Evolution of Dispersal in Heterogeneous Landscapes

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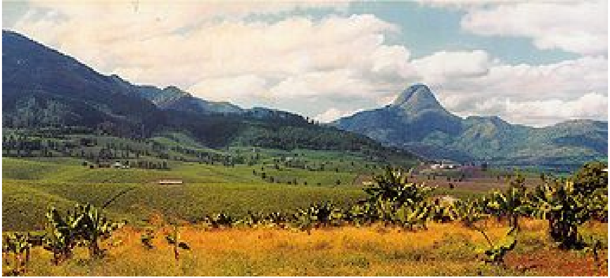
Talk Outline

1. Unbiased dispersal
2. Ideal free distribution (IFD)
3. Nonlocal/discrete dispersal and IFD
4. Biased dispersal
5. Fitness-dependent dispersal

Evolution of Dispersal



- How should organisms move “optimally" in heterogeneous landscapes?

Previous works

- Levin 76; Hastings 83; Holt 85; McPeek and Holt 92; Holt and McPeek 1996; Dockery et al. 1998; Kirkland et al. 2006; Abrams 2007; Armsworth and Roughgarden 2008; Amarasekare 2010

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- Johnson and Gaines 1990; Clobert et al. 2001; Levin, Muller-Landau, Nathan and Chave 2003; Bowler and Benton 2005; Holyoak et al. 2005; Amarasekare 2008

Evolution game theory

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- Evolutionary stable strategy (ESS): A strategy such that, if all the members of a population adopt it, no mutant strategy can invade
- Goal: To find dispersal strategies that are evolutionarily stable

Unbiased dispersal

Hastings (TPB, 83); Dockery et al. (JMB, 98)

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\begin{aligned}
u_t &= \quad u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \\
v_t &= \quad v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \qquad (1)
\end{aligned}
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- $u(x,t), v(x,t)$: densities at $x \in \Omega \subset R^N$

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- $u(x,t), v(x,t)$: densities at $x \in \Omega \subset R^N$
- $m(x)$: intrinsic growth rate of species

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$$u_t = d_1 \Delta u + u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$
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- d_1, d_2: dispersal rates

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\frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty).
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- $u(x, t), v(x, t)$: densities at $x \in \Omega \subset R^N$
- $m(x)$: intrinsic growth rate of species
- d_1, d_2: dispersal rates
- No-flux boundary condition

Hasting's approach

Suppose that species u is at equilibrium:

$$\begin{cases} d_1 \Delta u^* + u^*[m(x) - u^*] = 0 \quad \text{in } \Omega, \\ \frac{\partial u^*}{\partial n} = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{2}$$

Question. Can species v grow when it is rare?

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Question. Can species v grow when it is rare?

- Stability of $(u, v) = (u^*, 0)$: Let $\Lambda(d_1, d_2)$ denote the smallest eigenvalue of

$$d_2 \Delta\varphi + (m - u^*)\varphi + \lambda\varphi = 0 \quad \text{in } \Omega,$$

$$\nabla\varphi \cdot n = 0 \quad \text{on } \partial\Omega.$$

Evolution of slow dispersal

Hastings (1983)

Theorem

Suppose that $m(x)$ is non-constant, positive and continuous in $\bar{\Omega}$. Then, the sign of $\Lambda(d_1, d_2)$ is same as the sign of $d_2 - d_1$: If $d_1 < d_2$, then $(u^*, 0)$ is stable; if $d_1 > d_2$, $(u^*, 0)$ is unstable.

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- No dispersal rate is evolutionarily stable: Any mutant with a smaller dispersal rate can invade when rare!

Habitat selection theory

Fretwell and Lucas (70)

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- Assumption 2: Animals are capable of moving "freely"

Habitat selection theory

Fretwell and Lucas (70)

- How should organisms distribute themselves in heterogeneous habitat?
- Assumption 1: Animals are "ideal" in assessment of habitat
- Assumption 2: Animals are capable of moving "freely"
- Prediction: Animals aggregate proportionately to the amount of resources

Ideal free distribution (IFD)

- Milinski (79)

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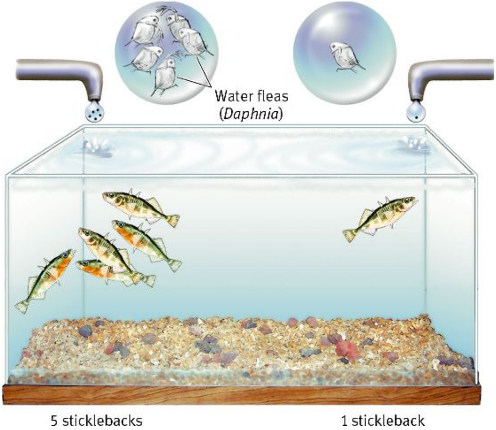

