

# Evolution of Conditional Dispersal in Spatially Heterogeneous Habitats

Yuan Lou

Department of Mathematics  
Mathematical Biosciences Institute  
Ohio State University

# Talk Outline

- 1 Random dispersal
- 2 Conditional dispersal
- 3 Ideal free dispersal
- 4 Some ideas of the proofs
- 5 Future directions

# Reaction-diffusion models

- A. Hastings (TPB, 83)

$$\begin{aligned} u_t &= uf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \\ v_t &= vf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \end{aligned} \quad (1)$$

- $u(x, t), v(x, t)$ : densities of species

# Reaction-diffusion models

- A. Hastings (TPB, 83)

$$\begin{aligned} u_t &= \mu \Delta u + uf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \\ v_t &= \nu \Delta v + vf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \end{aligned} \tag{1}$$

- $u(x, t), v(x, t)$ : densities of species
- $\mu, \nu > 0$ : random dispersal rates

# Reaction-diffusion models

- A. Hastings (TPB, 83)

$$\begin{aligned}
 u_t &= \mu \Delta u + uf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \\
 v_t &= \nu \Delta v + vf(u + v, x) \quad \text{in } \Omega \times (0, \infty), \\
 \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty).
 \end{aligned} \tag{1}$$

- $u(x, t), v(x, t)$ : densities of species
- $\mu, \nu > 0$ : random dispersal rates
- No-flux boundary condition

# Evolution of slow dispersal

# Evolution of slow dispersal

Dockery et al. (JMB 98):

# Evolution of slow dispersal

Dockery et al. (JMB 98):

- $f(u + v, x) = m(x) - u - v$ ,  $m(x)$  is positive and non-constant.



# Evolution of slow dispersal

Dockery et al. (JMB 98):

- $f(u + v, x) = m(x) - u - v$ ,  $m(x)$  is positive and non-constant.
- $\mu < \nu$ .

# Evolution of slow dispersal

Dockery et al. (JMB 98):

- $f(u + v, x) = m(x) - u - v$ ,  $m(x)$  is positive and non-constant.
- $\mu < \nu$ .
- Then  $(\tilde{u}, 0)$  is globally asymptotically stable,

# Evolution of slow dispersal

Dockery et al. (JMB 98):

- $f(u + v, x) = m(x) - u - v$ ,  $m(x)$  is positive and non-constant.
- $\mu < \nu$ .
- Then  $(\tilde{u}, 0)$  is globally asymptotically stable, where  $\tilde{u}$  is the unique positive steady-state of

$$\tilde{u}_t = \mu \Delta \tilde{u} + \tilde{u}(m - \tilde{u}) \quad \text{in } \Omega \times (0, \infty),$$

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

# Evolution of slow dispersal

Dockery et al. (JMB 98):

- $f(u + v, x) = m(x) - u - v$ ,  $m(x)$  is positive and non-constant.
- $\mu < \nu$ .
- Then  $(\tilde{u}, 0)$  is globally asymptotically stable, where  $\tilde{u}$  is the unique positive steady-state of

$$\tilde{u}_t = \mu \Delta \tilde{u} + \tilde{u}(m - \tilde{u}) \quad \text{in } \Omega \times (0, \infty),$$

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

- The slower diffuser is the winner.

# Discrete models

- A. Hastings (TPB, 83): discrete space and continuous time

# Discrete models

- A. Hastings (TPB, 83): discrete space and continuous time
- McPeck and Holt (Am. Nat. 92): discrete space and time, two patch

# Discrete models

- A. Hastings (TPB, 83): discrete space and continuous time
- McPeck and Holt (Am. Nat. 92): discrete space and time, two patch
- Kirkland et al (SIAM J. Appl. Math. 2006): discrete time and space, n-patch

# Conditional dispersal



# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues

# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues
- Discrete models: McPeck and Holt (Am. Nat. 92)

# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues
- Discrete models: McPeck and Holt (Am. Nat. 92)
- Continuous model: Cantrell et al (Math. Biosci. 2006); Chen et al (JMB 2008).

# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues
- Discrete models: McPeck and Holt (Am. Nat. 92)
- Continuous model: Cantrell et al (Math. Biosci. 2006); Chen et al (JMB 2008).

