Reaction-diffusion models that are cooperative at low densities and competitive at high densities

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Part 1: Movement models with switching

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Random dispersal in continuous time and space is most commonly modeled by diffusion, possibly with physical advection, or sometimes by nonlocal models of the form

$$\frac{\partial u}{\partial t} = \int J(x-y)u(y)dy - u.$$

Many organisms disperse in ways that are not random but depend on environmental conditions.

Conditional dispersal has been modeled by equations of the form

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu(x)\nabla u - uP\vec{(x)}],$$

sometimes with periodic time dependence, or related Fokker-Planck equations, or nonlocal models where $J(x-y)$ is replaced by $J(x,y)$.

However, all of those types of models assume that all individuals present at a given place and time will move in the same way.

In models for random dispersal the way is simple.

For conditional dispersal the way may be complex.

Recent advances in technology have greatly increased the amount of data on how animals actually move:

- Switching between different movement modes for extensive large scale search for discovery and intensive small scale search for exploitation.

- Each movement mode is often simple, for example diffusion

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}$$

or Ornstein-Uhlenbeck centered at some point x_0

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + c\frac{\partial}{\partial x}[(x - x_0)u] \quad \text{with } c > 0,$$

or similar diffusive/advective movement. (Statistical analyses do not usually support Lévy flights or more complicated movement modes.)

- Switching from extensive mode to intensive mode occurs when resource patches are discovered, switching back to extensive mode occurs when they are depleted.

Some math: A population model with switching

Let u and v be subpopulations of a single population consisting of individuals using different movement modes. We consider

$$\frac{\partial u}{\partial t} = Lu - \alpha(x)u + \beta(x)v + (m(x) - au - bv)u,$$
$$\frac{\partial v}{\partial t} = Mv + \alpha(x)u - \beta(x)v + (n(x) - cu - dv)v \quad \text{on} \quad \Omega \times (0, \infty)$$

with appropriate boundary conditions.

L and M are dispersal operators with diffusion and/or advection, for example

$$Lu = \nabla \cdot [\mu_u(x)\nabla u - u\vec{P}_u(x)].$$

Switching rates are given by $\alpha(x), \beta(x)$

This model is cooperative at low densities and competitive at high densities.

If L and M and their boundary conditions admit maximum principles there is an attracting invariant rectangle.

Some related work:

J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski studied models with n ecologically equivalent subpopulations, all switching rates the same and spatial variation only in growth rates (J. Math. Biol. 37(1998), no. 1, 61–83).

L. Girardin extensively studied traveling waves in systems with constant coefficients and n subpopulations (Nonlinearity, 31 (2018) 108–164 and Math. Models and Methods in Appl. Sci. 28 (2018)1067–1104).

L. Girardin and Q. Griette studied Liouville type theorems (Acta. Applicandae Mathematicae (2020): 1–17).

(Additional references in R.S. Cantrell, C., and X. Yu (Science China Mathematics, 63 (2020) 441-464, https://doi.org/10.1007/s11425-019-1623-2) or (arXiv:2001.03686).

Diffusion with $m(x) = n(x)$ or m and n constant

(R.S. Cantrell, C., X. Yu 2018, 2020, and notes). For $m(x) = n(x)$:

$$\frac{\partial u}{\partial t} = D_1 \Delta u - \alpha(x)u + \beta(x)v + u(m(x) - au - bv),$$
$$\frac{\partial v}{\partial t} = D_2 \Delta v + \alpha(x)u - \beta(x)v + v(m(x) - cu - dv) \text{ on } \Omega \times (0, \infty).$$

- If $\Omega \subset \mathbb{R}^N$ is bounded and the coefficients and $\partial\Omega$ are smooth and $m(x), a, b, c, d > 0$, the model has an attracting invariant rectangle $[B_1, 0] \times [0, B_2]$ for any classical homogeneous boundary conditions.
- Suppose the model has Neumann boundary condtions. Let

$$g_1(x, u, v) = (m(x) - \alpha(x) - u)u + (\beta(x) - bu)v,$$
$$g_2(x, u, v) = (m(x) - \beta(x) - v)v + (\alpha(x) - cv)u.$$

If there exist positive numbers A_1, A_2 with $g_1(x, A_1, v) > 0$ and $g_2(x, u, A_2) > 0$ for any $(x, u, v) \in \bar{\Omega} \times [A_1, B_1] \times [A_2, B_2]$, then the model has an attracting rectangle $[A_1, B_1] \times [A_2, B_2]$.

