

Evolutionary Aspects of Directed Movement

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Evolution of Dispersal in spatially varying but temporally constant environments

Basic questions:

1. What strategies can be expected to evolve?
2. What mechanisms can lead to such strategies?

Key ideas:

- Compare strategies in terms of evolutionary stability:
A strategy is evolutionarily stable if a resident population using it cannot be invaded by a small population using another strategy. ("ESS" ~ evolutionarily stable strategy)
- Use spatially explicit models for population dynamics and interactions to describe strategies in terms of mechanisms and to assess invasibility

A simple approach and a basic result (Hastings 1983)

Consider models of the form

$$\frac{\partial u}{\partial t} = D \nabla \cdot (\mu(x) \nabla u) + f(x, u)u = 0 \text{ on } \Omega \times (0, \infty)$$

$$\frac{\partial u}{\partial n} = 0 \text{ on } \partial \Omega \times (0, \infty) \text{ (no flux)}$$

(or in discrete space $\frac{du_i}{dt} = D \left(\sum_{j \neq i} c_{ij} u_j - \sum_{j \neq i} c_{ji} u_j \right) + f_i(u_i) u_i$,
 $i=1, \dots, N$, with $c_{ij} = c_{ji}$)

Suppose this model has a positive equilibrium u^* .

- Think of that as a resident population.
- Model an ecologically similar invading (small) population v by $\frac{\partial v}{\partial t} = d \nabla \cdot (\mu(x) \nabla v) + f(x, u^* + v)v$ on $\Omega \times (0, \infty)$

$$\frac{\partial v}{\partial n} = 0 \text{ on } \partial \Omega \times (0, \infty)$$

$v=0$ stable $\Leftrightarrow u^*$ not invaded by v .

Hastings' approach (continued)

For the resident:

$$\star D \nabla \cdot (\mu(x) \nabla u^*) + f(x, u^*) u^* = 0 \text{ in } \Omega, \quad \frac{\partial u^*}{\partial n} = 0 \text{ on } \partial\Omega$$

For the invader (linearized model at $v=0$)

$$\star \star d \nabla \cdot (\mu(x) \nabla \psi) + f(x, u^*) \psi = 0 \text{ in } \Omega, \quad \frac{\partial \psi}{\partial n} = 0 \text{ on } \partial\Omega$$

- Invasion is possible \Leftrightarrow principal eigenvalue $\sigma_1 > 0$ in $\star \star$.
- $\star \star$ can be viewed as an eigenvalue problem.
since $u^* > 0$, the principal eigenvalue is 0.

Key assumption: $f(x, u^*) \not\equiv 0$, so $\nabla u^* \neq 0$.

Suppose $d < D$:

$$0 = -D \int \mu |\nabla u^*|^2 dx + \int f(x, u^*) u^{*2} dx \geq -d \int \mu |\nabla u^*|^2 dx + \int f(x, u^*) u^{*2} dx$$

$$\frac{\int u^{*2} dx}{\int u^{*2} dx}$$

(all \int 's are
over Ω)

$$\leq \sup_{\phi \in W^{1,2}(\Omega)} \frac{-d \int \mu |\nabla \phi|^2 dx + \int f(x, u^*) \phi^2 dx}{\int \phi^2 dx}$$

$$= \sigma_1 \quad \text{so} \quad \sigma_1 > 0 \quad (\Rightarrow v \text{ can invade})$$

Conclusion from Hastings' approach:

If $u^* > 0$ is a stable equilibrium of

$$\frac{\partial u}{\partial t} = D \nabla^2 (\mu(x) \nabla u) + f(x, u) \text{ in } \Omega \times (0, \infty), \quad \frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega \times (0, \infty)$$

and $f(x, u^*) \not\equiv 0$, then u^* can be invaded by a small population using dispersal strategy $d \nabla^2 (\mu(x) \nabla v)$

$$\Leftrightarrow d < D.$$

Thus, no dispersal strategy with $D > 0$ and $f(x, u^*) \not\equiv 0$ can be evolutionarily stable. (Selection for slow dispersal)

What is behind this?