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

# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues
- Discrete models: McPeck and Holt (Am. Nat. 92)
- Continuous model: Cantrell et al (Math. Biosci. 2006); Chen et al (JMB 2008).

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

$$v_t = \nu \nabla \cdot [\nabla v - \beta \mathbf{v} \nabla \mathbf{m}] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty),$$

# Conditional dispersal

- Conditional dispersal: Organisms can sense and respond to local environmental cues
- Discrete models: McPeck and Holt (Am. Nat. 92)
- Continuous model: Cantrell et al (Math. Biosci. 2006); Chen et al (JMB 2008).

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

$$v_t = \nu \nabla \cdot [\nabla v - \beta \mathbf{v} \nabla \mathbf{m}] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - \alpha \mathbf{u} \nabla \mathbf{m}] \cdot \mathbf{n} = [\nabla v - \beta \mathbf{v} \nabla \mathbf{m}] \cdot \mathbf{n} = 0 \quad \text{on } \partial\Omega \times (0, \infty) \quad (2)$$

# Monotone dynamical system

# Monotone dynamical system

- Two species Lotka-Volterra competition systems are monotone



# Monotone dynamical system

- Two species Lotka-Volterra competition systems are monotone
- Matano (1984), Hirsch (1988), Thieme and Smith (1990, 1991), Dancer and Hess (1991), Hsu, Smith, and Waltman (1995), Smith (1995), Jiang, Liang and Zhao (2005)...

# Monotone dynamical system

- Two species Lotka-Volterra competition systems are monotone
- Matano (1984), Hirsch (1988), Thieme and Smith (1990, 1991), Dancer and Hess (1991), Hsu, Smith, and Waltman (1995), Smith (1995), Jiang, Liang and Zhao (2005)...
- Semi-trivial steady states: if  $m > 0$ ,  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  both exist

# Monotone dynamical system

- Two species Lotka-Volterra competition systems are monotone
- Matano (1984), Hirsch (1988), Thieme and Smith (1990, 1991), Dancer and Hess (1991), Hsu, Smith, and Waltman (1995), Smith (1995), Jiang, Liang and Zhao (2005)...
- Semi-trivial steady states: if  $m > 0$ ,  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  both exist
- Coexistence state: If both semi-trivial steady states are unstable, the system has one stable coexistence state

# Weak advection

Cantrell et al:  $\mu = \nu$ ,  $\beta = 0$  and  $\alpha > 0$  small.

# Weak advection

Cantrell et al:  $\mu = \nu$ ,  $\beta = 0$  and  $\alpha > 0$  small.

- If  $\Omega$  is convex,  $(\tilde{u}, 0)$  is globally asymptotically stable.

# Weak advection

Cantrell et al:  $\mu = \nu$ ,  $\beta = 0$  and  $\alpha > 0$  small.

- If  $\Omega$  is convex,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- There exist non-convex domains and  $m(x)$  such that  $(0, \tilde{v})$  is globally asymptotically stable.

# Weak advection

Cantrell et al:  $\mu = \nu$ ,  $\beta = 0$  and  $\alpha > 0$  small.

- If  $\Omega$  is convex,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- There exist non-convex domains and  $m(x)$  such that  $(0, \tilde{v})$  is globally asymptotically stable.
- Geometry of habitat matters

# Advection induced coexistence



# Advection induced coexistence

- What about large  $\alpha$ ?

# Advection induced coexistence

- What about large  $\alpha$ ?
- (Cantrell et al. 2007; Chen et al 2008) Suppose that  $m \in C^2(\bar{\Omega})$ , positive and non-constant.

# Advection induced coexistence

- What about large  $\alpha$ ?
- (Cantrell et al. 2007; Chen et al 2008) Suppose that  $m \in C^2(\bar{\Omega})$ , positive and non-constant. For any  $\mu$  and  $\nu$ ,  $\beta \leq 1 / \max_{\Omega} m$ , if  $\alpha$  is large, both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable, and system (2) has a stable positive steady state.

