

Models for the Evolution of Dispersal in
Spatially Heterogeneous Environments

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Classical models for population dynamics with dispersal:

Discrete diffusion: $u_i \sim$ density of population on patch i of n :

$$\frac{du_i}{dt} = \sum_{j=1}^n d_{ij} u_j - \left(\sum_{j=1}^n d_{ji} \right) u_i + f_i(u_i) u_i$$

or

$$u_i(t+1) = \sum_{j=1}^n D_{ij} F_j(u_j(t)) u_j(t) + \left(1 - \sum_{j=1}^n D_{ji} \right) F_i(u_i(t)) u_i(t)$$

(often $n=2$)

Diffusion: $u(x,t) \sim$ density of population relative to x ;
 $x \in \Omega \subseteq \mathbb{R}^n, (n=1,2,3)$

$$\frac{\partial u}{\partial t} = d \Delta u + f(x,u) u \text{ in } \Omega$$

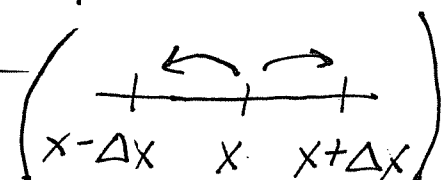
If Ω is bounded, $\alpha \frac{\partial u}{\partial n} + (1-\alpha)u = 0$ on $\partial\Omega$

(often f is independent of x)

These models have often been extended to more species —
BUT DO ORGANISMS REALLY MOVE LIKE THAT?

Movement in continuous space

I. Local movement (as a continuum limit)

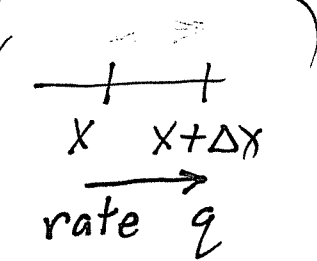
- At a small scale $(\Delta x, \Delta t)$ diffusion arises from random nearest neighbor movement —  but that may be conditioned on the environment at the departure point, arrival point, neither, or both. Scaling: $(\Delta x)^2 \sim \Delta t$ ($\Delta x \sim \sqrt{\Delta t}$)

Classical diffusion (unconditional): For density $u(x, t)$,

$$\frac{\partial u}{\partial t} = \nabla \cdot d(x, t) \nabla u.$$

Conditional diffusion: $\frac{\partial u}{\partial t} = \nabla \cdot d_1(x, t) \nabla (d_2(x, t) u).$

(Includes $\frac{\partial u}{\partial t} = \nabla^2 (d(x, t) u)$ as in cross-diffusion.)

- Advection arises from directed movement  scaling $\Delta x \sim \Delta t$; $\frac{\partial u}{\partial t} = \nabla \cdot \vec{q}(x, t) u.$

(extend to
 $x = (x_1, x_2)$
or (x_1, x_2, x_3))

Some sources/interpretations of local movement beyond simple diffusion:

- Physical processes and environmental structure
 - Physical advection in aquatic systems (e.g. rivers) (Hilker, Lewis, Lutscher, Nisbet, ...)
 - Landscape effects on movement, (e.g. different rates of movement in different terrain, interfaces between habitat types, anisotropy, etc.) (Ovaskainen, ...)
- Behavioral responses/movement strategies
 - Very small scale: alter diffusion rate based on local environment (kinesis; area restricted search)

$$\frac{\partial u}{\partial t} = \nabla \cdot d_1(x,t) \nabla (d_2(x,t) u), \quad d_1, d_2 \text{ decrease as habitat quality increases}$$

($\Delta x \sim \sqrt{\Delta t}$)
 - somewhat larger scale: advect on the basis of sensory information (taxis)

$$\frac{\partial u}{\partial t} = \nabla \cdot \vec{q}(x,t) u \quad (\text{Fagan and Mueller, ...})$$

($\Delta x \sim \Delta t$)

II. Nonlocal movement

Empirical results show that the dispersal patterns of some populations are not described well by diffusion-advection models because they involve (possibly rare) long distance dispersal events.