Integrating the equation for $u^* \Rightarrow \int_{\Omega} f(x, u^*) u^* dx = 0$

$\Rightarrow f(x, u^*)$ must change sign if $f(x, u^*) \not\equiv 0$

e.g.: logistic case: $f(x, u^*) = m(x) - u^*$ changing sign

$\Rightarrow \begin{cases} u^* > m(x) & \text{some places} \\ u^* < m(x) & \text{other places} \end{cases} \Rightarrow \begin{cases} u^* \text{ does not match} \\ \underline{\text{resource availability}} \end{cases}$

Alternative approach: Model a full competition system for u and v .

(McPeek and Holt 1992, two patch, discrete time)

(Dockery et al. 1998, reaction diffusion):

$$\frac{\partial u}{\partial t} = \mu \Delta u + (m(x) - u - v) u \quad \text{in } \Omega \times (0, \infty)$$

$$\frac{\partial v}{\partial t} = \nu \Delta v + (m(x) - u - v) v$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \partial \Omega \times (0, \infty).$$

Conclusion: $\nu < \mu \Rightarrow (u^*, 0)$ unstable, $(0, v^*)$ stable,
 v excludes u
(still selection for slow dispersal)

Notice: • No advection.

• Diffusion rate may vary but diffusion is of physical type based on Fick's law.

(No behavioral aspects of dispersal at micro scale)

(No direct connection to foraging)

McPeek and Holt: (numerical experiments)

$$\begin{cases} u_i'(t) = \exp \left[1 - \frac{(u_i(t) + v_i(t))}{K_i} \right] u_i(t) \\ v_i'(t) = \exp \left[1 - \frac{(u_i(t) + v_i(t))}{K_i} \right] v_i(t) \end{cases} \quad i=1,2$$

$$\begin{cases} u_i(t+1) = (1-d_{ij})u_i'(t) + d_{ji}u_j'(t) & i=1,2, \quad j \in \{1,2\}, j \neq i \\ v_i(t+1) = (1-D_{ij})v_i'(t) + D_{ji}v_j'(t) \end{cases}$$

If $D_{ij} = D_{ji}$, $d_{ij} = d_{ji}$ (unconditional dispersal)

then selection favors lower dispersal rates;

If $d_{ij} \neq d_{ji}$ is allowed (conditional dispersal) then selection favors strategies such that $d_{iz}/d_{zi} = K_z/K_i$

(so $K_i = (1-d_{ij})K_i + d_{ji}K_j$; that is,

(K_1, K_2) = equilibrium without dispersal = equilibrium with dispersal
 (and at equilibrium $\exp(1 - \frac{u_i}{K_i}) = \exp(1 - \frac{u_j}{K_j})$)

Hypothesis (suggested by work of Hastings, McPeek and Holt,

Dockery et al.): The dispersal strategies that are evolutionarily stable are those that allow organisms to match the spatial distribution of resources.

Mathematically (reaction-diffusion-advection case):

$$\text{For } \frac{\partial u}{\partial t} = \nabla \cdot [\mu(x, u) \nabla u - u \nabla e(x, u)] + (m(x) - u) u,$$

evolutionarily stable strategies should yield an equilibrium $u^* = m(x)$ (if $m(x) > 0$) or $u^* = m(x)_+$ (if $m(x)$ changes sign).

$$\Rightarrow \nabla \cdot [\mu \nabla m - m \nabla e] = 0, \text{ at least for } m > 0.$$

The key biological features:

- Fitness $= m(x) - u^* = \text{constant} (= 0)$ at equilibrium u^*
- $\nabla \cdot [\mu \nabla u^* - u^* \nabla e] = 0$ (No net movement at equilibrium)

Ecological theory: Ideal Free Distribution (Fretwell and Lucas 1970)

If individuals have complete knowledge of their environment and are free to move, they will locate themselves to optimize fitness.

- ⇒ • At equilibrium all individuals at all locations have equal fitness (otherwise some would move to improve theirs)
• At equilibrium there should be no net movement

Rephrased Hypothesis: Evolutionarily stable dispersal strategies are those that can produce ideal free population distributions.

Program:

- Check hypothesis in various modeling approaches
- Look for mechanisms that could allow dispersal behavior to induce ideal free distributions.
(microscale movement patterns; foraging behavior; ??)

More details (reaction-diffusion-advection case)

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

$$\frac{\mu \partial u}{\partial n} - \alpha u \frac{\partial v}{\partial n} = 0 \text{ on } \partial \Omega \times (0, \infty) \text{ (no flux B.C.)}$$

Interpret fitness as local intrinsic growth rate $f(x, u)$.