IFD and Dispersal

- Holt and Barfield (01), On the relationship between the ideal-free distribution and the evolution of dispersal

IFD and Dispersal

- Holt and Barfield (01), On the relationship between the ideal-free distribution and the evolution of dispersal
- Krivan, Cressman and Schneider (08), The ideal free distribution: A review and synthesis of the game-theoretic perspective

Unbiased dispersal

- Logistic model

$$\begin{aligned} & u_t = d\Delta u + u\,[m(x) - u] \quad \text{in } \Omega \times (0,\infty) \\ & \frac{\partial u}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0,\infty) \end{aligned} \tag{3}$$

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- If $u(x,0)$ is positive, $u(x,t) \to u^*(x)$ as $t \to \infty$

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- If $u(x, 0)$ is positive, $u(x, t) \to u^*(x)$ as $t \to \infty$
- Does u reach an IFD at equilibrium? That is,

$$
\frac{m(x)}{u^*(x)} = constant?
$$

Heterogeneous environment

Logistic model

$$d\Delta u^* + u^*(m(x) - u^*) = 0 \quad \text{in} \;\; \Omega, \tag{4}$$

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- No ideal free distribution: $m/u^* \not\equiv$ constant.

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$$\int_\Omega u^*(m - u^*) = 0.$$

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If m/u^* were a constant, then $m \equiv u^*$.

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- No ideal free distribution: $m/u^* \not\equiv$ constant. Integrating (4) in Ω,

$$\int_\Omega u^*(m - u^*) = 0.$$

If m/u^* were a constant, then $m \equiv u^*$. By (4),

$$\Delta m = 0 \quad \text{in } \Omega, \qquad \nabla m \cdot n = 0 \quad \text{on } \partial\Omega,$$

which implies that m must be a constant. Contradiction!

Two competing species

Dockery et al. (98)

$$\begin{aligned} & u_t = d_1 \Delta u + u(m - u - v) \quad \text{in } \Omega \times (0, \infty), \\ & v_t = d_2 \Delta v + v(m - u - v) \quad \text{in } \Omega \times (0, \infty), \\ & \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{5}$$

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Theorem

If $d_1 < d_2$, $(u^*, 0)$ is globally asymptotically stable.

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- Evolution of slow dispersal: Why?

Why smaller dispersal rate?

- Logistic model

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$$\lim_{d \to 0} \frac{m(x)}{u^*(x)} = 1.$$

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- It can be shown that

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- The smaller d is, the closer m/u^* to constant; i.e., the distribution of the species is closer to IFD for smaller dispersal rate

IFD and ESS

Question: Can we find evolutionarily stable dispersal strategies?

IFD and ESS

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- Idea: Find dispersal strategies which can produce ideal free distribution and show that they are evolutionarily stable

Single species

Cantrell, Cosner, L (MBE, 10)

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$$u_t = d_1 \nabla \cdot [\nabla u - u \nabla P(x)] + u[m(x) - u] \quad \text{in } \Omega \times (0, \infty)$$

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- $P(x) = \ln m(x)$ can produce ideal free distribution

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$$\nabla u - u \nabla P = \nabla m - m \nabla (\ln m) = 0$$

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- **Is the strategy $P = \ln m$ an ESS?**

Two species model

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- If $P = \ln m$, $(m, 0)$ is a steady state.

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- If $P = \ln m$, $(m, 0)$ is a steady state.
- Is $(m, 0)$ asymptotically stable? ($\Leftrightarrow$ Is $P = \ln m$ an ESS?)

Stability of $(m, 0)$

- Original system:

$$\begin{aligned} u_t &= d_1 \nabla \cdot [\nabla u - u \nabla \ln m] + u(m - u - v), \\ v_t &= d_2 \nabla \cdot [\nabla v - v \nabla Q] + v(m - u - v). \end{aligned} \tag{10}$$

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- Perturbation of $(m(x), 0)$:

$$
(u, v) = (m, 0) + (\epsilon\varphi(x)e^{-\lambda t}, \epsilon\psi(x)e^{-\lambda t})
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- Perturbation of $(m(x), 0)$:

$$(u, v) = (m, 0) + (\epsilon\varphi(x)e^{-\lambda t}, \epsilon\psi(x)e^{-\lambda t})$$