# Advection induced coexistence

- What about large  $\alpha$ ?
- (Cantrell et al. 2007; Chen et al 2008) Suppose that  $m \in C^2(\bar{\Omega})$ , positive and non-constant. For any  $\mu$  and  $\nu$ ,  $\beta \leq 1 / \max_{\Omega} m$ , if  $\alpha$  is large, both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable, and system (2) has a stable positive steady state.
- Chen and L. (Indiana Univ. Math. J, 08): for  $\beta = 0$  and large  $\alpha$ , if  $m$  has a unique local maximum, the species  $u$  concentrates around this maximum.

# Advection-induced extinction

Chen et al. JMB 2008: Suppose that  $\partial m / \partial n < 0$  on  $\partial \Omega$ ,  $m$  has only one critical point  $x_0$  in  $\overline{\Omega}$ , with  $x_0 \in \Omega$  and  $D^2 m(x_0) < 0$ .

# Advection-induced extinction

Chen et al. JMB 2008: Suppose that  $\partial m / \partial n < 0$  on  $\partial\Omega$ ,  $m$  has only one critical point  $x_0$  in  $\overline{\Omega}$ , with  $x_0 \in \Omega$  and  $D^2 m(x_0) < 0$ .

- If  $\beta \geq 1 / \min_{\overline{\Omega}} m$ ,  $(0, \tilde{v})$  is globally asymptotically stable for large  $\alpha$ .

# Advection-induced extinction

Chen et al. JMB 2008: Suppose that  $\partial m / \partial n < 0$  on  $\partial\Omega$ ,  $m$  has only one critical point  $x_0$  in  $\overline{\Omega}$ , with  $x_0 \in \Omega$  and  $D^2 m(x_0) < 0$ .

- If  $\beta \geq 1 / \min_{\overline{\Omega}} m$ ,  $(0, \tilde{v})$  is globally asymptotically stable for large  $\alpha$ .
- Strong biased movement of *single* species can induce the coexistence of both competing species

# Advection-induced extinction

Chen et al. JMB 2008: Suppose that  $\partial m / \partial n < 0$  on  $\partial\Omega$ ,  $m$  has only one critical point  $x_0$  in  $\overline{\Omega}$ , with  $x_0 \in \Omega$  and  $D^2 m(x_0) < 0$ .

- If  $\beta \geq 1 / \min_{\overline{\Omega}} m$ ,  $(0, \tilde{v})$  is globally asymptotically stable for large  $\alpha$ .
- Strong biased movement of *single* species can induce the coexistence of both competing species
- Strong biased movement of *both* species can induce the extinction of the species with the stronger biased movement



# Evolution of intermediate advection?

For  $\mu = \nu > 0$  and convex habitats, we conjecture that there exists some  $\alpha^* > 0$  such that

# Evolution of intermediate advection?

For  $\mu = \nu > 0$  and convex habitats, we conjecture that there exists some  $\alpha^* > 0$  such that

- If either  $\beta < \alpha \leq \alpha^*$  or  $\alpha^* \leq \alpha < \beta$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.

# Evolution of intermediate advection?

For  $\mu = \nu > 0$  and convex habitats, we conjecture that there exists some  $\alpha^* > 0$  such that

- If either  $\beta < \alpha \leq \alpha^*$  or  $\alpha^* \leq \alpha < \beta$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- If either  $\alpha < \alpha^* < \beta$  or  $\beta < \alpha^* < \alpha$ , both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable and there is one stable positive steady state.

# Evolution of intermediate advection?

For  $\mu = \nu > 0$  and convex habitats, we conjecture that there exists some  $\alpha^* > 0$  such that

- If either  $\beta < \alpha \leq \alpha^*$  or  $\alpha^* \leq \alpha < \beta$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- If either  $\alpha < \alpha^* < \beta$  or  $\beta < \alpha^* < \alpha$ , both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable and there is one stable positive steady state.
- How to estimate  $\alpha^*$ ?

# Two similar species

## Two similar species

(Hambrock and L. 2009) Suppose  $\mu = \nu$ ,  $\Omega = (0, 1)$ , and  $m_x > 0$  on  $[0, 1]$ .

## Two similar species

(Hambrock and L. 2009) Suppose  $\mu = \nu$ ,  $\Omega = (0, 1)$ , and  $m_x > 0$  on  $[0, 1]$ .