- Continuous time: integrodifferential models

$$\frac{\partial u}{\partial t} = (1 - \epsilon) \int_{\Omega} k(x, y) u(y, t) dy - \left(\int_{\Omega} k(y, x) dy \right) u(x, t) \quad \left(\begin{array}{l} \epsilon \geq 0 \sim \\ \text{loss in} \\ \text{transit} \end{array} \right)$$

(Medlock, Martinez, Jin and Lewis, Shen) (k might also depend on t)

Note: For all continuous time dispersal models we can separately add population dynamic terms:

$$\frac{\partial u}{\partial t} = \mathcal{D}(u) + f(x, t, u)u$$

\nwarrow dispersal \swarrow dynamics

(Also - dispersal terms may depend on density $u(x, t)$)

Nonlocal models - discrete time

- Integrodifference models:

$$u(x, T+1) = \int_{\Omega} K(x, y, t) F(y, T, u(y, T)) u(y, T) dy$$

(No simple separation between dispersal and growth terms)

(Wemberger (1980's); Kot; J. Clark, *Am. Nat.* 152 (1998); Lui)

(Allen, Fagan, Hsu, Lewis, Lutscher, Ruan, ...)

(Widely used in studying biological invasions.)

- Nonlocal models allow "fat tailed" and/or leptokurtic kernels.

More leptokurtic dispersal patterns: Skalski and Gilliam, *Am. Nat.* 161 (2003)

$u = F + S$ (fast and slow)

$$\frac{\partial F}{\partial t} = D_F \frac{\partial^2 F}{\partial x^2} - \beta_F \frac{\partial F}{\partial x} + aS - bF$$

$$\frac{\partial S}{\partial t} = D_S \frac{\partial^2 S}{\partial x^2} - \beta_S \frac{\partial S}{\partial x} - aS + bF$$

($D_S, \beta_S = 0$: Hadeler, Hillen, Lewis)

So why am I here?

Evolutionary ecology problems related to dispersal

In heterogeneous environments, given a class of sensory and movement mechanisms, which are optimal, and which will actually be observed?

- Which can evolve?

- Which can persist if they do evolve?

Ideas: [Motivated by game theory (Cressman, Krivan)
by way of adaptive dynamics (Diekmann-Beginner's Guide)]

Think of dispersal mechanisms, etc., as strategies, which may be

- Evolutionarily stable (ESS): If a population is using an ESS, no small population using another strategy can invade it.
- Convergent stable (CSS): Nearby strategies allow a small population to invade a population using a strategy that is further away from the CSS
- Neighborhood Invader (NIS): Allows small populations to invade

Historical background

(A. Hastings, *Theoretical Population Biology* 24 (1983), 244-251) (logistic type)

Consider a model of the form

$f(x, u)$ decreasing in u ,
 $f(x, 0) > 0$, $f(x, u) < 0$, u large

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

Note: classical diffusion - no dependence on arrival or departure point

Suppose $u^* > 0$ is a stable equilibrium

(think of u^* as a resident population)

Hastings also studied the discrete diffusion case
 $\frac{du_i}{dt} = D \sum_j \mu_{ij} u_j + f_i(u_i)$, $\mu_{ij} = \mu_{ji}$

Note that if $f(x, u)$ is nonconstant when $u > 0$ is constant then we cannot have $f(x, u^*) \equiv 0$. (If so then $\nabla \cdot [\mu \nabla u^*] = 0$ and the boundary condition $\Rightarrow u^* = \text{constant} \Rightarrow \text{contradiction}$)

Think of v as an invading small population with similar dispersal pattern but different rate; assume v has little impact on u .

$$\frac{\partial v}{\partial t} = d \nabla \cdot [\mu(x) \nabla v] + f(x, u^* + v) v \text{ in } \Omega \times (0, \infty), \quad \frac{\partial v}{\partial n} = 0 \text{ on } \partial \Omega \times (0, \infty)$$

Hastings' approach (continued)

For the resident:

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

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

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

- Invasion is possible \iff principal eigenvalue $\sigma_1 > 0$ in $\star \star$
- \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 $\nabla u^* \not\equiv 0$.

Suppose $d < D$.