- Equations for (φ, ψ, λ):

$$\begin{aligned} d_1 \nabla \cdot [\nabla \varphi - \varphi \nabla \ln m] - m\varphi - m\psi &= -\lambda\varphi, \\ d_2 \nabla \cdot [\nabla \psi - \psi \nabla Q] &= -\lambda\psi. \end{aligned} \tag{11}$$

Stability of $(m, 0)$

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- Eigenvalue problem for the stability of $(m, 0)$:

$$-d_2\nabla \cdot [\nabla\psi - \psi\nabla Q] = \lambda\psi \quad \text{in } \Omega,$$

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$$[\nabla \psi - \psi \nabla Q] = 0 \quad \text{on } \partial\Omega.$$

- $(\lambda, \psi) = (0, e^Q)$ is a solution
- *Bad news*: Zero is the smallest eigenvalue; i.e., $(m, 0)$ is neutrally stable

Evolutionary stable strategy

Cantrell et. al (10); Averill, Munther, L (JBD, 2012)

Theorem

Suppose that $m \in C^2(\bar{\Omega})$*, is non-constant and positive in* $\bar{\Omega}$*. If* $P = \ln m$ *and* $Q - \ln m$ *is non-constant, then* $(m, 0)$ *is globally stable.*

$P = lnm$ is an ESS:

- It can resist the invasion of any other strategy

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Theorem

Suppose that $m \in C^2(\bar{\Omega})$, is non-constant and positive in $\bar{\Omega}$. If $P = \ln m$ and $Q - \ln m$ is non-constant, then $(m, 0)$ is globally stable.

$P = lnm$ is an ESS:

- It can resist the invasion of any other strategy
- It can displace any other strategy

Proof

Proof

- Define

$$E(t) = \int_\Omega [u(x,t) + v(x,t) - m(x) \ln u(x,t)] \; dx.$$

Then $dE/dt \leq 0$ for all $t \geq 0$.

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$$E(t) = \int_\Omega [u(x,t) + v(x,t) - m(x) \ln u(x,t)] \, dx.$$

Then $dE/dt \leq 0$ for all $t \geq 0$.

- Three or more competing species: Gejji et al. (BMB 2012); Munther and L. (DCDS-A 2012)

Other dispersal strategies which can produce ideal free distribution:

- (Mark Lewis)

$$u_t = d\Delta\left(\frac{u}{m}\right) + u[m(x) - u] \tag{12}$$

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- (Mark Lewis)

$$u_t = d\Delta\left(\frac{u}{m}\right) + u[m(x) - u] \tag{12}$$

- (Dan Ryan)

$$u_t = d\nabla \cdot \left[mf(m,m)\nabla\left(\frac{u}{m}\right)\right] + u[m(x) - u], \tag{13}$$

where $f(m(x_1), m(x_2))$ is the probability moving from x_1 to x_2 which satisfies

$$D_2 f(m,m) - D_1 f(m,m) = \frac{f(m,m)}{m}.$$

Single species

- Cosner, Davilla and Martinez (JBD, 11)

$$u_t = \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x)-u] \quad (14)$$

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$$u_t = \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x)-u] \quad (14)$$

- Definition: $k(x,y)$ is an ideal free dispersal strategy if

$$\int_\Omega k(x,y)m(y)\,dy = m(x)\int_\Omega k(y,x)\,dy, \quad x\in\Omega. \quad (15)$$

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- Example: $k(x,y) = m^\tau(x)m^{\tau-1}(y)$.

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$$u_t = \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x)-u] \quad (14)$$

- Definition: $k(x,y)$ is an ideal free dispersal strategy if

$$\int_\Omega k(x,y)m(y)\,dy = m(x)\int_\Omega k(y,x)\,dy, \quad x\in\Omega. \quad (15)$$

- Example: $k(x,y) = m^\tau(x)m^{\tau-1}(y)$.

- $m(x)$ is an equilibrium of (14) $\Leftrightarrow$ $k(x,y)$ satisfies (15).

Two species model

Cantrell, Cosner, L and Ryan (Canadian Appl. Math. Quart., in press)

$$u_t = \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x) - u - v],$$
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Theorem

Suppose that both k and k^* are continuous and positive in $\bar\Omega \times \bar\Omega$, k is an ideal free dispersal strategy and k^* is not an ideal dispersal strategy. Then, $(m(x), 0)$ of (16) is globally stable in $C(\bar\Omega) \times C(\bar\Omega)$ for all positive initial data.