- If  $\beta < 1 / \max_{\overline{\Omega}} m$ , there exists  $\delta_1 > 0$  such that for  $\alpha \in (\beta, \beta + \delta_1)$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.

# Two similar species

(Hambrock and L. 2009) Suppose  $\mu = \nu$ ,  $\Omega = (0, 1)$ , and  $m_x > 0$  on  $[0, 1]$ .

- If  $\beta < 1 / \max_{\overline{\Omega}} m$ , there exists  $\delta_1 > 0$  such that for  $\alpha \in (\beta, \beta + \delta_1)$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- If  $\beta > 1 / \min_{\overline{\Omega}} m$ , there exists  $\delta_2 > 0$  such that for  $\alpha \in (\beta - \delta_2, \beta)$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.



# Two similar species

(Hambrock and L. 2009) Suppose  $\mu = \nu$ ,  $\Omega = (0, 1)$ , and  $m_x > 0$  on  $[0, 1]$ .

- If  $\beta < 1 / \max_{\overline{\Omega}} m$ , there exists  $\delta_1 > 0$  such that for  $\alpha \in (\beta, \beta + \delta_1)$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- If  $\beta > 1 / \min_{\overline{\Omega}} m$ , there exists  $\delta_2 > 0$  such that for  $\alpha \in (\beta - \delta_2, \beta)$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- $\alpha^* \in (1 / \max_{\overline{\Omega}} m, 1 / \min_{\overline{\Omega}} m)$

# Ideal free distribution

Consider

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

# Ideal free distribution

Consider

$$\begin{aligned} u_t &= \mu \nabla \cdot [\nabla u - \alpha \mathbf{u} \nabla \mathbf{P}(\mathbf{x})] + u(m - u) \quad \text{in } \Omega \times (0, \infty), \\ [\nabla u - \alpha u \nabla P(x)] \cdot n &= 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \tag{3}$$

# Ideal free distribution

Consider

$$\begin{aligned} u_t &= \mu \nabla \cdot [\nabla u - \alpha \mathbf{u} \nabla \mathbf{P}(\mathbf{x})] + u(m - u) \quad \text{in } \Omega \times (0, \infty), \\ [\nabla u - \alpha u \nabla P(x)] \cdot n &= 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \tag{3}$$

- If  $P(x) = \ln m$ , then  $\tilde{u} \equiv m$  is the unique positive equilibrium

# Ideal free distribution

Consider

$$\begin{aligned} u_t &= \mu \nabla \cdot [\nabla u - \alpha \mathbf{u} \nabla \mathbf{P}(\mathbf{x})] + u(m - u) \quad \text{in } \Omega \times (0, \infty), \\ [\nabla u - \alpha u \nabla P(x)] \cdot \mathbf{n} &= 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \tag{3}$$

- If  $P(x) = \ln m$ , then  $\tilde{u} \equiv m$  is the unique positive equilibrium
- The species with the dispersal strategy  $P = \ln m$  can perfectly match the environmental resource, which leads to its fitness equilibrated across the habitats; i.e.,  $m - \tilde{u} \equiv 0$ .

# Evolution of ideal free dispersal

(Cantrell et al, 2009)

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

# Evolution of ideal free dispersal

(Cantrell et al, 2009)

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

$$v_t = \nu \nabla \cdot [\nabla v - \beta \mathbf{v} \nabla \mathbf{Q}(\mathbf{x})] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty),$$

# Evolution of ideal free dispersal

(Cantrell et al, 2009)

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

$$v_t = \nu \nabla \cdot [\nabla v - \beta \mathbf{v} \nabla \mathbf{Q}(\mathbf{x})] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - \alpha u \nabla P(x)] \cdot n = [\nabla v - \beta v \nabla Q(x)] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty) \quad (4)$$



# Evolution of ideal free dispersal

(Cantrell et al, 2009)

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

$$v_t = \nu \nabla \cdot [\nabla v - \beta \mathbf{v} \nabla \mathbf{Q}(\mathbf{x})] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - \alpha u \nabla P(x)] \cdot n = [\nabla v - \beta v \nabla Q(x)] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty) \quad (4)$$

- Is the dispersal strategy  $P = \ln m$  evolutionarily stable?

