

Spatial population models with fitness based dispersal

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Research partially supported by various NSF grants, currently 15-14752

October 17, 2016

Reaction-diffusion-advection models for population dynamics and dispersal

Let Ω be a bounded domain in \mathbb{R}^n , $n = 1, 2$ or 3 .

A reasonably general class of population models with dispersal by diffusion and advection on environmental gradients can be written as

$$\frac{\partial u}{\partial t} = \nabla \cdot [d(x, u)\nabla u - \alpha u \nabla e(x, u)] + f(x, u)u \text{ in } \Omega \times (0, \infty)$$

If Ω represents a closed environment, no flux boundary conditions are suitable and are given by

$$[d(x, u)\nabla u - \alpha u \nabla e(x, u)] \cdot \vec{n} = 0 \text{ on } \partial\Omega \times (0, \infty).$$

Classical models typically use simple diffusion, where d is constant and e is zero. More recent models are still most often semilinear, that is, they assume d and e are independent of u , but may depend on x , so that dispersal is conditional on environmental features. However, if dispersal is also conditional on population density, d and e may depend on u as well. In these more general settings it is natural to ask which types of dispersal are optimal. (But what does “optimal” mean ?)

Fitness and the ideal free distribution

Ever since Darwin, the idea of fitness has been a key element of the theory of evolution and more recently evolutionary ecology. In a model of the form

$$\frac{\partial u}{\partial t} = \nabla \cdot [d(x, u)\nabla u - \alpha u \nabla e(x, u)] + f(x, u)u \text{ in } \Omega \times (0, \infty)$$

the term $f(x, u)$ represents the per capita reproductive rate for an individual at location x when the population density is u , so it is a likely candidate for local fitness, but local fitness by itself does not fully describe optimal dispersal

One hypothesis about optimal dispersal is the ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972). This is a verbal theory that individual organisms which can assess local fitness everywhere and are free to move as they wish will move to optimize their local fitness. This idea has two implications:

- at equilibrium, all individuals at all locations will have equal fitness, since otherwise some individuals would move from locations of lower fitness to those where fitness is higher, and if fitness depends on density, and
- there should be no net movement at equilibrium since all individuals have optimized their locations so moving to a new location would reduce an individual's fitness unless it traded places with another individual who was at that location.

The ideal free distribution in reaction-advection-diffusion equations

For reaction-advection-diffusion equations

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla \cdot [d(x, u)\nabla u - \alpha u \nabla e(x, u)] + f(x, u)u & \text{in } \Omega \times (0, \infty), \\ [d(x, u)\nabla u - \alpha u \nabla e(x, u)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty) : \end{cases}$$

Equal fitness means at a population equilibrium $u^*(x) \geq$ means $f(x, u^*) = c$.

The no-flux boundary condition implies $\int_{\Omega} f(x, u^*)u^*dx = 0$ so $f(x, u^*) \equiv 0$.

No net movement at equilibrium then means

$$\begin{cases} \nabla \cdot [d(x, u^*)\nabla u^* - \alpha u^* \nabla e(x, u^*)] = 0 & \text{in } \Omega, \\ [d(x, u^*)\nabla u^* - \alpha u^* \nabla e(x, u^*)] \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases}$$

If $f(x, u) = m(x) - u$ with $m(x) > 0$ then there are linear advection-diffusion operators which can produce an ideal free distribution: for $d_0 > 0$ constant,

$$d = \alpha = d_0, e(x) = \ln(m(x)) \text{ (so the operator is } d_0 \nabla \cdot [\nabla u - u \frac{\nabla m}{m}] \text{)}$$

(Cantrell, C., and Lou 2010), or

$$d = d_0/m(x), \alpha = d_0, e(x) = 1/(m(x)) \text{ (so the operator is } d_0 \Delta[u/m(x)] \text{)}$$

(Korobenko and Braverman 2014).

How is the ideal free distribution optimal?

Behavioral traits like dispersal patterns can be viewed as strategies and studied from the viewpoint of evolutionary stability and related ideas.

An evolutionarily stable strategy has the property that a population using it can resist invasion by any small population using any other available strategy.