The linearized system at $(0,0)$ is

$$\begin{aligned} D_1\Delta\phi - \alpha(x)\phi + \beta(x)\psi + m(x)\phi &= \lambda\phi, \\ D_2\Delta\psi + \alpha(x)\phi - \beta(x)\psi + m(x)\psi &= \lambda\psi \quad \text{on} \quad \Omega. \end{aligned}$$

It is cooperative so it has a principal eigenvalue λ_0.

If $\lambda_0 > 0$ then $(0,0)$ is unstable.

For no-flux boundary conditions, if $m(x) > 0$ then $\lambda_0 > 0$.

To see $\lambda_0 > 0$ integrate the equations and add them.

If $m(x)$ changes sign we only have partial results on the sign of λ_0.

If $\alpha, \beta > 0$ the model system cannot have semi-trivial equilibria, so if $(0,0)$ is unstable the system is uniformly persistent (permanent) by standard theory and thus has at least one positive equilibrium.

If $\lambda_0 < 0$ then note that solutions to the full model are sub-solutions to the dynamic linearized system

$$\frac{\partial u}{\partial t} = D_1 \Delta u - \alpha(x) u + \beta(x) v + m(x) u,$$
$$\frac{\partial v}{\partial t} = D_2 \Delta v + \alpha(x) u - \beta(x) v + m(x) v \quad \text{on} \quad \Omega \times (0, \infty),$$

and all solutions to that system go to $(0, 0)$ as $t \to \infty$.

The model without switching ($\alpha = \beta = 0$) is competitive.

If that model is bistable then for small α and β there may be multiple positive equilibria.

Idea: start with $\alpha = \beta = 0$, show that if there are stable semi-trivial equilibria then increasing α and β causes them to become positive in both components.

The model may be asymptotically cooperative or competitive.

For simplicity in stating a result, suppose the coefficients are constant but allow growth rates $m \neq n$, so the reaction terms are $(m - au - bv)u$, $(n - cu - dv)v$.

Let

$$L_1 = m - \alpha - \frac{a}{b}\beta, \; L_2 = n - \frac{d}{c}\alpha - \beta.$$

(1) If $L_1 < 0$ and $L_2 < 0$, then under homogeneous classical boundary conditions the model is cooperative in a globally attracting invariant set $[0, \beta/b] \times [0, \alpha/c]$.

(2) If $L_1 > 0$ and $L_2 > 0$, then under homogeneous Neumann boundary conditions the model is competitive in a globally attracting invariant set $[\beta/b, (m - \alpha)/a] \times [\alpha/c, (n - \beta)/d]$.

In applied settings Case (1) (fast switching) is more plausible.

Evolution of slow diffusion

J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski (J. Math. Biol. 37(1998), no. 1, 61–83) considered a two species competition model for two diffusing populations that were identical except for their diffusion rates:

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_1 \Delta u + [m(x) - u - v]u, \\ \frac{\partial v}{\partial t} &= D_2 \Delta v + +[m(x) - u - v]v \quad \text{on} \quad \Omega \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0 \quad \text{on} \quad \partial\Omega\end{aligned}$$

and showed that if $D_1 < D_2$ then the species with density u that has the slower diffusion rate excludes the species with density v that has the faster diffusion rate.

“The slower diffuser wins”

Comparison with simple diffusion

In the asymptotically cooperative case, for $\alpha, \beta > 0$ and $u(x,0) > 0$ or $v(x,0) > 0$, if t is sufficiently large the model is cooperative and subhomogeneous.

Thus it has a unique globally attracting positive equilibrium so the model behaves like a single diffusive logistic equation.
We compare it with one for an ecologically identical population.