# Evolutionarily stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $m \in C^2(\bar{\Omega})$  and  $m > 0$  in  $\bar{\Omega}$ .

# Evolutionarily stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $m \in C^2(\bar{\Omega})$  and  $m > 0$  in  $\bar{\Omega}$ .

- Suppose that  $P(x) = \ln m$ ,  $Q(x) = \ln m(x) + \epsilon R(x)$ , where  $R \in C^2(\bar{\Omega})$ . If  $R$  is non-constant, then  $(0, \tilde{v})$  is unstable and  $(\tilde{u}, 0)$  is globally asymptotically stable for  $0 < |\epsilon| \ll 1$ .

# Evolutionarily stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $m \in C^2(\bar{\Omega})$  and  $m > 0$  in  $\bar{\Omega}$ .

- Suppose that  $P(x) = Inm$ ,  $Q(x) = Inm(x) + \epsilon R(x)$ , where  $R \in C^2(\bar{\Omega})$ . If  $R$  is non-constant, then  $(0, \tilde{v})$  is unstable and  $(\tilde{u}, 0)$  is globally asymptotically stable for  $0 < |\epsilon| \ll 1$ .
- Suppose that  $P(x) - Inm$  is non-constant. There exists some  $R \in C^2(\bar{\Omega})$  such that for  $Q(x) = P(x) + \epsilon R(x)$ ,  $(\tilde{u}, 0)$  is unstable for  $0 < |\epsilon| \ll 1$ .

# Evolutionarily stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $m \in C^2(\bar{\Omega})$  and  $m > 0$  in  $\bar{\Omega}$ .

- Suppose that  $P(x) = Inm$ ,  $Q(x) = Inm(x) + \epsilon R(x)$ , where  $R \in C^2(\bar{\Omega})$ . If  $R$  is non-constant, then  $(0, \tilde{v})$  is unstable and  $(\tilde{u}, 0)$  is globally asymptotically stable for  $0 < |\epsilon| \ll 1$ .
- Suppose that  $P(x) - Inm$  is non-constant. There exists some  $R \in C^2(\bar{\Omega})$  such that for  $Q(x) = P(x) + \epsilon R(x)$ ,  $(\tilde{u}, 0)$  is unstable for  $0 < |\epsilon| \ll 1$ .
- $P = Inm$  is a local evolutionarily stable strategy (ESS), and no other strategy can be a local ESS.

# Convergent stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $P(x) = Inm + \alpha R$ ,  $Q(x) = Inm + \beta R$ ,  $m > 0$ ,  $\Omega = (0, 1)$  and  $R_x > 0$  in  $[0, 1]$ .

- If  $\alpha < \beta < 0$  or  $0 < \beta < \alpha$ ,  $(\tilde{u}, 0)$  is unstable and  $(0, \tilde{v})$  is stable.

# Convergent stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $P(x) = Inm + \alpha R$ ,  $Q(x) = Inm + \beta R$ ,  $m > 0$ ,  $\Omega = (0, 1)$  and  $R_x > 0$  in  $[0, 1]$ .

- If  $\alpha < \beta < 0$  or  $0 < \beta < \alpha$ ,  $(\tilde{u}, 0)$  is unstable and  $(0, \tilde{v})$  is stable.
- Given any  $\eta > 0$ , there exists  $\kappa > 0$  such that if either (i)  $\alpha, \beta \in [-\eta, 0]$  and  $0 < \beta - \alpha < \kappa$  or (ii)  $\alpha, \beta \in [0, \eta]$  and  $-\kappa < \beta - \alpha < 0$ ,  $(0, \tilde{v})$  is globally asymptotically stable.

# Convergent stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $P(x) = Inm + \alpha R$ ,  $Q(x) = Inm + \beta R$ ,  $m > 0$ ,  $\Omega = (0, 1)$  and  $R_x > 0$  in  $[0, 1]$ .