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

(all \int 's are over Ω)

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

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

Conclusion from Hastings' approach:

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

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

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

$$\iff d < D.$$

Thus, no dispersal strategy with $D > 0$ and $f(x, u^*) \not\equiv 0$ can be evolutionarily stable, and $D = 0$ is convergent stable

What is behind this? (selection for slower diffusion)

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

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

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

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

Related work: Dockery, Hutson, Mischaikow, Pernarowski, *J. Math. Biol.* 37 (1998), 61-83

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

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

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

(General
Competition
theory)

If $\int_{\Omega} m(x) dx > 0$ then there are unique single species equilibria

$(u^*, 0)$ and $(0, v^*)$.

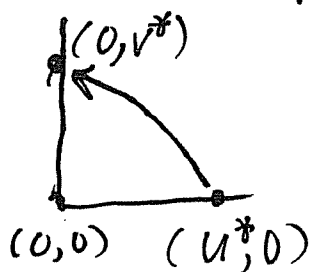
The system is monotone with respect to the ordering $(u_1, v_1) \geq (u_2, v_2)$ if $u_1 \geq u_2$ and $v_1 \leq v_2$.

Thus, solutions can be studied using sub- and super solutions.

If $(u^*, 0)$ is unstable, solutions starting at (u^*, v_0) with v_0 small will increase (in that ordering) toward another equilibrium.

Results from DHMP (1998):

$\nu < \mu \Rightarrow (u^*, 0)$ unstable, $(0, v^*)$ stable, no coexistence state (u^{**}, v^{**}) .
 $\Rightarrow v$ excludes u . (selection for slower random dispersal)



Why selection for slower random dispersal?

Suppose $\mu \Delta u^* + (m(x) - u^*)u^* = 0$ in Ω ; $\frac{\partial u^*}{\partial n} = 0$ on $\partial \Omega$, $u^* > 0$, $m > 0$

As $\mu \rightarrow 0$, $u^* \rightarrow m(x)$ uniformly on any closed subset of Ω , so u^* matches "resources" (as described by $m(x)$) better as $\mu \rightarrow 0$.

What about conditional dispersal? Introduce some advection, see if it is possible to match $m(x)$.

First guess: Try advection up the gradient of $m(x)$ (Belgacem, C.)

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

$$\mu \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega \times (0, \infty) \quad (\text{no flux b.c.})$$

Results:

(Using $w = e^{-\alpha/\mu m}$ converts b.c. to Neumann)

Roughly: $\alpha > 0$, small, allows u^* to match $m(x)$ better than simple diffusion but not perfectly

α large causes u^* to concentrate near peaks of $m(x)$, matching $m(x)$ less well. (Cantrell, C., Lou; Lou et al.; Ni, Lam)

$(u^*, 0), (0, v^*)$ equilibria for

m : _____
 u^* :
 v^* : - - - - -

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + (m(x) - u - v)u \quad (\text{no flux b.c.})$$

$$\frac{\partial v}{\partial t} = \nabla \cdot [\nu \nabla v - \beta v \nabla m] + (m(x) - u - v)v$$

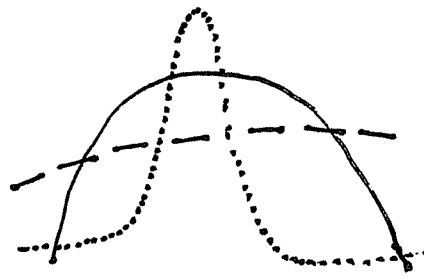
$\mu \approx \nu, \beta = 0, \alpha > 0$
 $\alpha \approx 0$
 (u wins)

μ, ν arbitrary
 β small, α large
 (Coexistence)

μ, ν arbitrary,
 β large, α very large
 (v wins)

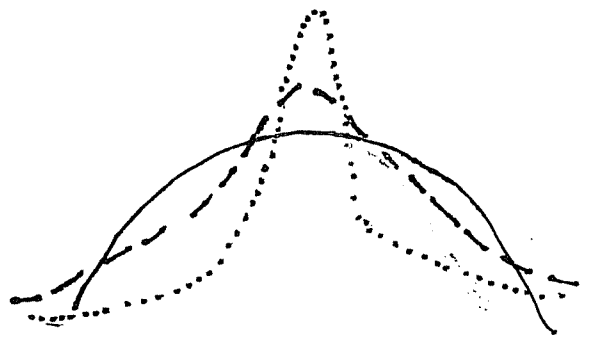


u^* matches m better than v^*



u^* overmatches m where m is large, undermatches when m is small.

v^* overmatches m when m is small, undermatches when m is large.
 (spatial separation of competitors)



u^* and v^* both overmatch m when m is large, undermatch when m is small, but v^* matches m better than u^* .