This property can be characterized by pairwise invasibility analysis: assume that two populations are ecologically equivalent except for a single trait (strategy), and ask if a population using a particular strategy can resist invasion by any population using another strategy. That leads to competition models, for example

$$\begin{cases} u_t = \nabla \cdot [\mu(x)\nabla u - \alpha u \nabla e(x, u, v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nabla \cdot [\nu(x)\nabla v - \beta v \nabla E(x, u, v)] + v f(x, u + v) & \text{in } \Omega \times (0, \infty). \\ [\mu(x)\nabla u - \alpha u \nabla e(x, u, v)] \cdot \vec{n} = [\nu(x)\nabla v - \beta v \nabla E(x, u, v)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

In cases where $f(x, u) = m(x) - u$ with $m(x) > 0$, populations using linear dispersal strategies that lead to an ideal free distribution, such as $d_0 \Delta[u/m(x)]$ or $d_0 \nabla \cdot [\nabla u - u \frac{\nabla m}{m}]$, can invade (and even exclude) populations using strategies that do not produce an ideal free distribution. See (Averill, Lou and Munther 2012), (Cantrell, C., and Lou 2010), or (Korobenko and Braverman 2014).

What if $f(x, u) = m(x) - u$ and $m(x)$ changes sign ?

If $m(x)$ changes sign and $f(x, u^*) = m(x) - u^* = c$ for constant c then to have $\int_{\Omega} f(x, u^*)u^* dx = c \int_{\Omega} u^* dx = 0$ (from the no-flux b.c.)

we must have either $c = 0$ so $u^*(x) = m(x)$ or $\int_{\Omega} u^* dx = 0$.

In both of those cases the population density u^* must change sign, which is not reasonable, so an ideal free distribution seems impossible in the linear case.

However : a nonnegative ideal free distribution on $\{x \in \Omega : m(x) > 0\}$ with $f(x, u^*) = 0$ on that set could be attained if we can find dispersal terms so that $u^*(x) = m_+(x)$, that is, $u^*(x) = m(x)$ if $m(x) > 0$ and $u^*(x) = 0$ otherwise, provided we could choose d and e so that

$$\begin{cases} \nabla \cdot [d(x, u^*)\nabla u^* - \alpha u^*\nabla e(x, u^*)] = 0 & \text{in } \Omega, \\ [d(x, u^*)\nabla u^* - \alpha u^*\nabla e(x, u^*)] \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases}$$

for $u^*(x) = m_+(x)$.

Problem: For the dispersal strategies with $d(x, u) > 0$ this is impossible because of the strong maximum principle and elliptic/parabolic regularity theory. A possible solution is to allow $d = 0$ some places (degenerate diffusion).

Advection on fitness and degenerate diffusion 1

A standard approach to deriving transport-type models in continuum mechanics for the way a density $u(x, t)$ varies in time is based on the formula

$$\frac{\partial u}{\partial t} = -\nabla \cdot J$$

where J is a vector that represents flux. For advection given by a vector \vec{v} , the flux is $J = u\vec{v}$. For standard diffusion, Fick's law says that $J = -\nabla u$.

To model movement based on advection up the gradient of fitness with fitness given by $f(x, u) = m(x) - u$ with rate scaled by α one would use

$$J = [\nabla f(x, u)]u = \alpha \nabla [m(x) - u]u = \alpha(u \nabla m(x) - u \nabla u),$$

so that for the dispersal terms in our model

$$\begin{aligned} \frac{\partial u}{\partial t} &= -\alpha \nabla \cdot [u \nabla (m(x) - u)] \\ &= \alpha \nabla \cdot [u \nabla u] - \alpha \cdot \nabla [u \nabla m]. \end{aligned}$$

Taking just the first term on the right gives the porous medium equation

$$\frac{\partial u}{\partial t} = (\alpha/2) \Delta(u^2),$$

which has been widely studied: (Aronson 1985), (Otto 2001), (Vasquez 2007).

Advection on fitness and degenerate diffusion 2

The porous medium equation

$$\frac{\partial u}{\partial t} = (\alpha/2)\Delta(u^2) = \alpha \nabla \cdot [u \nabla u]$$

has the properties that:

- It admits (weak) solutions that are positive on compact sets and zero elsewhere.
- The support of a nonnegative solution which is initially positive on an open set but zero outside a compact set expands with finite speed of propagation.
- Solutions are Hölder continuous. (They will be smooth where they are positive.) (See (Aronson 1985), (Vasquez 2007)).