- If  $\alpha < \beta < 0$  or  $0 < \beta < \alpha$ ,  $(\tilde{u}, 0)$  is unstable and  $(0, \tilde{v})$  is stable.
- Given any  $\eta > 0$ , there exists  $\kappa > 0$  such that if either (i)  $\alpha, \beta \in [-\eta, 0]$  and  $0 < \beta - \alpha < \kappa$  or (ii)  $\alpha, \beta \in [0, \eta]$  and  $-\kappa < \beta - \alpha < 0$ ,  $(0, \tilde{v})$  is globally asymptotically stable.
- If either  $\alpha < 0 < \beta$  or  $\beta < 0 < \alpha$ , both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable, and system (4) has one stable positive steady state.



# Convergent stable strategy

(Cantrell et al. 2009) Suppose that  $\mu = \nu$ ,  $P(x) = Inm + \alpha R$ ,  $Q(x) = Inm + \beta R$ ,  $m > 0$ ,  $\Omega = (0, 1)$  and  $R_x > 0$  in  $[0, 1]$ .

- If  $\alpha < \beta < 0$  or  $0 < \beta < \alpha$ ,  $(\tilde{u}, 0)$  is unstable and  $(0, \tilde{v})$  is stable.
- Given any  $\eta > 0$ , there exists  $\kappa > 0$  such that if either (i)  $\alpha, \beta \in [-\eta, 0]$  and  $0 < \beta - \alpha < \kappa$  or (ii)  $\alpha, \beta \in [0, \eta]$  and  $-\kappa < \beta - \alpha < 0$ ,  $(0, \tilde{v})$  is globally asymptotically stable.
- If either  $\alpha < 0 < \beta$  or  $\beta < 0 < \alpha$ , both  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  are unstable, and system (4) has one stable positive steady state.
- $P(x) = Inm$  is a CSS.

# Stability of $(0, \tilde{v})$

- Stability of  $(0, \tilde{v})$ : The sign of the principal eigenvalue  $\lambda(\alpha)$  of

$$\mu \nabla \cdot [\nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \tilde{v}) = -\lambda \varphi \quad \text{in } \Omega,$$

$$\frac{\partial \varphi}{\partial n} - \alpha \varphi \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega$$

# Stability of $(0, \tilde{v})$

- Stability of  $(0, \tilde{v})$ : The sign of the principal eigenvalue  $\lambda(\alpha)$  of

$$\mu \nabla \cdot [\nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \tilde{v}) = -\lambda \varphi \quad \text{in } \Omega,$$

$$\frac{\partial \varphi}{\partial n} - \alpha \varphi \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega$$

- Set  $\psi = e^{-\alpha m} \varphi$ .

# Stability of $(0, \tilde{v})$

- Stability of  $(0, \tilde{v})$ : The sign of the principal eigenvalue  $\lambda(\alpha)$  of

$$\mu \nabla \cdot [\nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \tilde{v}) = -\lambda \varphi \quad \text{in } \Omega,$$

$$\frac{\partial \varphi}{\partial n} - \alpha \varphi \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega$$

- Set  $\psi = e^{-\alpha m} \varphi$ . Then  $\psi$  satisfies

$$-\mu[\Delta \psi + \alpha \nabla m \cdot \nabla \psi] + \psi(\tilde{v} - m) = \lambda(\alpha) \psi \quad \text{in } \Omega,$$

$$\frac{\partial \psi}{\partial n} = 0 \quad \text{on } \partial \Omega.$$

# Stability of $(0, \tilde{v})$

- Stability of  $(0, \tilde{v})$ : The sign of the principal eigenvalue  $\lambda(\alpha)$  of

$$\mu \nabla \cdot [\nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \tilde{v}) = -\lambda \varphi \quad \text{in } \Omega,$$

$$\frac{\partial \varphi}{\partial n} - \alpha \varphi \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial \Omega$$

- Set  $\psi = e^{-\alpha m} \varphi$ . Then  $\psi$  satisfies

$$-\mu[\Delta \psi + \alpha \nabla m \cdot \nabla \psi] + \psi(\tilde{v} - m) = \lambda(\alpha) \psi \quad \text{in } \Omega,$$

$$\frac{\partial \psi}{\partial n} = 0 \quad \text{on } \partial \Omega.$$

- What is the behavior of  $\lambda(\alpha)$  for large  $\alpha$ ?