Technical note - principal eigenvalues are a key tool (Berestycki, Lopez-Gomez) also, monotone methods (Smith)

Question: If we require $\mu, \nu \geq \mu_0 > 0$, are there any evolutionarily stable strategies in this class?
 (Perfect match to $m(x)$ impossible)

Historical background again
(Source of many interesting ideas about evolution of dispersal)

M. McPeck, R. Holt, *American Naturalist* 140 (1992), 1010-1027

Discrete time and space (2 patch) models based on Ricker model

$$u(t+1) = \left[r \exp \left(1 - \frac{u(t)}{K} \right) \right] u(t) \quad (\text{with parameters so that } K \sim \text{stable equilibrium})$$

2 patches, carrying capacities $K_1 \neq K_2$.

Dynamics:
$$\begin{cases} \tilde{u}_i(t+1) = \left[r_i \exp \left(1 - \frac{u_i(t) + v_i(t)}{K_i} \right) \right] u_i(t) \\ \tilde{v}_i(t+1) = \left[r_i \exp \left(1 - \frac{u_i(t) + v_i(t)}{K_i} \right) \right] v_i(t) \end{cases} \quad (\text{symmetric competition; ecologically identical competitors})$$

($i=1,2$)
($j \neq i$)

Dispersal: For $0 \leq d_{12}, d_{21}, D_{12}, D_{21} \leq 1$

($i=1,2$)
($j \neq i$)

$$\begin{cases} u_i(t+1) = D_{ij} \tilde{u}_j(t+1) + (1 - D_{ji}) \tilde{u}_i(t+1) \\ v_i(t+1) = d_{ij} \tilde{v}_j(t+1) + (1 - d_{ji}) \tilde{v}_i(t+1) \end{cases}$$

Methods: feed in different competitors with different d_{ij} ; simulate; see who survives

Conclusions: If $d_{ij} = d_{ji}$, $D_{ij} = D_{ji}$, selection favors slower dispersal
($d_{ij} = d_{ji} \sim$ "unconditional" dispersal, since $K_1 \neq K_2$ is irrelevant.
"conditional" dispersal depending on K_i is a different story. (more later))

Evolution Again

- Mathematical analysis suggests that in logistic-type models

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu_2(x, u) \nabla (\mu_1(x) u) - u \nabla e(x, u)] + (m(x) - u) u \quad \text{on } \Omega \times (0, \infty),$$

$$[\mu_2 \nabla (\mu_1 u) - u \nabla e] \cdot \vec{n} = 0 \quad \text{on } \partial \Omega \times (0, \infty),$$

the competitive advantage goes to strategies that allow u to "best match" $m(x)$.

- Back to McPeck and Holt (1992): Two patches, indexed by $i = 1, 2$:

$$\begin{cases} \tilde{u}_i(t+1) = f_i(u_i(t) + v_i(t)) u_i(t) \\ \tilde{v}_i(t+1) = f_i(u_i(t) + v_i(t)) v_i(t) \end{cases} \begin{matrix} \nearrow \\ \nearrow \end{matrix} \begin{cases} u_i(t+1) = D_{ij} \tilde{u}_j(t+1) + (1 - D_{ji}) \tilde{u}_i(t+1) \\ v_i(t+1) = d_{ij} \tilde{v}_j(t+1) + (1 - d_{ji}) \tilde{v}_i(t+1) \end{cases}$$

Assume that the models $w(t+1) = f_i(w(t)) w(t)$ have stable equilibria K_i .

- In numerical experiments, McPeck and Holt found that strategies with $K_i / D_{ij} = K_j / D_{ji}$ would persist in competition with other strategies.

(Those dispersal strategies keep $(u_1, u_2) = (K_1, K_2)$ fixed, so allow the populations to match resources exactly with no net movement at equilibrium.)