Comparison system (assume α, β constant, $m(x)$ nonconstant):

$$\begin{aligned}
\frac{\partial u}{\partial t} &= D_1 \Delta u - \alpha u + \beta v + [m(x) - u - v - w]u, \\
\frac{\partial v}{\partial t} &= D_2 \Delta v + \alpha u - \beta v + [m(x) - u - v - w]v \\
\frac{\partial w}{\partial t} &= D_3 \Delta w + [m(x) - u - v - w]w \ \text{ on } \ \Omega \\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega.
\end{aligned}$$

The subsystem with $w = 0$ for the population with switching

$$\begin{aligned}
\frac{\partial u}{\partial t} &= D_1 \Delta u - \alpha u + \beta v + [m(x) - u - v]u, \\
\frac{\partial v}{\partial t} &= D_2 \Delta v + \alpha u - \beta v + [m(x) - u - v]v \ \text{ on } \ \Omega \\
\frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega,
\end{aligned}$$

is asymptotically cooperative and has a unique globally attracting equilibrium (u^*, v^*) if

$$\int_\Omega m(x)dx > 0, \quad \max_{x \in \Omega} m(x) < \alpha + \beta.$$

For $(u, v) = 0$, w satisfies a diffusive logistic equation that has a unique globally attracting equilibrium w^* under the same condition.

The full system is monotone with respect to the ordering

$$(u_1, v_1, w_1) \leq (u_2, v_2, w_2) \iff u_1 \leq u_2, \ \ v_1 \leq v_2, \ \ w_1 \geq w_2.$$

The comparison system is monotone so, as in the case of 2×2 competition, if there is no coexistence state and $(u^*, v^*, 0)$ is unstable then the first population excludes the second, while if $(0, 0, w^*)$ is unstable the second population excludes the first.

The eigenvalue problems determining the stability of semi-trivial equilibria are 3×3 systems but the signs of the principal eigenvalues at $(u^*, v^*, 0)$ and $(0, 0, w^*)$ respectively are determined by the single equation

$$\begin{gathered} D_3 \Delta \phi + (m(x) - u^* - v^*)\phi = \lambda \phi \ \text{ on } \ \Omega, \\ \frac{\partial \phi}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega \end{gathered}$$

and the system

$$\begin{gathered} D_1 \Delta \phi + (m(x) - w^* - \alpha)\phi + \beta\psi = \lambda\phi \\ D_2 \Delta \psi + \alpha\phi + (m(x) - \beta - w^*)\psi = \lambda\psi \ \text{ on } \ \Omega, \\ \frac{\partial \phi}{\partial \nu} = \frac{\partial \psi}{\partial \nu} = 0 \text{ on } \ \partial\Omega. \end{gathered}$$

Results: (recall we assumed $D_1 < D_2$)

Based on analysis of the eigenvalue problems and possible positive equilibria, and monotone dynamical systems theory we have the following results:

If $D_3 \leq D_1$ then $(0, 0, w^*)$ is globally asymptotically stable.
If $D_3 \geq D_2$ then $(u^* v^*, 0)$ is globally asymptotically stable.

If $D_1 < D_3 < D_2$ then there exist C_1, C_2 with $D_1 < C_1 \leq C_2 < \frac{\beta}{\alpha+\beta} D_1 + \frac{\alpha}{\alpha+\beta} D_2$ such that

$(0, 0, w^*)$ is globally asymptotically stable if $D_3 < C_1$,
$(u^*, v^*, 0)$ is globally asymptotically stable if $D_3 > C_2$.

Remark: If $\alpha = \beta$ then for $C_2 < D_3 < (D_1 + D_2)/2$ the equilibrium $(u^*, v^*, 0)$ is globally asymptotically stable. The strict inequality for C_2 suggests that there is an advantage to switching.

Some mathematical biology: Experimental observation from
J. A. Prevedello et al. Journal of Zoology 284 (2011)53–59.