To obtain a full population model with advection on fitness we would add population dynamics to the movement terms

$$\frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla (m(x) - u \nabla u)]$$

yielding

$$\frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla u - u \nabla (m(x))] + (m(x) - u)u.$$

This model is in (McCall 1990) and (Cosner 2005). It is expected to have properties somewhat similar to logistic models with porous medium type diffusion.

Related models

Models with degenerate diffusion and nonlinear dynamics (including logistic dynamics)

$$\frac{\partial u}{\partial t} = \Delta\phi(u) + f(x, u)u$$

were proposed as population models by Gurtin and MacCamy (1977) and Dirichlet boundary value problems for those and for predator-prey and competition systems were studied by Pozio and Tesi (1985,1987). Models with Allee effects were studied by D.G. Aronson, M.G. Crandall, and L.A. Peletier (1982).

The original cross diffusion models of Shigesada, Kawasaki, and Teramoto (1979) included advection on an environmental gradient ∇U :

$$\begin{cases} \frac{\partial u_1}{\partial t} = \nabla \cdot [\nabla\{(\alpha_1 + \beta_{11}u_1 + \beta_{12}u_2)\}u_1] - \gamma_1 u_1 \nabla U + f_1(x, u_1, u_2)u_1 \\ \frac{\partial u_2}{\partial t} = \nabla \cdot [\nabla\{(\alpha_2 + \beta_{21}u_1 + \beta_{22}u_2)\}u_2] - \gamma_2 u_2 \nabla U + f_2(x, u_1, u_2)u_2. \end{cases}$$

(Models with population dynamics or species interactions and linear dispersal terms including spatially varying diffusion and/or advection on environmental gradients have been studied by various researchers.)

Results on models with diffusion and advection on fitness

In models with both diffusion and advection on fitness, as the diffusion rate $\rightarrow 0$, positive equilibria approximate $m(x)$ if $m(x) > 0$ or $m_+(x)$ if $m(x)$ changes sign. Consider the equation

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla \cdot [\mu \nabla u - \alpha u \nabla(m(x) - u)] + u(m(x) - u) & \text{in } \Omega \times (0, \infty) \\ [\mu \nabla u - \alpha u \nabla(m(x) - u)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

Assume $m \in C^{2,\tau}(\bar{\Omega})$, $m(x) > 0$ somewhere. Then from (Cantrell, C, Lou 2008):

Theorem 1. *Suppose that $\mu > 0$ and $\alpha \geq 0$. Then the equation has a unique solution $u \in C^{2,1}(\bar{\Omega} \times (0, \infty)) \cap C(\bar{\Omega} \times [0, \infty))$.*

It is not obvious that the equation has a comparison principle or monotonicity, but it turns out that it does. (That requires a change of variables).

Theorem 2. *If $u = 0$ is linearly unstable, then there exists at least one positive steady state. Moreover, there exist two steady states (which might be equal), denoted by u_* and u^* , such that for any positive steady state u $u_* \leq u \leq u^*$ in $\bar{\Omega}$. If $m(x) > 0$ then for α/μ large there is a unique positive steady state that is globally asymptotically stable.*

Models with diffusion and advection on fitness (continued)

Still considering

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla \cdot [\mu \nabla u - \alpha u \nabla(m(x) - u)] + u(m(x) - u) & \text{in } \Omega \times (0, \infty) \\ [\mu \nabla u - \alpha u \nabla(m(x) - u)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

again from (Cantrell, C, Lou 2008) we have

Theorem 3. *For any positive steady state u , $u \rightarrow m_+(x)$ weakly in H^1 and strongly in L^2 as $\alpha/\mu \rightarrow \infty$. For any given $\eta > 0$, if $\alpha \geq \eta$ and $\alpha/\mu \rightarrow \infty$, then in general $u \rightarrow m_+(x)$ in $C^\gamma(\bar{\Omega})$ for some $\gamma \in (0, 1)$ and if in addition $m(x) > 0$ then $u \rightarrow m(x)$ in $C^2(\bar{\Omega})$.*

In that sense the model approximates the ideal free distribution as $\alpha/\mu \rightarrow \infty$, but it never actually achieves it. Also, as long as $\mu > 0$ the population density is always positive everywhere.

The model is quasilinear but it is nondegenerate so that it can be studied in terms of classical solutions by fairly standard PDE methods.