- The features are related to certain ecological theories about how organisms are expected to distribute themselves

Ecological Theory: Ideal Free Distribution

S.D. Fretwell, *Populations in a Seasonal Environment*, Princeton University Press, 1972

S.D. Fretwell, H.L. Lucas Jr., *Acta Biotheoretica* 19 (1970), 16-36.

Verbal description of how individuals will locate themselves:

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

(Here fitness is interpreted in the evolutionary sense of expected reproductive success rate. It typically depends on habitat and crowding.)

Implications:

- At equilibrium, all individuals at all locations will have equal fitness. (Otherwise some individuals would move to increase their fitness.)
- At equilibrium there should be no net movement (since individuals have optimized their location.)
(Individuals could trade places.)

Meso-scale interpretations of ideal free distribution

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

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

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

- Dynamic idea for ideal free dispersal: move up gradient of $f(x, u)$ or some related quantity.
- Equilibrium idea for ideal free dispersal: $u^* > 0$ equilibrium

Equal fitness: $f(x, u^*) = \text{constant}$

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:

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

Micro scale issue: What strategies allow this with $u^* > 0$?

Macro scale issue: Are these strategies stable?

Alternative dispersal strategies leading to an ideal free distribution

- Conditional dispersal requires knowledge of conditions
- Knowledge of conditions requires sensory information

Suppose that the sensory response to a stimulus s is $G(s)$ (s might represent the number of resource items or other individuals encountered in unit time.) To make sense $G(s)$ should be increasing. Suppose individuals advect on the gradient of the difference between sensory responses to resources and to density:

$$\frac{\partial u}{\partial t} = -\nabla \cdot [u(\nabla G(m) - \nabla G(u))] + (m(x) - u)u = 0. \text{ Assume } m(x) > 0.$$

This model supports an equilibrium $u^* = m(x)$ (ideal free distribution). Any model of this type is interesting, but:

* Weber-Fechner Law: The intensity of sensory response to stimulus is logarithmic ($G(s) = \gamma \ln(s)$, so $\nabla G(m) = \gamma \nabla m/m$)

(S. Dehaene, Trends in Cognitive Science 7 (2003), 146-147) (refers to number sense)

$$\text{Then: } \frac{\partial u}{\partial t} = -\nabla \cdot \gamma [u \frac{\nabla m}{m} - u \frac{\nabla u}{u}] + (m(x) - u)u = \gamma \nabla \cdot [\nabla u - u \frac{\nabla m}{m}] + (m(x) - u)u$$

* (Used in original Keller-Segeel Chemotaxis Model, JTB 30 (1971), 235-248)

Alternative strategies (continued) ($m(x) > 0$)

- Advection on sensory response, using Weber-Fechner law: (taxis)

$$\frac{\partial u}{\partial t} = \gamma \nabla \cdot \left[\nabla u - u \frac{\nabla m}{m} \right] + (m(x) - u - v) u \quad \text{in } \Omega \times (0, \infty)$$

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

Note: No direct density dependence in dispersal—so this strategy is not directly fitness dependent, does not require density information.

(It can be interpreted as "move up ∇m but go slower if m is large")

- A different mechanism: Recall that in micro-scale diffusion processes where the probability of moving depends on departure point as $p_1(x)$ and on arrival point as $p_2(x)$, the diffusion equation is

$$\frac{\partial u}{\partial t} = \gamma \nabla \cdot \left[p_2(x)^2 \nabla \left(\frac{p_1(x) u}{p_2(x)} \right) \right] + (m(x) - u) u. \quad \text{(kinesis)}$$

If $\frac{p_1(x)}{p_2(x)} = \frac{\gamma_0}{m}$ this supports an ideal free distribution $u \equiv m$.