- Dynamic idea for ideal free dispersal - move up gradient of $f(x, u)$.
- Equilibrium idea for ideal free dispersal: $u^* > 0$ equilibrium
Equal fitness $\sim f(x, u^*) = \text{constant}$
Since $\int f(x, u^*) u^* dx = 0$ (by no-flux boundary condition)
this implies $f(x, u^*) \equiv 0$ (Directly contradicting key assumption in Hastings' analysis)

No net movement \sim

$$\nabla \cdot [\mu(x, u^*) \nabla u^* - \alpha u^* \nabla v(x, u^*)] = 0 \text{ in } \Omega \text{ (+B.C.)}$$

Mechanisms

(Micro scale) (Following Okubo 1980)

$u(x)$ = density at x J = flux from $(x-\Delta x, x)$ to $(x, x+\Delta x)$

(rate of movement per time step Δt)

In general: As $\Delta x, \Delta t \rightarrow 0$, $\frac{\partial u}{\partial t} = -\frac{\partial J}{\partial x}$

1. Simple diffusion: At each time step Δt , individuals move randomly from $x-\Delta x$ to x or x to $x-\Delta x$ at the same rate $p_0(x)$ (no patch dependence at microscale)

$$\begin{aligned} J &= \frac{1}{\Delta t} p_0(x) [u(x-\Delta x, t) \Delta x - u(x, t) \Delta x] \\ &= \frac{(\Delta x)^2}{\Delta t} p_0(x) \left[\frac{u(x-\Delta x, t) - u(x, t)}{\Delta x} \right] \end{aligned}$$

Diffusive scaling : $\frac{(\Delta x)^2}{\Delta t} = D_0$; $D(x) = D_0 p_0(x)$ as $\Delta x, \Delta t \rightarrow 0$

Then: $J \rightarrow -D(x) \frac{\partial u}{\partial x}$ so

$$\boxed{\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} (D(x) \frac{\partial u}{\partial x})}$$

2. dispersal probability depends on departure point

$$\begin{aligned} J &= \frac{1}{\Delta t} [p_1(x-\Delta x) u(x-\Delta x, t) \Delta x - p_1(x) u(x, t) \Delta x] \\ &= \frac{(\Delta x)^2}{\Delta t} \left[\frac{p_1(x-\Delta x) u(x-\Delta x, t) - p_1(x) u(x, t)}{\Delta x} \right] \end{aligned}$$

Again, diffusive scaling $\frac{(\Delta x)^2}{\Delta t} = D_0$; $D(x) = D_0 p_1(x)$

but in this case as $\Delta x, \Delta t \rightarrow 0$,

$$J \rightarrow -\frac{\partial}{\partial x} (D(x) u) \text{ so}$$

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

3. dispersal probability depends on arrival patch

$$J = \frac{1}{\Delta t} [p_2(x) u(x-\Delta x, t) \Delta x - p_2(x-\Delta x) u(x, t) \Delta x]$$

$$= \frac{(\Delta x)^2}{\Delta t} p_2(x) p_2(x-\Delta x) \left[\left(\frac{u(x-\Delta x, t)}{p_2(x-\Delta x)} - \frac{u(x, t)}{p_2(x)} \right) \right] / \Delta x$$

$$J \rightarrow -D(x)^2 \frac{\partial}{\partial x} \left(\frac{u}{D(x)} \right) \text{ so}$$

$$\boxed{\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left[D(x)^2 \frac{\partial}{\partial x} \left(\frac{u}{D(x)} \right) \right]}$$

$$D(x) = D_0 p_2(x)$$

4. Advection $J = \frac{1}{\Delta t} \left[g(x-\Delta x) u(x-\Delta x) \Delta x \right]$

Advective scaling $\frac{\Delta x}{\Delta t} = e_0$, $e(x) = e_0 g(x)$, $\Delta x, \Delta t \rightarrow 0$

so $J \rightarrow e(x)u(x)$

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} (e(x)u)$$

Possible forms of conditional dispersal:

- Kinesis: random movement rate $D(x)$ depends on environmental quality or on $u(x)$ or other densities. (Details depend on microscale movement behavior)
- Taxis: advection rate $e(x)$ depends on environment, $u(x)$, etc.

