Evolutionarily Stable Dispersal Strategies in Heterogeneous Environments

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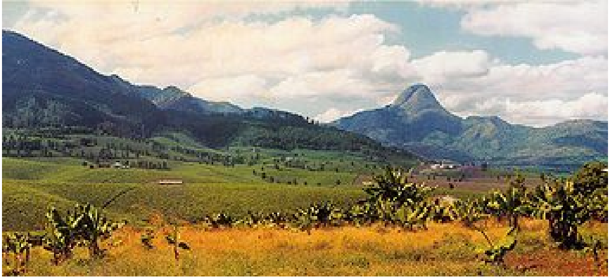
Talk Outline

1. Unbiased dispersal
2. Balanced dispersal
3. Biased dispersal
4. Fitness-dependent dispersal

Evolution of Dispersal



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

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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- Surveys: 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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- “Optimal" movement strategy: Dispersal strategies that are evolutionarily stable

Unbiased dispersal

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

$$\begin{aligned} u_t &= u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \\ v_t &= v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \end{aligned} \tag{1}$$

- $u(x,t), v(x,t)$: densities at $x \in \Omega \subset R^N$

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- d_1, d_2: dispersal rates (**strategies**)

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- $m(x)$: intrinsic growth rate of species
- d_1, d_2: dispersal rates (**strategies**)
- No-flux boundary condition

Hasting's approach

Suppose that u (resident species) is at equilibrium:

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

Question. Can mutant v grow when it is rare?

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Question. Can mutant 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

Theorem

(Hastings 1983) Suppose that $m(x)$ is non-constant, positive and continuous in $\bar{\Omega}$. If $d_1 < d_2$, then $(u^*, 0)$ is stable; if $d_1 > d_2$, $(u^*, 0)$ is unstable.

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- $\Lambda(d_1, d_1) = 0$
- $\Lambda(d_1, d_2)$ is increasing in d_2
- No dispersal rate is evolutionarily stable: Any mutant with a smaller dispersal rate can invade!

Ideal free distribution (IFD)

Fretwell and Lucas (70)

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- How should organisms distribute in heterogeneous habitat?

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

Ideal free distribution (IFD)

Fretwell and Lucas (70)

- How should organisms distribute 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

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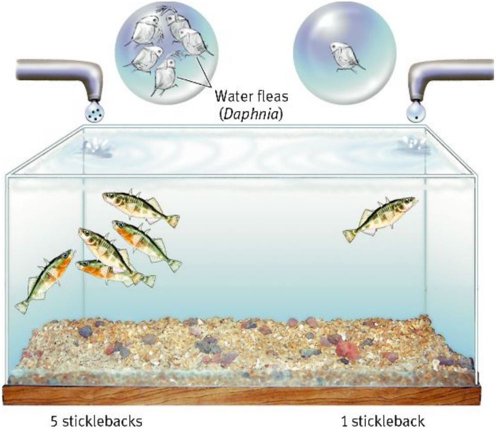

Unbiased dispersal

- 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

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

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

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), \qquad (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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- 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

Q: Are there dispersal strategies that can produce ideal free distribution?

Single species

Cantrell, Cosner, L (MBE, 10)

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

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

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

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- Equations for (φ, ψ, λ):

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

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

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- $(\lambda, \psi) = (0, e^Q)$ 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

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

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

- 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)

$$
\begin{aligned}
u_t &= \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x)-u-v],\\
v_t &= \int_\Omega k^*(x,y)v(y,t)\,dy - v(x,t)\int_\Omega k^*(y,x)\,dy + v[m(x)-u-v].
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$$

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. $\displaystyle\int_\Omega h(x, y)\, dy = \int_\Omega h(y, x)\, dy$ for all $x \in \Omega$.

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

Summary

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- Balanced dispersal strategies are generally evolutionarily stable

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- What happens if dispersal strategies are unbalanced?

