Nonlinear Diffusion and Resource Matching in Population Dynamics

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Set-Up

Consider a resident biological species in a spatial habitat that equilibrates over time to a stable spatially dependent carrying capacity. Suppose that an ecologically identical species (e.g., a mutant) is introduced into the habitat in small numbers. Suppose the second species (which we call the invader) differs from the resident only in the way that it disperses across the habitat. Will the invader be able to establish itself in the habitat or will the resident species be able to repel the invasion? To address this question, we regard the two species as competitors and determine whether the steady state given by the carrying capacity of the resident and the absence of the invader is stable or unstable relative to the introduction of small numbers of invaders. If the spatial distribution that is set up by the resident’s dispersal process is ecologically stable relative to invasion by an ecologically identical species using a different dispersal strategy, we will regard the resident as being non-invasive. If the resident is non-invasive relative to any ecologically identical invader employing a dispersal strategy from some class of strategies, we borrow nomenclature from adaptive dynamics and say the resident employs an EVOLUTIONARILY STABLE DISPERSAL STRATEGY. This approach involves a pairwise invasibility analysis.
Hastings (TPB, 1983)

\( u_t = D \nabla [\mu(x) \nabla u] + F(x,u) \ u \quad \text{in} \quad \Omega \times (0,\infty) \)
\( \nabla u \cdot \eta = 0 \quad \text{on} \quad \partial \Omega \times (0,\infty) \)

\( v_t = d \nabla [\mu(x) \nabla v] + F(x,u^* + v) \ v \quad \text{in} \quad \Omega \times (0,\infty) \)
\( \nabla v \cdot \eta = 0 \quad \text{on} \quad \partial \Omega \times (0,\infty) \)

\( 0 = D \nabla [\mu(x) \nabla u^*] + F(x,u^*) \ u^* \quad \text{in} \quad \Omega \times (0,\infty) \)
\( \nabla u^* \cdot \eta = 0 \quad \text{on} \quad \partial \Omega \times (0,\infty) \)

\( F(x,u^*) \neq 0 \quad \text{and} \quad 0 < d < D \Rightarrow \text{invasion when rare} \)
Observations

1. The “D” strategy here would be an **ESS** relative to a “d” strategy if d > D.

   2. Slower movement has the advantage here. To this end, we again borrow from adaptive dynamics nomenclature to say that no movement is a **CONVERGENT STABLE STRATEGY (CSS)**.

3. \( F(x,u^*) \neq 0 \). So for any \( D > 0 \), \( D \nabla [\mu(x) \nabla u^*] \neq 0 \). Here \( F \) is called the per capita growth rate or fitness.

4. Frequently if \( F(x,u) = 0 \) has the unique solution \( u_\#(x) \) with \( u_\#(x_0) > 0 \) for some \( x_0 \in \Omega \), then \( u^*(x) \to (u_\#)^+(x) \) as \( D \to 0 \), uniformly on compact subsets of \( \Omega \), where \( (u_\#)^+(x) = u_\#(x) \) when \( u_\#(x) > 0 \) and 0 otherwise. In such a case \( u^*(D) \) approximates resource availability better as \( D \to 0 \).

5. Hastings’ single equation approach allows us to assess evolutionary advantage. Using a two species competition model allows us to consider full ecological dynamics, allowing us the possibility of observing competitive exclusion.
Dockery et al JMB (1998)

\[ u_t = \mu \Delta u + u[ m(x) - u - v] \]
\[ v_t = v \Delta v + v[ m(x) - u - v] \quad \text{in} \quad \Omega \times (0, \infty) \]
\[ \nabla u \cdot \eta = \nabla v \cdot \eta = 0 \quad \text{on} \quad \partial \Omega \times (0, \infty) \]

\[ v < \mu \implies \text{species with density } u \text{ is eliminated by species with density } v \]

(convergent stability)
More Context

Pure diffusion and diffusion with physical advection are thought of as unconditional forms of dispersal. As we have noted, these forms of dispersal can lead to a mismatch between the distribution of the population and the distribution of the resources. The mismatch is diminished as the dispersal rate is lowered, an example of a phenomenon Altenberg (PNAS 2012) has called the reduction principle. Conditional dispersal refers to dispersal that is influenced by the environment or the presence of other organisms. For certain types of conditional dispersal, evolution can favor faster dispersal over slower dispersal if faster dispersal allows the population to track resources more efficiently. A landmark contribution in this direction is that of McPeek and Holt (Am Nat 1992). They suggested in the context of discrete time two patch models that among conditional dispersal strategies in a spatially heterogeneous but temporally constant environment, a strategy which results in an ideal free distribution for a single species at equilibrium is an ESS.
Notes

1. In the context of discrete diffusion patch models, Cantrell, Cosner and Lou (JMB 2012) showed that when there are patches that can be regarded as net favorable (source patches) and patches that can be regarded as net unfavorable (sink patches), no movement is the dispersal strategy favored by selection. When all patches are sources, we show that movement which can be regarded as ideal free is an ESS. These results are valid for an arbitrary number of patches and competitors. They expand earlier results of Cantrell, Cosner, DeAngelis and Padron (JBD 2007.)