Dynamic models for the Ideal Free Distribution: Advection I. (C., 2005)

Assume individuals can sense resource and population gradients and advect along them.

$$\text{Logistic fitness: } f(x, u) = m(x) - u$$

$$\begin{aligned} \text{Advection up fitness gradient } \frac{du}{dt} &= -\alpha \nabla \cdot [u \nabla (m-u)] \\ &= \alpha \nabla \cdot u \nabla u - \alpha \nabla \cdot u \nabla m \end{aligned}$$

(porous medium type diffusion - degenerate parabolic)

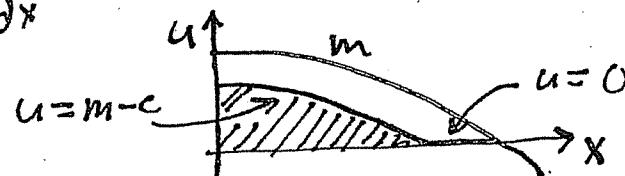
- Without population dynamics: $\Omega = (0, \infty)$, no flux b.c. at $x=0$

Let $E(t) = \frac{1}{2} \int_0^\infty u^2 \left[\frac{\partial}{\partial x} (m-u) \right]^2 dx$. Formally compute E' .

$$E'(t) = - \int_0^\infty u \left(\frac{du}{dt} \right)^2 dx + \frac{1}{2} \int_0^\infty \left(\frac{\partial^2 m}{\partial x^2} \right) u^2 \left[\frac{\partial}{\partial x} (m-u) \right]^2 dx$$

If $\frac{\partial^2 m}{\partial x^2} \leq 0$ then $E' \leq 0$, so the model is expected to stabilize

with $u \frac{\partial (m-u)}{\partial x} = 0$ so fitness = constant ($= m - u$) where $u \neq 0$.



Dynamic IFD; Advection I. (continued)

- With population dynamics:

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

$$u \frac{\partial (m-u)}{\partial n} = 0 \quad \text{on } \partial \Omega \times (0, \infty)$$

Clearly $u^* = m(x)$ satisfies $m-u^* = 0$, $-\alpha \nabla \cdot [u^* \nabla (m-u^*)] = 0$
so model supports an ideal free equilibrium.

(Rigorous treatment remains open for time dependent problem,
uniqueness, stability.)

- Approximate ideal free dispersal: (Cantrell, C., Lou 2008)

Add some diffusion μ ; assume α is bounded below;
consider

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

$$\mu \frac{\partial u}{\partial n} - \alpha u \left(\frac{\partial m}{\partial n} - \frac{\partial u}{\partial n} \right) = 0 \quad \text{on } \partial \Omega \times (0, \infty)$$

Results: If $u=0$ is unstable then ★ has a positive equilibrium.

As $\alpha \rightarrow \infty$, any positive equilibrium $\rightarrow m(x)$ in $C^2(\bar{\Omega})$.

For α large, the positive equilibrium is unique and stable.

Equilibrium Ideal Free Dispersal (from microscale behavior)

Based on taxis: ($m = m(x)$ throughout) (Cantrell, C., Lou preprint)

$$\frac{\partial u}{\partial t} = \mu \nabla \cdot \left[\nabla u - u \left(\frac{\nabla m}{m} \right) \right] + (m-u)u \quad (\text{advec up } \nabla m, \text{ with rate } \sim \frac{1}{m}, \text{ i.e. up } \nabla \ln m)$$

Based on kinesis:

1. Diffusion rate depends on departure point (Lewis, preprint)

$$\frac{\partial u}{\partial t} = \mu \nabla^2 \left(\frac{u}{m} \right) + (m-u)u \quad (D(x) = \frac{1}{m(x)})$$

2. Diffusion rate depends on arrival point

$$\frac{\partial u}{\partial t} = \mu \nabla \cdot \left[m^2 \nabla \left(\frac{u}{m} \right) \right] + (m-u)u \quad (D(x) = m(x))$$

Nonlocal dispersal: $\frac{\partial u}{\partial t} = \int_{\Omega} K(x, y)u(y)dy - \int_{\Omega} K(y, x)u(x)dy + (m-u)u$
 (C., Davila, Martinez preprint)

$K(x, y)$ = movement rate from y to x

$$K(x, y) = m(x)^{\alpha} \cdot m(y)^{\alpha-1} \sim \text{ideal free} \sim \begin{cases} 1/m(y) & (\text{departure}) \\ m(x) & (\text{arrival}) \end{cases}$$