Single species

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Weak advection

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Theorem

Suppose that $m \in C^2(\bar{\Omega})$, positive, non-constant.

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

Strong advection

Cantrell et al. (07); Chen, Hambrock, L (JMB, 08)

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- Strong advection can induce coexistence of competing species

Aggregation

Theorem

Let (u, v) *be a positive steady state of system* (18). *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

$$
\begin{aligned}
u_t &= d\nabla \cdot [\nabla u - \alpha u \nabla m] + u(m - u - v) \text{ in } \Omega \times (0, \infty), \\
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[\nabla u - \alpha u \nabla m] \cdot n &= [\nabla v - \beta v \nabla m] \cdot n = 0 \text{ on } \partial\Omega
\end{aligned}
\tag{19}
$$

Question. Can we find some advection rate which is evolutionarily stable?

Hasting's approach revisited

Suppose that species u is at equilibrium:

$$\begin{aligned} & d\nabla \cdot [\nabla u^* - \alpha u^* \nabla m] + u^*[m(x) - u^*] = 0 \quad \text{in} \;\; \Omega, \\ & [\nabla u^* - \alpha u^* \nabla m] \cdot n = 0 \quad \text{on} \;\; \partial\Omega. \end{aligned} \tag{20}$$

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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

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

Adaptive Dynamics

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

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- Step 1. Find α^* such that

$$\frac{\partial \Lambda}{\partial \beta}(\alpha^*, \alpha^*) = 0.$$

Such α^* is called evolutionarily singular strategy.

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  Such α^* is called evolutionarily singular strategy.

- Step 2. If α^* is an evolutionarily singular strategy, determine the sign of

$$\frac{\partial^2 \Lambda}{\partial \beta^2}(\alpha^*, \alpha^*)$$

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

Theorem

Suppose that $m > 0$, $C^2(\bar{\Omega})$,

$$1 < \frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq 3 + 2\sqrt{2}.$$

Given any $\gamma > 0$, if d is small, there exists exactly exactly one evolutionarily singular strategy, denoted as α^*, in $(0, \gamma]$.

- As $d \to 0$, $\alpha^* \to \eta^*$, where η^* is the unique positive root of

$$\int_\Omega e^{-\eta m}(1 - \eta m)m|\nabla m|^2 = 0.$$

- For some functions m satisfying $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} > 3 + 2\sqrt{2}$, there are at least 3 evolutionarily singular strategies.

Theorem

Suppose that Ω is convex and

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

where $\alpha_0 \approx 0.814$, then for small d, $\alpha = \alpha^*$, $\beta \neq \alpha^*$ and $\beta \approx \alpha^*$, $(u^*, 0)$ is asymptotically stable.

- $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq e^{\alpha_0} \approx 2.257 < 3 + 2\sqrt{2}$.
- For some function m satisfying $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} > 3 + 2\sqrt{2}$, there exists some evolutionarily singular strategy which is not an ESS.

One ingredient of the proof is the following celebrated theorem of Payne and Weinberger:

Theorem

Suppose that Ω is a convex domain in R^N. Let μ_2 denote the second eigenvalue of the Laplacian with Neumann boundary condition. Then

$$\mu_2 \geq \left(\frac{\pi}{diam(\Omega)} \right)^2.$$

Single species

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Fitness-dependent vs unbiased dispersal

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- Dispersal in random environments: Evans et al. JMB 2012; S. Schreiber, Am. Nat, in press

Acknowledgment

Collaborators:

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- Isabel Averill, Richard Hambrock
- Xinfu Chen (University of Pittsburgh)
- King-Yeung Lam (MBI)
- Dan Munther (York University)
- Dan Ryan (NIMBioS)

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MBI Emphasis Year on Cancer and Its Environment: 2014-15

- Ecology and Evolution of Cancer
- Metastasis and Angiogenesis
- Cancer and the Immune System
- Tumor Heterogeneity and the Microenvironment
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Thank you!