2. In the case of pairwise interactions, we have “IFD =ESS” results in the context of reaction-diffusion-advection models (Cantrell, Cosner and Lou (MBE 2010), Averill, Lou and Munther (JBD 2012) and Gejji, Lou, Munther and Peyton (BMB 2102) and integro-difference non-local models (Cantrell, Cosner, Lou and Ryan, CAMQ 2013).
Ideal Free Distribution

1. Verbal description in the ecology literature (Fretwell and Lucas, Acta Biotheoretica 1970) of how organisms would locate themselves if they could move to optimize fitness. In the original formulation, a finite number of sites is envisioned and fitness is decreased by an increased number of conspecifics.

2. Example. Suppose four sites with intrinsic growth rates (fitness at zero density) $m_1 > m_2 > m_3 > m_4$. (Site 1 has the best resources.) Assume fitness is diminished linearly by average density (logistic). The organism with average density $u_i$ in Site $i$ fills up Site 1 until $m_1 - u_1 = m_2$ at which point the organism continues to fill up Site 1 and starts to fill up Site 2. This process continues until $m_1 - u_1 = m_2 - u_2 = m_3$. At the end of the process an ideal free distribution is reached when $m_1 - u_1 = m_2 - u_2 = m_3 - u_3 = m_4 - u_4$. If the overall population is fixed $m_i - u_i$ may be positive. If one has underlying population dynamics the process must continue until fitness reaches zero, at which point the population stops growing. In that case $m_1 - u_1 = m_2 - u_2 = m_3 - u_3 = m_4 - u_4 = 0$. In either event there can now be no net movement after an IFD is reached. (Net movement would enable some members of the population to move to increase fitness, which they would do.)
3. Continuum formulation (Cosner and Kshatriya, TPB 2001)

4. Advection-reaction model with IDF as equilibrium (Cosner TPB 2005)

\[
\frac{du}{dt} = -\alpha \nabla \cdot [u \nabla (m-u)] + u (m-u) \quad \text{in } \Omega \times (0,\infty)
\]
\[
u \nabla (m-u) \cdot \eta = 0 \quad \text{on } \partial \Omega \times (0,\infty)
\]

Here fitness is \( m-u \), we assume \( m(x) > 0 \) throughout \( \Omega \) and \( u(x) \equiv m(x) \) is an equilibrium solution for which
\[
-\alpha \nabla \cdot [u \nabla (m-u)] \equiv 0.
\]

So we regard \( m(x) \) as an IFD and the equilibrium position is achieved by perfectly matching resources.

5. Contrast with

\[
\frac{du}{dt} = \mu \nabla^2 u + u (m-u) \quad \text{in } \Omega \times (0,\infty)
\]
\[
\nabla u \cdot \eta = 0 \quad \text{on } \partial \Omega \times (0,\infty).
\]

Diffusion under-matches the best resources and over-matches the poorest. Dockery et al (1998) show that a slower disperser is favored over a faster disperser in this context. In the limit as \( \mu \to 0 \) \( u(x) \equiv m(x) \) (assuming \( m > 0 \)) is an equilibrium solution that arises from perfectly matching resources.
1. One might modify the random dispersal model by adding advection up the resource to get
\[
\begin{align*}
    u_t &= \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u (m-u) \text{ in } \Omega \times (0,\infty) \\
    [\mu \nabla u - \alpha u \nabla m] \cdot \eta &= 0 \text{ on } \partial \Omega \times (0,\infty).
\end{align*}
\]

What happens in a model of the form
\[
\begin{align*}
    u_t &= \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u (m-u - v) \\
    v_t &= \nu \nabla^2 v + v (m-u - v) \\
\end{align*}
\]
in \(\Omega \times (0,\infty)\) with
\[
[\mu \nabla u - \alpha u \nabla m] \cdot \eta = 0 = \nabla v \cdot \eta
\]
on \(\partial \Omega \times (0,\infty)\) ? Assume \(\int m > 0\), the set of critical points of \(m\) has measure 0, and \(\nu < \mu\).