# Asymptotic behavior

- Consider

$$-\mu[\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi] + c(x)\varphi = \lambda\varphi \quad \text{in } \Omega, \quad \frac{\partial\varphi}{\partial n}|_{\partial\Omega} = 0.$$

# Asymptotic behavior

- Consider

$$-\mu[\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi] + c(x)\varphi = \lambda\varphi \quad \text{in } \Omega, \quad \frac{\partial\varphi}{\partial n}|_{\partial\Omega} = 0.$$

- Chen and L. (Indiana Math Univ. J, 08): suppose that  $m \in C^2(\bar{\Omega})$  and all critical points of  $m$  are non-degenerate.

# Asymptotic behavior

- Consider

$$-\mu[\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi] + c(x)\varphi = \lambda\varphi \quad \text{in } \Omega, \quad \frac{\partial\varphi}{\partial n}|_{\partial\Omega} = 0.$$

- Chen and L. (Indiana Math Univ. J, 08): suppose that  $m \in C^2(\bar{\Omega})$  and all critical points of  $m$  are non-degenerate. Then

$$\lim_{\alpha \rightarrow \infty} \lambda(\alpha) = \min_{x \in \mathcal{M}} c(x),$$



# Asymptotic behavior

- Consider

$$-\mu[\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi] + c(x)\varphi = \lambda\varphi \quad \text{in } \Omega, \quad \frac{\partial\varphi}{\partial n}|_{\partial\Omega} = 0.$$

- Chen and L. (Indiana Math Univ. J, 08): suppose that  $m \in C^2(\bar{\Omega})$  and all critical points of  $m$  are non-degenerate. Then

$$\lim_{\alpha \rightarrow \infty} \lambda(\alpha) = \min_{x \in \mathcal{M}} c(x),$$

where  $\mathcal{M}$  is the set of points of local maximum of  $m$ .

# Back to dispersal

# Back to dispersal

- Recall

$$-\mu[\Delta\psi + \alpha\nabla m \cdot \nabla\psi] + \psi(\tilde{\nu} - m) = \lambda(\alpha)\psi \quad \text{in } \Omega,$$

$$\frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

# Back to dispersal

- Recall

$$-\mu[\Delta\psi + \alpha\nabla m \cdot \nabla\psi] + \psi(\tilde{v} - m) = \lambda(\alpha)\psi \quad \text{in } \Omega,$$

$$\frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

- It follows from previous result of Chen and L. that

$$\lim_{\alpha \rightarrow \infty} \lambda(\alpha) = \min_{\mathcal{M}}(\tilde{v} - m),$$

where  $\mathcal{M}$ =the set of points of local maximum of  $m(x)$ .

# Resource undermatching and overmatching

# Resource undermatching and overmatching

- Recall

$$\nu \nabla \cdot [\nabla \tilde{v} - \beta \tilde{v} \nabla m] + \tilde{v}(m - \tilde{v}) = 0 \quad \text{in } \Omega,$$

$$\frac{\partial \tilde{v}}{\partial n} - \beta \tilde{v} \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

# Resource undermatching and overmatching

- Recall

$$\nu \nabla \cdot [\nabla \tilde{v} - \beta \tilde{v} \nabla m] + \tilde{v}(m - \tilde{v}) = 0 \quad \text{in } \Omega,$$

$$\frac{\partial \tilde{v}}{\partial n} - \beta \tilde{v} \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

- If  $\beta \leq 1 / \max_{\overline{\Omega}} m$ ,

# Resource undermatching and overmatching

- Recall

$$\nu \nabla \cdot [\nabla \tilde{v} - \beta \tilde{v} \nabla m] + \tilde{v}(m - \tilde{v}) = 0 \quad \text{in } \Omega,$$

$$\frac{\partial \tilde{v}}{\partial n} - \beta \tilde{v} \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

- If  $\beta \leq 1 / \max_{\bar{\Omega}} m$ ,

$$\tilde{v} < \max_{\bar{\Omega}} m \cdot e^{\beta[m(x) - \max_{\bar{\Omega}} m]}, \quad \forall x \in \bar{\Omega}.$$