If $p_1(x) = \gamma_1 \sqrt{m}$ and $p_2(x) = \gamma_2 \sqrt{m}$ this last equation becomes

$$\frac{\partial u}{\partial t} = \gamma_3 \nabla \cdot \left[m(x) \nabla \left(\frac{u}{m(x)} \right) \right] + (m(x) - u) u = \gamma_3 \nabla \cdot \left[\nabla u - u \frac{\nabla m}{m} \right] + (m(x) - u) u !!$$

(Obviously there are more possibilities)

Evolutionary stability of ideal free dispersal based on advection

Consider
$$\frac{\partial u}{\partial t} = \mu \nabla \cdot [\nabla u - u \nabla P] + (m(x) - u - v) u$$

$$\frac{\partial v}{\partial t} = \nu \nabla \cdot [\nabla v - v \nabla Q] + (m(x) - u - v) v$$
on $\Omega \times (0, \infty)$

$$[\nabla u - u \nabla P] \cdot \vec{n} = [\nabla v - v \nabla Q] \cdot \vec{n} = 0 \text{ on } \partial \Omega \times (0, \infty)$$

$P, Q, m \in C^2(\bar{\Omega})$; $\mu, \nu, m(x) > 0$. (Then $\exists! (u^*, 0), (0, v^*)$)

R.S. Cantrell, C. Cosner, Y. Lou, *Math. Biosciences and Engineering* 7 (2010), 17-36

I. Averill, Y. Lou, D. Munther, *J. Biological Dynamics*, to appear

R. Gejji, Y. Lou, D. Munther, J. Peyton, *Bull. Math. Biology*, to appear

Thm: (Averill, Lou, Munther): Suppose $P = \ln m$ and $Q = \ln m$ is not constant. Then $(u^*, 0)$ is globally asymptotically stable

Remarks: This shows that within the class of strategies of the form $\mu \nabla \cdot [\nabla u - u \nabla P]$, the strategies with $P = \ln m$ are the only possible evolutionarily stable strategies (since they can invade any other type of strategy) and are evolutionarily stable (because they cannot be invaded by other types.)

(However, two strategies with $P = \ln m$ but $\mu \neq \nu$ could coexist.)

Nonlocal models:

$$\frac{\partial u}{\partial t} = \int_{\Omega} k_u(x, y) u(y) dy - \left(\int_{\Omega} k_u(y, x) dy \right) u(x) + (m(x) - u - v) u$$

$$\frac{\partial v}{\partial t} = \int_{\Omega} k_v(x, y) v(y) dy - \left(\int_{\Omega} k_v(y, x) dy \right) v(x) + (m(x) - u - v) v.$$

If $k_u(x, y) = \mu k(x, y)$, $k_v(x, y) = \nu k(x, y)$, $\mu < \nu$,
then in general u wins. (selection for slower dispersal)

(Hutson, Martinez, Mischaikow, Vickers, JMB 47 (2003), 483-517)

Ideal free condition: $\int_{\Omega} k(x, y) m(y) dy = \left(\int_{\Omega} k(y, x) dy \right) m(x)$

(example: $k(x, y) = m(x)^{\alpha} m(y)^{\alpha-1}$)

Consider single species equilibrium u^* ; take Hastings approach;

$$\frac{\partial v}{\partial t} = \int_{\Omega} k_v(x, y) v(y) dy - \left(\int_{\Omega} k_v(y, x) dy \right) v(x) + (m(x) - u^* - v) v$$

If $k_u(x, y) \sim$ ideal free strategy, v cannot invade

If $k_u(x, y)$ is not ideal free, some choices of k_v allow invasion

(C., Davila, Martinez) (Note: Kao, Lou, Shen 2010 - diffusion vs. nonlocal - "slower" wins)

Technical issues -
• lack of regularity/
compactness
• existence
of
eigenfunctions

Back to "basics": patch models of various sorts

- Sometimes environments are really patchy, and important phenomena arise from patchiness
- Finite dimensional models may be technically less difficult, and may give insights into more technically difficult models
(Abrams, Allen, Cantrell, C., DeAngelis, Fagan, Hastings, Holt, Hsu, Lou, Ovaskainen, Ruan, Tyson, ... (probably missed some people...))