(a) When \(\alpha << 1\) species with density \(v\) competitively excludes the species with density \(u\).
(b) Once \(\alpha\) increases beyond a small threshold, the species with density \(u\) competitively excludes the species with density \(v\). (c) For large values of \(\alpha\), each species can invade the other at carrying capacity and we have coexistence. What happens here is that the species with density \(u\) concentrates so heavily on the most favorable parts of the environment that it leaves room for its competitor to persist. So this form of advection when strong mediates coexistence instead of promoting evolutionary advantage.
2. Adding advection up the gradient of the resource is thus not the best mechanism for trying to gain evolutionary advantage through conditional dispersal. A natural idea is to modify the form of advection in some way. If $m > 0$ in $\Omega$, replacing $\nabla m$ with $\nabla m/m = \nabla(\ln(m))$ gives the equation

$$u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln(m)] + u (m-u) \text{ in } \Omega \times (0,\infty)$$

$$[\mu \nabla u - \alpha u \nabla \ln(m)] \cdot \eta = 0 \text{ on } \partial \Omega \times (0,\infty).$$

In this case, if $\mu = \alpha$, $u \equiv m$ is an equilibrium which can be regarded as ideal free and which matches resources perfectly. Notice also that that an IFD is generated on the basis of purely local information (the species has to be “smart but not omniscient” (S. Ellner, personal communication)). “IFD = ESS” in the model has been explored in Cantrell, Cosner and Lou (MBE 2010), Averill, Lou and Munther (JBD 2012), and Gejji, Lou Munther and Peyton (BMB 2012).
3. Another possibility would be to advect up the gradient of fitness as in the Cosner model. (Equivalently one could think of so doing as adding a diffusive component to the Cosner model.) There are several good reasons, both mathematical and biological, to proceed in this way.

(1) While such a strategy is not ideal free, as $\alpha/\mu$ becomes large the dispersal is predominately advective and it is reasonable to consider whether it might be “approximately ideal free” and thus confer evolutionary advantage over say a purely random dispersal strategy.

(2) Some degree of random motion is probably a realistic assumption about the way many organisms move.

(3) One does not require $m$ to be positive everywhere, as in the preceding model.

(4) Adding diffusion to the Cosner model brings us into the realm of quasi-linear parabolic problems, which gives some theory to work with but also much to think about mathematically.
Random Dispersal versus Fitness Dependent Dispersal

The Competition Model

\[ u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla (m - u - v)] + u (m - u - v) \]

\[ v_t = \nabla \cdot [v \nabla v] + v (m - u - v) \]

in \( \Omega \times (0, \infty) \) and

\[ [\mu \nabla u - \alpha u \nabla (m - u - v)] \cdot \eta = 0 = \nabla v \cdot \eta \]

on \( \partial \Omega \times (0, \infty) \).
Single Species Model with Fitness Dependent Dispersal

\[ u_t = \nabla \cdot (\mu \nabla u - \alpha u \nabla (m - u)) + u (m-u) \quad \text{in } \Omega \times (0, \infty) \]

\[ [\mu \nabla u - \alpha u \nabla (m - u)] \cdot \eta = 0 \quad \text{on } \partial \Omega \times (0, \infty) \]
References


Results

Theorem 1 (A,B) Suppose that $\Omega \subseteq \mathbb{R}^N$ with $\partial \Omega$ of class $C^{2+\gamma}$, $m \in C^{2+\gamma}(\text{cl } \Omega)$ for some $\gamma \in (0,1)$. If $\mu > 0$ and $\alpha \geq 0$, the single species model with fitness dependent dispersal has a unique solution $u \in C^{2,1}(\text{cl } \Omega \times (0,\infty)) \cap C(\text{cl } \Omega \times [0,\infty))$. If $\mu > 0$, $v > 0$, and $\alpha > 0$, solutions to the competition model corresponding to bounded nonnegative initial data exist globally for $N = 1, 2$ and also for $N \geq 3$ provided $v > \mu$. By (C), we may remove the restriction $v > \mu$ when $N \geq 3$ if $\Omega$ is convex.

Theorem 2 (A) If $u = 0$ is linearly unstable, the single species model with fitness dependent dispersal has at least one positive steady state. (The condition $\int m > 0$ guarantees the existence of a steady state for any $\mu > 0$ and $\alpha \geq 0$.)
Theorem 3 (A) (i) Any positive steady state $u$ of the single species model with fitness dependent dispersal converges to $m_+$ (the positive part of $m$) weakly in $H^1(\Omega)$ and strongly in $L^2(\Omega)$ as $\alpha/\mu \to \infty$. Given $\eta > 0$, if $\alpha \geq \eta$ and $\alpha/\mu \to \infty$, $u \to m_+$ in $C^{\gamma}(\text{cl } \Omega)$ for some $\gamma \in (0,1)$.