A key ingredient

Let $h : \bar{\Omega} \times \bar{\Omega} \to [0, \infty)$ be a continuous function. Then the following two statements are equivalent:

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1. $\int_\Omega h(x, y)\, dy = \int_\Omega h(y, x)\, dy$ for all $x \in \Omega$.
2. $\int_\Omega \int_\Omega h(x, y) \frac{f(x) - f(y)}{f(y)}\, dx\, dy \geq 0$ for any $f \in C(\overline{\Omega})$, $f > 0$ on $\overline{\Omega}$.

Discrete models

- Discrete-space and continuous-time model

$$\frac{du_{ki}}{dt} = \sum_{j=1}^{n} \left(d_{ij}^{k} u_{kj} - d_{ji}^{k} u_{ki} \right) + u_{ki} f_i \left(\sum_{l=1}^{m} u_{li} \right), \quad t > 0, \qquad (17)$$

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- Discrete-time and discrete-space models: Ideal free dispersal strategies may not be able to displace other non-ideal free dispersal strategies; Kirkland, Li and Schreiber, SIAP 2006.

Summary

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- What happens if dispersal strategies can not produce ideal free distribution?

Single species

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- For some non-convex Ω and $m(x)$, $(0, v^*)$ is globally stable

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- Strong advection can induce coexistence of competing species

Aggregation

Theorem

Let (u, v) *be a positive steady state of system* (19)*. As* $\alpha \to \infty$*,* $v(x) \to v^*$ *and*

$$u(x) = e^{-\alpha[m(x_0)-m(x)]} \cdot \left\{ 2^{\frac{N}{2}} \left[m(x_0) - v^*(x_0) \right] + o(1) \right\},$$

where x_0 *is a local maximum of* m *such that* $m(x_0) - v^*(x_0) > 0$*.*

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- Lam (SIMA, 12): *m* finite many local maxima, $N \geq 1$

Consider

$$\begin{aligned} u_t &= d_1 \nabla \cdot [\nabla u - \alpha u \nabla m] + u(m - u - v) \text{ in } \Omega \times (0, \infty), \\ v_t &= d_2 \nabla \cdot [\nabla v - \beta v \nabla m] + v(m - u - v) \text{ in } \Omega \times (0, \infty), \qquad (20) \\ [\nabla u &- \alpha u \nabla m] \cdot n = [\nabla v - \beta v \nabla m] \cdot n = 0 \text{ on } \partial\Omega \end{aligned}$$

Question. If $d_1 = d_2$, can we find some advection rate which is evolutionarily stable?

Hasting's approach revisited

Suppose that species u is at equilibrium:

$$\begin{aligned} & d_1 \nabla \cdot [\nabla u^* - \alpha u^* \nabla m] + u^* [m(x) - u^*] = 0 \quad \text{in } \Omega, \\ & [\nabla u^* - \alpha u^* \nabla m] \cdot n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{21}$$

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Question. Can species v grow when it is rare?

- Stability of $(u, v) = (u^*, 0)$: Let $\Lambda(\alpha, \beta)$ denote the smallest eigenvalue of

$$\begin{aligned} & d_1 \nabla \cdot [\nabla \varphi - \beta \varphi \nabla m] + (m - u^*)\varphi + \lambda \varphi = 0 \quad \text{in } \Omega, \\ & [\nabla \varphi - \beta \varphi \nabla m] \cdot n = 0 \quad \text{on } \partial\Omega. \end{aligned}$$

ESS

Question: Is there an ESS? That is, there exists some $\alpha^* > 0$ such that

$$\Lambda(\alpha^*, \beta) > 0, \quad \forall \beta \neq \alpha^*$$

Two similar species

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- The species with the stronger advection wins the competition if both advection rates are small, but loses if both advection rates are large.
- Some ESS $\alpha^* \in \left(\frac{1}{\max_{\overline{\Omega}} m}, \frac{1}{\min_{\overline{\Omega}} m}\right)$?

K.-Y. Lam and L. (2012)

Theorem

Suppose that Ω is convex and

$$\|\nabla ln(m)\|_{L^\infty} \le \frac{\alpha_0}{diam(\Omega)},$$

where $\alpha_0 \approx 0.814$, then for $d_1 = d_2$ small, there exists a unique $\hat{\alpha} > 0$ such that if $\alpha = \hat{\alpha}$, $\beta \neq \hat{\alpha}$ and $\beta \approx \hat{\alpha}$, $(u^*, 0)$ is asymptotically stable.

This theorem fails for some functions m satisfying

$$\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} > 3 + 2\sqrt{2}.$$

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Fitness-dependent dispersal vs unbiased dispersal

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Recent developments

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Acknowledgment

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Support:

- NSF, Mathematical Biosciences Institute

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Happy Birthday, Chris!