- The researchers took forest animals (South American marsupials, “possums”) out of the forest and released them at different distances from their favored habitat.
- When they could not detect the forest they moved randomly at a fairly large scale.
- When they could detect the forest, they moved toward it quickly in a directed way.

To model this we used a combination of switching and nonlocal information.
(W. F. Fagan, T. Hoffman, D. Dahiya, E. Gurarie, R. S. Cantrell, and C. Improved foraging by switching between diffusion and advection: benefits from movement that depends on spatial context, Theoretical Ecology 13 (2020), 127-136)

Modeling set up:
The model is set in a finite one dimensional domain Ω

Let $u(x,t) =$ population density (total population constant).
Let $m(x) =$ resource density or habitat quality. In this case good habitat is forest and the boundary between habitats is sharp so we used a step function.
The marsupials could detect the forest at a distance so we used nonlocal information, and modeled directed movement toward the forest as advection on the gradient of sensory perception of good habitat together with a little diffusion.

Perception model: Let $B_R(x) =$ ball of radius R centered at x. Let

$$h(x,t) = \frac{1}{|B_R(x)|} \int_{B_R(x)} m(x-y)dy.$$

Here $R =$ sensory radius. h is an average of $m(x)$ over $B_R(x)$ that encodes information at a distance up to R from x.

Movement model:(recall $h(x)$ is perceived habitat quality)

Random search $\dfrac{\partial u}{\partial t} = D\dfrac{\partial^2 u}{\partial x^2}$ (D large)
Directed movement $\dfrac{\partial v}{\partial t} = \epsilon\dfrac{\partial^2 v}{\partial x^2} - \gamma\dfrac{\partial}{\partial x}\left(v\dfrac{\partial h(x)}{\partial x}\right)$ (ϵ small)

Switching model:
$\alpha(x)$ = rate of switching to random search
$\beta(x)$ = rate of switching to directed movement

In good habitat ($m(x) = 1$) they switch from search to directed movement at a fixed rate β_0. If they are in directed mode they stay in it.
In bad habitat ($m(x) = 0$) they switch from search to directed movement if the gradient of perceived habitat quality is large enough and switch back if it is too small.

Rate of switching from directed movement to search

$$\alpha(x) = \begin{cases} 0 \ \text{ if } \ m(x) = 1 \\[2ex] \alpha_0 - \alpha_1 \left|\dfrac{dh}{dx}\right| \ \text{ if } \ m(x) = 0 \text{ and } \ \left|\dfrac{dh}{dx}\right| \leq \dfrac{\alpha_0}{\alpha_1} \\[2ex] 0 \ \text{ if } \ m(x) = 0 \text{ and } \ \left|\dfrac{dh}{dx}\right| > \dfrac{\alpha_0}{\alpha_1} \end{cases}$$

Rate of switching from search to directed movement

$$\beta(x) = \begin{cases} \beta_0 \ \text{ if } \ m(x) = 1 \\[2ex] 0 \ \text{ if } \ m(x) = 0 \text{ and } \ \left|\dfrac{dh}{dx}\right| \leq h_1 \\[2ex] \dfrac{\beta_0 \left(\left|\frac{dh}{dx}\right| - h_1\right)}{1 + \beta_1 \left(\left|\frac{dh}{dx}\right| - h_1\right)} \ \text{ if } \ m(x) = 0 \text{ and } \ \left|\dfrac{dh}{dx}\right| > h_1 \end{cases}$$

Full movement model: $\Omega = (0, L)$

$$\begin{aligned}
&\frac{\partial u}{\partial t} = D\frac{\partial^2 v}{\partial x^2}u - \alpha(x)u + \beta(x)v,\\
&\frac{\partial v}{\partial t} = \epsilon\frac{\partial^2 v}{\partial x^2} - \gamma\frac{\partial}{\partial x}\left(v\frac{\partial h(x)}{\partial x}\right) + \alpha(x)u - \beta(x)v \ \text{ on } \ \Omega \times (0, T)\\
&\frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = 0 \ \text{ on } \ \partial\Omega \times (0, T).
\end{aligned}$$

The model makes sense in two or three dimensions as well if d/dx is replaced by ∇.
It provides a simple "toy" model that captures qualitative features of actual animal movement.