Connections to foraging (First passage time analysis... McKenzie, Lewis, Merrill 2009)

u = predator N = prey

Prey do not disperse; predators diffuse; effective contact rate between predators and prey depends on predator diffusion rate:

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla^2 [d(x)u] + \alpha d(x)N^2 u - \delta u \\ \frac{\partial N}{\partial t} = g(x) - \beta N^2 d(x)u \end{cases}$$

Use prey pseudoequilibrium: $N^2 d(x)u = g(x)/\beta$. Then

$$\frac{\partial u}{\partial t} = \nabla^2 [d(x)u] + \alpha \frac{g(x)}{\beta} - \delta u$$

u^* = predator equilibrium without dispersal = $\frac{\alpha g(x)}{\beta \delta}$

Then $\nabla^2 [d(x)u^*] = 0$ if $d(x) = \frac{d_0}{g(x)}$ (ideal free dispersal)

(diffusion rate based on departure point,
inversely proportional to prey growth rate)

Evolutionary Stability of Ideal Free Dispersal

Game Theoretic Approach: (Cressman and Krivan 2006):
The ideal free distribution is an evolutionarily stable strategy. (Discrete space model)

Invasibility Approaches

- Hastings approach (model dynamics of invader only)
 - Discrete space (discrete diffusion): Ideal free dispersal is generally necessary and often sufficient for evolutionary stability. (Cantrell, C., DeAngelis, Padrón 2007; considerable previous work by various researchers)
 - Nonlocal dispersal: similar to discrete diffusion. (C., Davila, Martinez, preprint)
- McPeek-Holt, Dockery et al. approach (model invader and resident dynamics)
 - Constant diffusion, linear advection: Ideal free dispersal is locally evolutionarily stable relative to choice of advection. (Cantrell, C., Lou preprint)

Discrete Diffusion

$$\text{Basic model: } \frac{du_i}{dt} = \sum_{\substack{j \neq i \\ j=1}}^n (d_{ij}u_j - d_{ji}u_i) + F_i(u_i)u_i, \quad i=1, \dots, n$$

(single species case - extends to multiple species)

Equilibrium without dispersal: $u_i = u_i^*$ so that $F_i(u_i^*) = 0$.

Ideal free dispersal: $\sum_{j \neq i} (d_{ij}u_j^* - d_{ji}u_i^*) = 0$

General equilibrium $u_i = u_i^{**}$

$$\text{Invasibility system: } \frac{dv_i}{dt} = \sum_{\substack{j \neq i \\ j=1}}^n (D_{ij}v_j - D_{ji}v_i) + F_i(u_i^{**} + v_i)v_i$$

Results: If $u_i^{**} = u_i^*$ (ideal free resident strategy) and $F'_i(u_i^*) < 0$ for $i=1, \dots, n$ then $\vec{v} = 0$ is stable (Lyapunov methods)
(so ideal free dispersal is an ESS)

If \vec{u}^{**} has $F_i(u_i^{**}) \neq 0$ for some i , then there is a strategy $((D_{ij}))$ so that $v = 0$ is unstable.

(so any ESS is ideal free.) (Cantrell, C., DeAngelis, Padrón 2007)

Discrete Diffusion (continued) Observation:

Linearized invasibility model (at $v=0$):

$$\star \quad \sum_{\substack{j \neq i \\ j=1}}^n (D_{ij}\phi_j - D_{ji}\phi_i) + F_i(u_i^{**})\phi_i = \sigma\phi_i$$

Define $D_{ii} = -\sum_{\substack{j \neq i \\ j=1}} D_{ji}$. Then $((D_{ij}))$ has 0 principal eigenvalue.

If $u_i^{**} = u_i^*$ (ideal free resident) then $F_i(u_i^*) = 0$ so $\sigma = 0$ is the principal eigenvalue in \star , so linearly $v=0$ is neutrally stable. (Nonlinear analysis is required. This feature is present across model types.)

Nonlocal dispersal: Analogous to discrete diffusion

$$\frac{du(x,t)}{dt} = \int_{\Omega} k(x,y)u(y)dy - \int_{\Omega} k(y,x)u(x)dy + F(x,u)$$

Similar methods (some technical modifications) \Rightarrow similar results
(IFD generally necessary, often sufficient for ESS.)