Models with advection on fitness only

The situation is quite different if $\mu = 0$ so that the model becomes

$$\begin{cases} \frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla u - u \nabla(m(x))] + (m(x) - u)u & \text{in } \Omega \times [0, \infty), \\ [u \nabla u - u \nabla(m(x))] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times [0, \infty) \\ u(x, 0) = u_0(x). \end{cases}$$

As in the case of the porous medium equation and related equations, “solutions” which are initially zero on part of Ω may remain zero in some places and will not necessarily be smooth so we must think in terms of weak solutions. In (C. and Winkler 2014) we considered the model (with space scaled so that $\alpha = 1$) and obtained:

Theorem 4. *Assume that $m(x)$ and $\partial\Omega$ are smooth. Let $u_0 \in C^0(\bar{\Omega})$ be nonnegative. Then the model has a unique nonnegative global weak solution*

$$u \in C^0([0, \infty); L^1(\Omega)) \cap L_{loc}^2([0, \infty); W^{1,2}(\Omega)) \cap L_{loc}^\infty(\bar{\Omega} \times [0, \infty)).$$

This solution is bounded and continuous in $\bar{\Omega} \times [0, \infty)$. Finally, the solution depends continuously on the initial data relative to $L^1(\Omega)$.

(A weak solution of

$$\begin{cases} \frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla u - u \nabla(m(x))] + (m(x) - u)u & \text{in } \Omega \times [0, \infty), \\ [u \nabla u - u \nabla(m(x))] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times [0, \infty) \\ u(x, 0) = u_0(x). \end{cases}$$

with

$$u \in C^0([0, \infty); L^1(\Omega)) \cap L_{loc}^2([0, \infty); W^{1,2}(\Omega)) \cap L_{loc}^\infty(\bar{\Omega} \times [0, \infty))$$

satisfies the integrated equation

$$-\int_0^t \int_{\Omega} u \varphi_t + \int_{\Omega} u(\cdot, t) \varphi(\cdot, t) = \int_{\Omega} u_0 \varphi(\cdot, 0) - \int_0^t \int_{\Omega} u \nabla(u-m) \cdot \nabla \varphi + \int_0^t \int_{\Omega} u(m-u) \varphi$$

for any nonnegative $\varphi \in C^1(\bar{\Omega} \times [0, t])$.

Models with advection on fitness only (continued)

Still considering

$$\begin{cases} \frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla u - u \nabla(m(x))] + (m(x) - u)u & \text{in } \Omega \times [0, \infty), \\ [u \nabla u - u \nabla(m(x))] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times [0, \infty) \\ u(x, 0) = u_0(x). \end{cases}$$

What are the possible equilibria? Again from (C. and Winkler 2014):

Let G_1, G_2, \dots denote the mutually disjoint connected components of the set $\{m > 0\} := \{x \in \Omega \mid m(x) > 0\}$.

(If there are only finitely many such components set $G_i := \emptyset$ for large $i \in \mathbb{N}$).

Theorem 5. *A function $w \in L^\infty(\Omega) \cap W^{1,2}(\Omega)$ is a stationary weak solution of the model if and only if for some sequence $\sigma = (\sigma_i)_{i \in \mathbb{N}} \subset \{0, 1\}$,*

$$w = m_\sigma(x) := \sum_{i \in \mathbb{N}} \sigma_i \chi_{G_i}(x) m(x) \quad x \in \Omega,$$

in other words the stationary weak solutions have the form

$$m_\sigma(x) = \begin{cases} = m(x) & \text{if } x \in G_i \text{ for some } i \in \mathbb{N} \text{ with } \sigma_i = 1, \\ = 0 & \text{otherwise} \end{cases}$$

Models with advection on fitness only (continued)

The model with only advection on fitness has equilibria

$$m_\sigma(x) = \begin{cases} = m(x) & \text{if } x \in G_i \text{ for some } i \in \mathbb{N} \text{ with } \sigma_i = 1, \\ = 0 & \text{otherwise} \end{cases}$$

where $\{G_i : i \in \mathbb{N}\}$ is the set of connected components of $\{x \in \Omega : m(x) > 0\}$.

The equilibria include $m_+(x)$ as a possible equilibrium, so the models can produce an ideal free distribution and will do so if $u(x, 0) > 0$.

However, there may be places where $m > 0$ but $u = 0$, depending on the initial data. The set of i with $\sigma_i \neq 0$ may be empty so $m_\sigma(x) \equiv 0$ is included in the set of equilibria.