Numerical simulations show that this movement model can be effective in concentrating a population in the region of good habitat.

Future directions:

- Pure mathematics: Build up better general theory of PDE systems that are cooperative at low densities but are competitive at high densities.

- Mathematical ecology: Determine which switching rates are optimal, perhaps from the viewpoint of adaptive dynamics. Build more realistic movement models with switching and test them with movement data.

- Models with switching between movement modes involving diffusion and advection arise in other biological applications:

M.-V. Ciocanel et al., Modeling microtubule-based transport and anchoring of mRNA. SIAM J Appl Dyn Sys 17(4) (2018), 2855–2881.

V. Bitsouni et al., Aggregation and travelling wave dynamics in a two-population model of cancer cell growth and invasion. Mathematical Medicine and Biology 35(4)(2018), 541-577.

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R.S. Cantrell , C., and X. Yu, Dynamics of populations with individual variation in dispersal on bounded domains, Journal of Biological Dynamics, 12 (2018), 288-317.

R.S. Cantrell, C., and X. Yu, Populations with individual variation in dispersal in heterogeneous environments: dynamics and competition with simply diffusing populations, Science China Mathematics, 63 (2020), 441-464, https://doi.org/10.1007/s11425-019-1623-2

W. F. Fagan, T. Hoffman, D. Dahiya, E. Gurarie, R. S. Cantrell, and C., Improved foraging by switching between diffusion and advection: benefits from movement that depends on spatial context, Theoretical Ecology 13 (2020), 127-136

Part 2: Persistence for a two-stage reaction-diffusion system

R. S. Cantrell, C., and S. Martínez, MDPI Mathematics 8(3) (2020), 396; https://doi.org/10.3390/math8030396

(Open access)

In the diffusive logistic model

$$\frac{\partial u}{\partial t} = d\Delta u + [m(x) - u]u \ \text{ in } \Omega,$$

$$\frac{\partial u}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega,$$

the population growth rate at low density, given by the principal eigenvalue of

$$d\Delta\phi + m(x)\phi = \lambda\phi \quad \text{ on } \ \Omega,$$
$$\frac{\partial \phi}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega,$$

is decreasing in d.

Recall that in competition between two competing and diffusing populations that are structured only by spatial distribution and are ecologically identical except for their diffusion rates, the slower diffuser wins.

In contrast, in patch models with age structure there are examples where some positive rates of dispersal are evolutionarily stable (Greenwood-Lee and Taylor, 2001)

We consider a spatial population model for a stage structured population introduced by Brown and Zhang (2003) where u and v represent the densities of juveniles and adults respectively:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + r(x)v - s(x)u - a(x)u - b(x)u^2 - c(x)uv \ \text{ in } \Omega, \\[2em] \dfrac{\partial v}{\partial t} = d_2 \Delta v + s(x)u - e(x)v - f(x)v^2 - g(x)uv \text{ in } \Omega, \\[2em] \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega. \end{cases}$$

$r(x)$ = rate of reproduction by adults

$s(x)$ = rate of survival and maturation into adulthood by juveniles

$a(x)$ and $e(x)$ = rates of density independent mortality

$b(x), c(x), f(x)$ and $g(x)$ = rates of density dependent mortality.

General features of the model

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + r(x)v - s(x)u - a(x)u - b(x)u^2 - c(x)uv \ \text{ in } \Omega, \\[2ex] \dfrac{\partial v}{\partial t} = d_2 \Delta v + s(x)u - e(x)v - f(x)v^2 - g(x)uv \text{ in } \Omega, \\[2ex] \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0 \ \text{ on } \ \partial\Omega. \end{cases}$$

• If c and g are positive the model is cooperative at low densities, competitive at high densities.
• It always has the equilibrium $(0, 0)$. Any other nonnegative equilibrium must have both $u > 0$ and $v > 0$.
• The linearized system at $(0, 0)$ is cooperative and has a principal eigenvalue λ_1 (López-Gómez and Molina-Meyer 1994). If $\lambda_1 > 0$ then $(0, 0)$ is unstable and the system is uniformly persistent.
• If $c = g = 0$ the system is cooperative and if $\lambda_1 > 0$ it has a unique globally attracting positive equilibrium (Molina-Meyer 1996).

