

Sketch of key arguments......

- convergence in Ω : given solns (u^k, v^k), there exists (u^{k_n}, v^{k_n}) such that

$$u^{k_n} \to \overline{u}, \quad v^{k_n} \to \overline{v} \quad \text{in } W_0^{1,2}(\Omega) \text{ as } k_n \to \infty, \quad \text{and}$$

$$\overline{w} := \alpha\overline{u} - \overline{v} \in C^{1,\lambda}(\overline{\Omega}) \text{ for all } \lambda \in (0,1)$$

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- convergence in $\Omega \setminus A$:

$$0 = \Delta\overline{u} + f(\overline{u}) - r\overline{u}\,\overline{v} \quad \text{in } \Omega \setminus A$$

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- convergence in A : $u^k v^k \to 0$ uniformly in A as $k \to \infty$, and linear combination $w^k := \alpha u^k - v^k$ satisfies

$$-\Delta w^k = \alpha f(u^k) - g(v^k) - (\alpha s - r) u^k v^k \quad \text{in } \Omega,$$

$$\therefore \quad -\Delta \overline{w} = \alpha f(\alpha^{-1} \overline{w}^+) - g(-\overline{w}^-) \;\; a.e. \text{ in } A$$

The limit problem

The limit pair $(\overline{u}, \overline{v})$ and the function $\overline{w} = \alpha\overline{u} - \overline{v}$ satisfy the problem

$$
\begin{aligned}
-\Delta\overline{w} &= \alpha f(\alpha^{-1}\overline{w}^{+}) - g(-\overline{w}^{-}) && a.e. \text{ in } A,\\
\overline{w} &= \psi && \text{on } \partial A,\\
\overline{u} &= \alpha^{-1}\overline{w}^{+}, \quad \overline{v} = -\overline{w}^{-} && a.e. \text{ in } A,\\
-\Delta\overline{u} &= f(\overline{u}) - s\,\overline{u}\,\overline{v} && \text{in } \Omega\setminus\overline{A},\\
-\Delta\overline{v} &= g(\overline{v}) - r\,\overline{u}\,\overline{v} && \text{in } \Omega\setminus\overline{A},\\
\overline{u} &= \overline{v} = 0 && \text{on } \partial\Omega,\\
\overline{u} &= \alpha^{-1}\psi^{+}, \quad \overline{v} = -\psi^{-} && \text{on } \partial A,\\
\alpha\frac{\partial\overline{u}}{\partial\nu} - \frac{\partial\overline{w}^{+}}{\partial\nu} &= \frac{\partial\overline{v}}{\partial\nu} - \frac{\partial(-\overline{w}^{-})}{\partial\nu} && \text{on } \partial A,\\
\overline{u} &\geq 0, \ \overline{v} \geq 0 && \text{in } \Omega
\end{aligned}
$$

where boundary function ψ is given by $\overline{w}|_A$ and ν is the normal direction to ∂A pointing into A

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e.g. if $g(v) = av(1 - v)$ where $a > \lambda_1$, the least eigenvalue of $-\Delta$ on Ω with $v = 0$ on $\partial\Omega$, there exists a unique positive solution of (*)

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- But if positive solutions $(u^k, v^k) \to (0, \overline{v})$ as $k \to \infty$, then $f'(0)$ has to be an eigenvalue of the linear problem

$$-\Delta y + s\bar{v}y = \lambda\, y \text{ in } \Omega \setminus A,$$
$$y = 0 \quad \text{on } \partial(\Omega \setminus A)$$

with a non-negative eigenfunction (idea of proof : take limits of $u^k/\|u^k\|_\infty$)

Further work on elliptic and parabolic $k \to \infty$ problems

- systems of 2 equations

(1) elliptic systems

- *Dancer and Yihong Du; Dancer and Zongming Guo; C. and Dancer; Zhou, Zhang, Liu+Lin*

(2) parabolic systems

general d_1, d_2: convergence of (u^k, v^k) as $k \to \infty$ on $Q_T = \Omega \times [0, T]$ to $(w^+, -w^-)$, where w is the unique (suitably defined) weak solution of

$$w_t = d_1 \Delta w^+ + d_2 \Delta w^- + f(w^+) - g(-w^-), \quad (x,t) \in Q_T$$