Solutions stabilize, that is, for any nonnegative weak solution $u(x, t)$, $u(x, t) \rightarrow m_\sigma(x)$ (in $C^0(\bar{\Omega})$) for some σ as $t \rightarrow \infty$.

However, solutions with nontrivial nonnegative initial data may $\rightarrow 0$.

Ecological traps

Still considering

$$\begin{cases} \frac{\partial u}{\partial t} = \alpha \nabla \cdot [u \nabla u - u \nabla(m(x))] + (m(x) - u)u & \text{in } \Omega \times [0, \infty), \\ [u \nabla u - u \nabla(m(x))] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times [0, \infty) \\ u(x, 0) = u_0(x). \end{cases}$$

Theorem 6. *Suppose that m is such that for some open subset Ω_1 of Ω , the inequalities*

$$\sup_{x \in \partial\Omega_1 \cap \Omega} m(x) < \sup_{x \in \Omega_1} m(x) \leq 0$$

hold. Then there exists a nontrivial nonnegative $w \in C^0(\bar{\Omega})$ with the property that for any nonnegative $u_0 \in C^0(\bar{\Omega})$ such that $0 \not\equiv u_0 \leq w$ in Ω , the solution u with $u(x, 0) = u_0$ satisfies $u \not\equiv 0$ but

$$u(\cdot, t) \rightarrow 0 \quad \text{in } C^0(\bar{\Omega}) \quad \text{as } t \rightarrow \infty.$$

In particular, such a function w can be found whenever m attains a strict nonpositive local maximum at some point in $\bar{\Omega}$.

The idea is that individuals will move up the fitness gradient toward better but still unsuitable habitat, with no true diffusion to spread the population further.

A recent result for a related system

S. Kondratyev, L. Monsaingeon, and D. Vorotnikov (2016) have a preprint on arXiv (arXiv:1603.06431v1 [math.AP]) on the system

$$\frac{\partial u_i}{\partial t} = -\nabla \cdot (u_i \nabla f_i) + u_i f_i, \quad i = 1 \dots N,$$

with

$$f_i = m_i(x) - (A(x)\vec{u})_i$$

where $A(x)$ is a positive definite matrix.

The results are spirit of those developed by Otto (2001) for the porous medium equation; specifically they show that the system generates a gradient flow (on a space of Radon measures) and obtain the existence of weak solutions that converge to an ideal free distribution. The methods are largely based on recent ideas from optimal transport theory.

Random dispersal versus fitness dependent dispersal

Intuition suggests that fitness dependent dispersal should be advantageous versus random dispersal. Cantrell, C., Lou, and Xie (2013) considered competition between ecologically similar populations, one with random dispersal versus one with random and fitness dependent dispersal:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla f(x, u + v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \Delta v + v f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla f(x, u + v)] \cdot \vec{n} = \nabla v \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $f(x, u) = m(x) - u$.

This model is a second order quasilinear system. The right side of the system and its linearizations have the property of *Normal Ellipticity*: If an $n \times n$ system of linear second order differential operators on a domain $\Omega \subset \mathbb{R}^N$ has principal symbol $A(x, \xi) = \sum_{i,j=1}^N a_{ij}(x) \xi_i \xi_j$ where $a_{ij} = (a_{ij}^{rs})$ is an $n \times n$ matrix for $i, j = 1 \dots N$, the system is *normally elliptic* if the spectrum of the matrix $A(x, \xi)$ is contained in $\{z \in \mathbb{C} : \text{Re } z > 0\}$ for all $x \in \bar{\Omega}$ and $\xi \in \mathbb{R}^N \setminus \{0\}$. Normal ellipticity is weaker than uniform ellipticity but is sufficient for local existence for the time dependent model and implies that linearized operators for the equilibrium model have Fredholm properties needed for global bifurcation.

Random dispersal versus fitness dependent dispersal (continued)

Still considering

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla f(x, u + v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \Delta v + v f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla f(x, u + v)] \cdot \vec{n} = \nabla v \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $f(x, u) = m(x) - u$, μ and ν are positive, and $\Omega \subset \mathbb{R}^n$ is bounded.

Some results from (Cantrell, C., Lou, and Xie 2013), roughly stated:

Global existence for the time dependent model if $n = 1, 2$, and if $\nu > \mu$, for $n \geq 3$.