Detailed assumptions and linearized problem

Assume

(i) $r, s, a, b, c, e, f, g \in C^{\alpha}(\overline{\Omega})$, $\partial\Omega$ is of class $C^{2,\alpha}$
(ii) $a(x), c(x), e(x), g(x)r(x), s(x) \geq 0$ in Ω
(iii) $r(x)$ and $s(x)$ not identically 0, $b(x), f(x) > 0$

The linearized problem at $(0, 0)$:

$$\begin{cases} d_1\Delta\phi + r(x)\psi - (s(x) + a(x))\phi = \lambda\phi \ \text{ in } \Omega, \\ d_2\Delta\psi + s(x)\phi - e(x)\psi = \lambda\psi \ \text{ in } \Omega, \\ \dfrac{\partial u}{\partial\nu} = \dfrac{\partial v}{\partial\nu} = 0 \ \text{ on } \ \partial\Omega. \end{cases}$$

Let λ_1 be the principal eigenvalue.

Theorem: If $\lambda_1 > 0$ then the population persists if its initial density is nonzero. If $\lambda_1 \leq 0$ then $(0, 0)$ is globally asymptotically stable.

(Proof by standard methods of reaction-diffusion theory)

Small diffusion

If $d_1 = d_2 = 0$ the eigenvalues of the linearization around (0,0) are the roots of $\det(A(x) - \lambda I)$ where

$$A(x) = \begin{bmatrix} -(s(x) + a(x)) & r(x) \\ s(x) & -e(x) \end{bmatrix}$$

The maximum eigenvalue is given by

$$\Lambda(x) = \frac{1}{2}\left[-(s(x) + a(x) + e(x)) + \sqrt{(s(x) + a(x) - e(x))^2 + 4r(x)s(x)}\right].$$

Then then $\Lambda(x) > 0$ if and only if $r(x)s(x) > (s(x) + a(x))e(x)$.

By (K.-Y. Lam and Y. Lou, J. Dyn. Diff. Equat. 29 (2016), 29–48), Theorem 1.4,

$$\lambda_1 \to \max_{x \in \overline{\Omega}} \Lambda(x) \text{ as } d_1, d_2 \to 0.$$

Thus, the model predicts persistence for small d_1, d_2 if and only if

$$\max_{x \in \overline{\Omega}} (r(x)s(x) - (s(x) + a(x))e(x)) > 0.$$

Large diffusion

For this case we verify and use a "folk theorem" that is more general than what we need. Consider the eigenvalue problem

$$d_i L^i \phi_i + \sum_{j=1}^{N} a_{ij}\phi_j = \lambda \phi_j, \quad i = 1 \ldots N,$$

$$\text{with } \; L^i u = \nabla u \cdot \mu_i(x)[\nabla u - u \nabla \alpha_i(x)] \quad \text{for} \quad x \in \Omega,$$

$$\text{and } \; [\nabla u - u\nabla \alpha_i] \cdot \nu = 0 \quad \text{for} \quad x \in \partial\Omega,$$

with $\mu_i(x) \geq \mu_0 > 0$, $A = ((a_{ij}(x)))$ irreducible, $a_{ij} \geq 0$ if $i \neq j$.
Let λ_1 be the principal eigenvalue.

Let $\overline{A}_{ij} = \int_\Omega a_{ij} exp(\alpha_i) dx / \int_\Omega exp(\alpha_i) dx$.
Let $\overline{\Lambda}$ be the principal eigenvalue of $((\overline{A}_{ij}))$.

Theorem: If $\min\limits_{i=1,\ldots,N} d_i \to \infty$ then $\lambda_1 \to \overline{\Lambda}$.

Proof by compactness argument.
If $L^i = d_i \Delta$ for all i then $\overline{A}_{ij}$ is the spatial average of A_{ij}.