(C., Davila, Martinez, preprint.)

Constant diffusion with advection (contrell, C., Lou, preprint)

Consider

$$\begin{aligned}
 (\star\star) \quad \frac{\partial u}{\partial t} &= \nabla \cdot [\nabla u - u \nabla P] + (m - u - v) u \\
 \frac{\partial v}{\partial t} &= \nabla \cdot [\nabla v - u \nabla Q] + (m - u - v) v \quad \text{in } \Omega \times (0, \infty) \\
 \frac{\partial u}{\partial n} - u \frac{\partial P}{\partial n} &= 0, \quad \frac{\partial v}{\partial n} - v \frac{\partial Q}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty)
 \end{aligned}$$

$P = P(x), Q = Q(x); P, Q, m \in C^2(\bar{\Omega}), m(x) > 0.$

Semitrivial equilibria: $(u^*, 0), (0, v^*)$

- $P = \ln m \sim$ Ideal Free Case $u^* = m$

Theorem 1: If $P(x) = \ln m(x)$ and $Q(x) = \ln m(x) + \epsilon R(x)$

with $R(x)$ nonconstant then for $|\epsilon|$ small, $(u^*, 0)$ is

globally asymptotically stable and $(0, v^*)$ is unstable \Rightarrow v invades u

(so $P = \ln m(x)$ is evolutionarily stable, locally). v, v
cannot invade u

If $P(x) - \ln m(x)$ is nonconstant then there exists $R(x)$ so that for $Q(x) = P(x) + \epsilon R(x)$, $(u^*, 0)$ is unstable

(so if $P(x) - \ln m(x)$ is nonconstant, P cannot be evolutionarily stable)

(Eigenvalue estimates, Lyapunov-Schmidt analysis of equilibria for $|\epsilon|$ small,
competition theory (monotonicity))

Constant diffusion with advection (continued)

$$\begin{aligned}
 (\star\star) \quad \frac{\partial u}{\partial t} &= \frac{\partial}{\partial x} \left(\frac{\partial u}{\partial x} - u \frac{\partial P}{\partial x} \right) + (m - u - v) u \\
 (R') \quad \frac{\partial v}{\partial t} &= \frac{\partial}{\partial x} \left(\frac{\partial v}{\partial x} - v \frac{\partial Q}{\partial x} \right) + (m - u - v) v \\
 &\quad + \text{no flux B.C.}
 \end{aligned}$$

on $(0, 1) \times (0, \infty)$

Theorem 2: Assume $R_x \neq 0$, $P = \ln m + \alpha R$, $Q = \ln m + \beta R$.

If $\alpha < 0 < \beta$ or $\beta < 0 < \alpha$ then $(0, v^*)$ and $(u^*, 0)$ are both unstable
 $(\Rightarrow$ coexistence)

If $0 < \alpha < \beta$ or $\beta < \alpha < 0$ then $(u^*, 0)$ is stable
but $(0, v^*)$ is unstable.

(selection for strategy closer to ideal free)

(This shows a type of "convergent stability" for the ideal free strategy.)

Conclusion: The strategy $P(x) = \ln m(x)$ to an ideal free equilibrium, is "evolutionarily stable" in a robust sense

Return to the big picture. ($\text{IFD} \sim \text{ideal free distribution}$)

microscale

Simple diffusion

mesoscale

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

no IFD

macroscale

evolutionarily unstable
(selection for slow dispersal)

nonlinear advection,
no true diffusion

$$-\nabla \cdot [u \nabla f(x, u)]$$

IFD possible

??

simple diffusion
with linear advection

$$\nabla \cdot [\mu(x) \nabla u - u \nabla P(x)]$$

IFD possible

In some cases, IFD is
evolutionarily stable within this
class of strategies

diffusion with
movement rate
based on departure
point

$$\nabla^2 (\mu(x) u)$$

IFD possible -
use $u = 1/\mu(x)$
in logistic case

??

diffusion with
movement rate
based on arrival
point

$$\nabla \cdot [\mu(x)^2 \nabla \left(\frac{u}{\mu(x)} \right)]$$

IFD possible - use
 $\mu(x) = m(x)$ in logistic case

??

Many other
possibilities

Many technical
issues in PDE

Many questions about
evolutionary stability in
larger classes of strategies