$+$ appropriate boundary conditions

- *Dancer, Hilhorst, Mimura and Peletier; C., Dancer, Hilhorst, Mimura and Ninomiya; Hilhorst, Martin and Mimura*

Further work on elliptic and parabolic $k \to \infty$ problems.....ctd

$d_1 = d_2$: long-time convergence to stationary solutions of the system when k is large under a non-degeneracy condition on stationary solutions of limit problem, by using the Lyapunov function

$$\int_\Omega \frac{d_1}{2}|\nabla w|^2 - H(w)\,dx$$

for the limit equation

$$w_t = d_1 \Delta w + h(w),$$

where

$$h(w) := f(w^+) - g(-w^-)$$

- *Dancer and Zhitao Zhang JDE 2002; C., Hilhorst and Dancer*

Further work on elliptic and parabolic $k \to \infty$ problems.....ctd

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  - some results require symmetric competition terms $-b_{ij}u_iu_j$; that is

$$b_{ij} = b_{ji}$$

Further work on elliptic and parabolic $k \to \infty$ problems.....ctd

(1) elliptic systems

- *Conti, Terracini and Verzini; Conti and Felli; Kelei Wang and Zhitao Zhang; Caffarelli, Karakhanyan and Lin*

(2) parabolic systems

equal d_i:

- some results on long-time convergence when k is large under non-degeneracy conditions on stationary solutions
- *Kelei Wang and Zhitao Zhang; Dancer, Kelei Wang and Zhitao Zhang*

general d_i:

- variational structure for limit problem as gradient flow for harmonic maps into a metric space with non-positive curvature

- *Kelei Wang, DCDS A 2015*

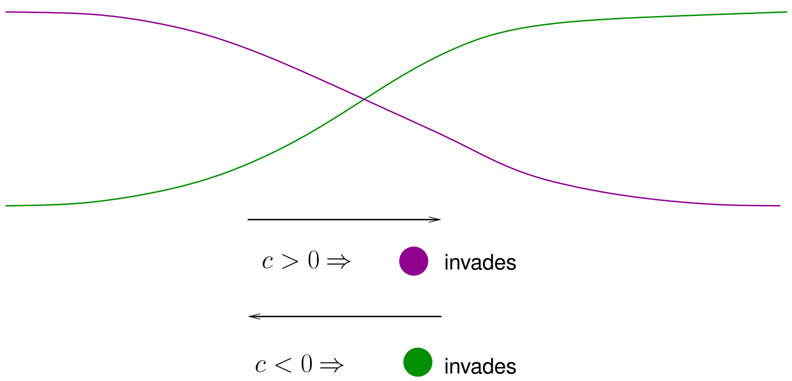
Further work on elliptic and parabolic $k \to \infty$ problems.....ctd

- applications to biological invasions of strongly competing species

(i) sign of speed $c \in \mathbb{R}$ of travelling wave

$$(u_1, u_2)(x,t) = (w_1, w_2)(x - ct)$$

connecting two stable steady states can be determined by the free-boundary condition in a limit problem



$\Rightarrow$ up to constants, the <u>more</u> diffusive species is the invading species (contrasts with results for heterogenous Ω of *Dockery et al, 1998*, where the <u>least</u> diffusive species was the invader)

- *Girardin and Nadin, 2015; 2018*

Further work on elliptic and parabolic $k \to \infty$ problems.....ctd

- applications to biological invasions of strongly competing species...ctd

(ii) diffusion depends periodically on space, *e.g.*,

$$\nabla \cdot (d(x)\nabla u)$$

- homogenisation and strong competition limits used to study the influence of high-frequency oscillations in the diffusion on the direction of invasion

  - *Hutridurga and Venkataraman, 2018*

(iii) rôle of movement-response/taxis terms in determining speed of invasion *e.g.*,

$$u_t = \ldots\ldots - c_1\nabla \cdot (u\nabla v) + \ldots..$$

$$v_t = \ldots\ldots - c_2\nabla \cdot (v\nabla u) + \ldots..$$

  - *Petrovskii and Potts, 2017*

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  - *Petrovskii and Potts, 2017*

Thank you for your attention....