Basic applied results 1

For our diffusion model with $A(x) = \begin{bmatrix} -(s(x)+a(x)) & r(x) \\ s(x) & -e(x) \end{bmatrix}$, the principal eigenvalue λ_1 for the linearized model at $(0,0)$ is positive for d_1, d_2 large if and only if $\overline{\Lambda} > 0$.

We have $\overline{\Lambda} > 0$ if and only if $\overline{r}\ \overline{s} - (\overline{s} + \overline{a})\overline{e} > 0$, where $\overline{r}$ etc. are spatial averages. Thus the model predicts persistence for large d_1, d_2 if and only if

$$\overline{r}\ \overline{s} - (\overline{s} + \overline{a})\overline{e} > 0.$$

Recall that the model predicts persistence for small d_1, d_2 if and only if

$$\max_{x \in \overline{\Omega}} (r(x)s(x) - (s(x) + a(x))e(x)) > 0.$$

These conditions can depend on details of the spatial arrangement of regions favorable for reproduction and those favorable for survival and maturation.

Basic applied results 2

If $r(x)s(x) \equiv 0$, i.e. the supports of $r(x)$ and $s(x)$ are disjoint, but $\overline{r}$ and $\overline{s}$ are both large, then the model predicts extinction for small diffusion rates but can predict persistence for large diffusion rates, specifically if $\overline{r}$ is sufficiently large.

If $s(x) \geq s_0 > 0$ on Ω, $r(x) \equiv 0$ on $\Omega \backslash \Omega_0$ where $\Omega_0 \subset \Omega$ with $|\Omega_0|$ small, but $\max_{x \in \overline{\Omega}}(r(x)$ is large, the model can predict extinction for large diffusion rates but persistence for small ones, because $\overline{r}$ could be arbitrarily small while $\max_{x \in \overline{\Omega}} r(x)$ is arbitrarily large, depending on the size of Ω_0.

The first general conclusion is that this type of structured population model may select for or against slower diffusion, since either sufficiently fast or sufficiently slow diffusion can be necessary for persistence of the population, depending on the environment.

Future directions

- Consider competing stage structured populations that are identical except for their diffusion rates with diffusivities d_1, d_2 versus those with diffusivities D_1, D_2.

(If adults only compete with adults and juveniles with juveniles, so that $c \equiv g \equiv 0$, the single species models would be cooperative so monotone dynamical systems theory could be used. Otherwise the single species models are cooperative at low densities but competitive at high densities so it would be harder).

- Try to model systems with directed movement and periodic time dependence.

(Many species migrate seasonally between habitats where adults can find resources and habitats where juveniles are safe. It might require more complicated models to really capture that, perhaps Droop type models that track the nutritional status of populations.)

Part 3: Evolution of dispersal in models with Allee effects

N. Rodriguez and C., in progress

Part 3: Comparison of dispersal strategies again

There has been a large amount of work on comparing dispersal strategies by using models for populations that are otherwise identical and which by themselves have logistic dynamics.That leads to systems like

$$\frac{\partial u}{\partial t} = L_1\, u + [m(x) - u - v]u,$$
$$\frac{\partial v}{\partial t} = L_2 v + [m(x) - u - v]v$$

where L_1 and L_2 are diffusion-advection operators with no-flux boundary conditions or other dispersal operators.

This type of system is competitive, and for two species, competitive systems generate monotone flows or semiflows, which greatly simplifies the analysis.

Allee effects

For a model with Allee effects, we would replace the logistic term with a function $f(x, u) = g(x, u)u$ where $g(x, u)$ is increasing for smalll u and decreasing for large u. For example:

$g(x, u) = (m(x) - u)(u - \theta(x))$ where $0 < \theta(x) < m(x)$.

The comparison system now becomes

$$\frac{\partial u}{\partial t} = L_1 \, u + g(x, u + v)u,$$
$$\frac{\partial v}{\partial t} = L_2 v + g(x, u + v)v.$$

This produces another system which is cooperative at lo densities but competitive at large densities.

We have some partial results on comparing strategies in this case.

THANK YOU!