If $m(x)$ is nonconstant and positive somewhere then for α/μ large, the semi-trivial equilibrium $(0, v^*)$ is unstable if it exists. (It will exist if $\int_{\Omega} m > 0$ or ν is small.)

If either $m(x)$ changes sign or $m(x)$ is non-constant and $m(x) > 0$, then for α/μ and α both large, the semi-trivial equilibrium $(u^*, 0)$ is stable.

If $m(x)$ changes sign then for α large there is no positive equilibrium (u^{**}, v^{**}) .

These results suggest that fitness based dispersal can be advantageous. However:

Open Question: If $m(x)$ changes sign and $\alpha, \alpha/\mu$ are large, is $(u^*, 0)$ globally stable? (That would be true in a semilinear system because of monotonicity.)

More on random dispersal versus fitness dependent dispersal

Again,

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla f(x, u + v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \Delta v + v f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla f(x, u + v)] \cdot \vec{n} = \nabla v \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $f(x, u) = m(x) - u$.

There is a bifurcation analysis of coexistence states, with α as bifurcation parameter in (Cantrell, C., Lou, and Xie 2013) but only for the case where Ω is convex and the Hessian of $m(x)$ is negative definite, and the analysis of the global behavior of the bifurcating branch requires that $m(x)$ changes sign.

Global existence for the time dependent system was obtained for any space dimension by Y. Lou, Y. Tao, and M. Winkler (2014) without conditions other than positivity on μ and ν in the case that the domain Ω is convex.

The convexity condition was removed by X. Li (2015).

No dispersal versus fitness dependent dispersal

Y. Lou, Y. Tao, and M. Winkler (2014) (the same paper cited before) also considered a model for a population with purely fitness-based dispersal versus one with no dispersal at all:

$$\begin{cases} u_t = -\alpha \nabla \cdot [u \nabla f(x, u + v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = v f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ [u \nabla f(x, u + v)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where again $f(x, u) = m(x) - u$.

They obtained global existence of nonnegative weak solutions in the case Ω is convex.

They also showed that if $u(x, 0) \geq 0$ and $v(x, 0) > 0$ then the weak solution stabilizes to (u_∞, v_∞) with $v_\infty > 0$ a.e. on $\{x \in \Omega : m(x) > 0\}$ and $u_\infty + v_\infty = m_+$ so in fact $u + v \xrightarrow{*} m_+$ (convergence in the weak* sense) in $L^\infty(\Omega)$.

Note that both pure advection on fitness and no movement at all are dispersal strategies that can produce an ideal free distribution.

Some related work

D. Ryan and R. S. Cantrell (2015): They studied an intraguild predation model (top predator eats intraguild prey, both of them eat a resource) where the dispersal of the intraguild prey is related to fitness. They obtained existence of a global attractor and persistence results. (Cantrell and collaborators have work in progress on related models.)

Y.-J. Kim, O. Kwon, and F. Li (2013), (2014): They studied population models with a different form of nonlinear diffusion related to starvation.

J. T. Rowell (2009), (2010): He used models with fitness based dispersal to address ecological problems such as range limits and the spatial distribution of populations more generally. (These papers are in theoretical biology journals and do not have much mathematical analysis)

Possible future directions

As noted before, many of the results in existing papers are incomplete or have only been proved under hypotheses that seem too restrictive.

Essentially nothing is known about the general case

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla f(x, u + v)] + u f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nabla \cdot [\nu \nabla u - \beta u \nabla f(x, u + v)] + v f(x, u + v) & \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla f(x, u + v)] \cdot \vec{n} = [\nu \nabla u - \beta u \nabla f(x, u + v)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

This type of system seems especially challenging if $\mu \neq 0$ but $\nu = 0$ since the approaches used so far for degenerate and nondegenerate diffusion are different.

A somewhat reasonable conjecture is that dispersal strategies that can produce an ideal free distribution are evolutionarily stable in more general models

$$u_t = \nabla \cdot [d(x, u) \nabla u - \alpha u \nabla e(x, u)] + f(x, u)u \text{ in } \Omega \times (0, \infty).$$

What are those strategies? (Advection on fitness is one.) Is the conjecture true?

The case where $m(x)$ changes sign seems especially challenging.

(For $m(x) > 0$ there are linear nondegenerate dispersal strategies that produce an ideal free distribution, and they are known to be evolutionarily stable.)

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