(ii) If $m > 0$ in $\text{cl } \Omega$, given $\eta > 0$, if $\alpha \geq \eta$ and $\alpha/\mu \to \infty$, $u \to m$ in $C^2(\text{cl } \Omega)$.

(iii) If $m > 0$ in $\text{cl } \Omega$, then for large values of $\alpha/\mu$, the single species model with fitness dependent dispersal has a unique positive steady state which is globally asymptotically stable.

Now let $u^\sim$ denote a positive steady state of the single species model with fitness dependent dispersal and $\theta$ denote the unique positive steady state of the single species model with purely random dispersal.

Theorem 4 (B) Suppose that $m$ is non-constant and positive somewhere in $\Omega$. (i) If $\mu < \nu$, then for small $\alpha > 0$, $(u^\sim,0)$ is linearly stable and $(0, \theta)$ is linearly unstable, whenever they exist.

(ii) If $\mu > \nu$, then for small $\alpha > 0$, $(u^\sim,0)$ is linearly unstable and $(0, \theta)$ is linearly stable, whenever they exist.
**Theorem 5 (B)** Suppose that $m$ changes sign in $\text{cl } \Omega$ or that $m > 0$ in $\text{cl } \Omega$ and non-constant. Then for any $\nu$ and $\eta > 0$, there is a positive constant $\Lambda_1(\nu, \eta, m, \Omega)$ so that if $\alpha \geq \eta$ and $\alpha/\mu \geq \Lambda_1(\nu, \eta, m, \Omega)$, $(u^\sim, 0)$ is linearly stable. Moreover, for any $\nu > 0$, there is a uniquely determined constant $\Lambda_2(\nu, m, \Omega)$ so that if $\alpha/\mu \geq \Lambda_2(\nu, m, \Omega)$, $(0, \theta)$ is linearly unstable whenever it exists.

Theorem 5 implies that random dispersal compares unfavorably to an approximately ideal free dispersal strategy.

**Theorem 6 (B)** Suppose that $m$ changes sign in $\Omega$. Then for any $\mu, \nu > 0$, there is a constant $\Lambda_3(\mu, \nu, m, \Omega)$ so that if $\alpha \geq \Lambda_3(\mu, \nu, m, \Omega)$, the competition model admits no coexistence state.

Theorems 5 and 6 strongly suggest that $(u^\sim, 0)$ should be the global attractor. We cannot yet verify that such is the case.
**Theorem 7 (B)** Suppose that $\Omega$ is convex and that the Hessian matrix of $m$ is negative definite for all $x$ in $\text{cl } \Omega$. Then there is an $\nu_0(m, \Omega)$ so that:

(i) If $\nu > \max(\nu_0, \mu)$, $(0, \theta)$ is linearly unstable for every $\alpha \geq 0$.

(ii) If $\mu > \nu > \nu_0$, there is a unique $\alpha^* = \alpha^*(\mu, \nu, m, \Omega)$ so that $(0, \theta)$ is linearly stable for $\alpha \in [0, \alpha^*)$ and linearly unstable for $\alpha > \alpha^*$.

**Theorem 8 (B)** Suppose that $\Omega$ is convex and that the Hessian matrix of $m$ is negative definite for all $x$ in $\text{cl } \Omega$ and that $\mu > \nu > \nu_0$.

(i) **(Local bifurcation)** There exist an $\epsilon > 0$ and continuous functions $\alpha(s) : (\alpha^* - \epsilon, \alpha^* + \epsilon) \to \mathbb{R}^1$ and $\phi(s), \psi(s) : (-\epsilon, \epsilon) \to C^2(\text{cl } \Omega)$ so that $\alpha(0) = \alpha^*$, $\phi(0) = \phi^* > 0$, $\psi(0) = \psi^*$ and steady-state solutions of the competition model near $(\alpha^*, 0, \theta)$ consist precisely of $(\alpha, 0, \theta)$ and $\{(\alpha(s), s\phi(s), \theta + s\psi(s)) | s \in (-\epsilon, \epsilon)\}$.

(ii) **(Global bifurcation)** Assume further that $m$ changes sign in $\Omega$. Then the component-wise positive steady-states of the competition model that emanate from $(\alpha, 0, \theta)$ at $(\alpha^*, 0, \theta)$ contain a continuum which meets $(\alpha^{**}, u^\sim, 0)$, where $u^\sim$ is a positive steady-state of the single species model with fitness dependent dispersal with $\alpha = \alpha^{**}$. 