Single population, two dispersal strategies; patches $i=1, \dots, n$

$$\frac{du_i}{dt} = \sum_{j=1}^n d_{ij} u_j - \left(\sum_{j=1}^n d_{ji} \right) u_i + f_i(u_i + v_i) u_i \quad i=1, \dots, n$$

$$\frac{dv_i}{dt} = \sum_{j=1}^n D_{ij} v_j - \left(\sum_{j=1}^n D_{ji} \right) v_i + f_i(u_i + v_i) v_i$$

f_i logistic type - $f_i(0) > 0$, $f_i' < 0$, $f_i(k_i) = 0$ for $i=1, \dots, n$

unconditional dispersal if $d_{ij} = d_{ji}$; ideal free if $\sum_{j=1}^n d_{ij} k_j = \left(\sum_{j=1}^n d_{ji} \right) k_i$
($i, j=1, \dots, n$) ($i=1, \dots, n$)

Patch models (continued)

$$\frac{du_i}{dt} = \sum_{j=1}^n d_{ij} u_j - \left(\sum_{j=1}^n d_{ji} \right) u_i + f_i(u_i + v_i) u_i$$

$$\frac{dv_i}{dt} = \sum_{j=1}^n D_{ij} v_j - \left(\sum_{j=1}^n D_{ji} \right) v_i + f_i(u_i + v_i) v_i \quad f_i \sim \text{logistic type}$$

or discrete time equivalents without cycles or chaos

Summary of results:

- Selection for slower unconditional dispersal
- For situations that can be described by these models, selection against dispersal into sinks ($f_i(0) < 0$), but other factors can change that.
- Ideal free dispersal strategies are evolutionarily stable, non-IFD strategies are not. (Multiple IFD strategies are mutually neutrally stable. [Even for single species, discrete time])
- Results extend to some multispecies models if there are no cycles or chaos but fail if there are.

(Hastings, Holt & McPeck, Abrams, Schreiber et al., Cantrell, C., DeAngelis, Padron; Lou ...)

What if there are no strategies leading to an ideal free distribution?

(The strategy of no dispersal at all usually produces an IFD, so those situations where some dispersal is unavoidable are the ones that are interesting.)

Models with travel loss (DeAngelis et al., Lou & Wu):

$$\frac{du_i}{dt} = (1-\epsilon) \sum_{j=1}^n d_{ij} u_j - \left(\sum_{j=1}^n d_{ji} \right) u_i + f_i(u_i)$$

with $d_{ij} > 0$ fixed for some i, j .

(motivated by aquatic systems with physical transport between some patches)

No IFD is possible in general but there do exist evolutionarily stable strategies in some cases; those can be explicitly described. What about other model types?

Time dependent environments

Discrete time and space (with some assumptions)

Possible phenomena (McPeck and Holt 1992)

- selection for some positive amount of dispersal among unconditional strategies
- Fast/slow polymorphism
- selection of a specific strategy that would be ideal free for the mean carrying capacity (as opposed to a continuum of IFD strategies in the case of spatially varying but temporally constant environments.)

Continuum models:

$$\frac{\partial u}{\partial t} = \mu \Delta u + (m(x,t) - u - v)u \quad m(x,t+T) = m(x,t) \text{ (periodic)}$$

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

(Various results, including principal eigenvalues:

Lazer, Hess, Ruan, Shen, Zhao)

Hutson, Mischaikow, Polacik (2001): sometimes selection for faster diffusion.

What about conditional advective/diffusive strategies???

Integrodifference models

$$u(x, T+1) = \int_{\Omega} K(x, y) F(y, T, u(y, T)) u(y, T) dy$$

Linear case: $u(x, T+1) = \int_{\Omega} K(x, y) \lambda(y, T) u(y, T) dy \equiv K_{\lambda}(u(\cdot, T))$

For population growth: $\text{spr}(K_{\lambda}) > 1$

Hardin, Takac, Webb, SIAM J. Appl. Math 48 (1988) 1396-1423:

Allow $\lambda = \lambda(y) \in \Lambda$, where $\Lambda \subseteq C_+(\bar{\Omega})$, $\inf \{ \|\lambda\|_{\infty} : \lambda \in \Lambda \} > 0$.

Require $\int_{\Omega} K(x, y) dx \leq 1 \quad \forall y \in \Omega$ (no gain in population from K)

Extend class of operators to be measure valued (dual of $C(\bar{\Omega})$)

→ Try to choose K to maximize $s(K, \Lambda) = \inf \{ \text{spr}(K_{\lambda}) : \lambda \in \Lambda \}$

($s(K, \Lambda) > 1 \Rightarrow$ persistence for any $\lambda \in \Lambda$)

Result: No movement, that is, $K(x, y) = \delta(x-y)$, is a maximizer.

What else is true? What about ESS, IFD, etc.??