# Resource undermatching and overmatching

- Recall

$$\nu \nabla \cdot [\nabla \tilde{v} - \beta \tilde{v} \nabla m] + \tilde{v}(m - \tilde{v}) = 0 \quad \text{in } \Omega,$$

$$\frac{\partial \tilde{v}}{\partial n} - \beta \tilde{v} \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

- If  $\beta \leq 1 / \max_{\bar{\Omega}} m$ ,

$$\tilde{v} < \max_{\bar{\Omega}} m \cdot e^{\beta[m(x) - \max_{\bar{\Omega}} m]}, \quad \forall x \in \bar{\Omega}.$$

- If  $\beta \geq 1 / \min_{\bar{\Omega}} m$ ,

# Resource undermatching and overmatching

- Recall

$$\nu \nabla \cdot [\nabla \tilde{v} - \beta \tilde{v} \nabla m] + \tilde{v}(m - \tilde{v}) = 0 \quad \text{in } \Omega,$$

$$\frac{\partial \tilde{v}}{\partial n} - \beta \tilde{v} \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

- If  $\beta \leq 1 / \max_{\bar{\Omega}} m$ ,

$$\tilde{v} < \max_{\bar{\Omega}} m \cdot e^{\beta[m(x) - \max_{\bar{\Omega}} m]}, \quad \forall x \in \bar{\Omega}.$$

- If  $\beta \geq 1 / \min_{\bar{\Omega}} m$ ,

$$\tilde{v} > \max_{\bar{\Omega}} m \cdot e^{\beta[m(x) - \max_{\bar{\Omega}} m]}, \quad \forall x \in \bar{\Omega}.$$

# Overmatching resource

# Overmatching resource

- A. Bezugly: Let  $x_0 \in \Omega$  be a non-degenerate local maximum of  $m(x)$ . Then there exist some  $\delta > 0$  and  $\Lambda > 0$  such that for every  $|x - x_0| < \delta$  and  $\beta > \Lambda$ ,

$$\tilde{v}(x) > m(x_0)e^{\beta[m(x)-m(x_0)]}.$$

# Overmatching resource

- A. Bezugly: Let  $x_0 \in \Omega$  be a non-degenerate local maximum of  $m(x)$ . Then there exist some  $\delta > 0$  and  $\Lambda > 0$  such that for every  $|x - x_0| < \delta$  and  $\beta > \Lambda$ ,

$$\tilde{v}(x) > m(x_0)e^{\beta[m(x)-m(x_0)]}.$$

- Ni (private communication): At each local maximum  $x_0$  of  $m(x)$ ,

$$\liminf_{\beta \rightarrow \infty} \tilde{v} \geq m(x_0);$$

Furthermore, as  $\beta \rightarrow \infty$ ,  $\tilde{v} \rightarrow 0$  uniformly in any compact set which does not contain any local maximum of  $m$ .

# Questions

# Questions

- Resource with multiple peaks? Evolution branching?

# Questions

- Resource with multiple peaks? Evolution branching?
- Multiple traits: e.g., dispersal rate ( $\mu$ ) and advection rate ( $\alpha$ ); Connections with IFD.



# Questions

- Resource with multiple peaks? Evolution branching?
- Multiple traits: e.g., dispersal rate ( $\mu$ ) and advection rate ( $\alpha$ ); Connections with IFD.
- Density-dependent dispersal? Tracking fitness gradient?

# Questions

- Resource with multiple peaks? Evolution branching?
- Multiple traits: e.g., dispersal rate ( $\mu$ ) and advection rate ( $\alpha$ ); Connections with IFD.
- Density-dependent dispersal? Tracking fitness gradient?
- Temporal variability? Include resource dynamics?

# Acknowledgement

## Collaborators:

- Stephen Cantrell (University of Miami)
- Xinfu Chen (University of Pittsburgh)
- Chris Cosner (University of Miami)
- Richard Hambrock (Ohio State University)

# Acknowledgement

## Collaborators:

- Stephen Cantrell (University of Miami)
- Xinfu Chen (University of Pittsburgh)
- Chris Cosner (University of Miami)
- Richard Hambrock (Ohio State University)

## Support:

- NSF
- Mathematical Biosciences Institute

# MBI 2010-2011 Emphasis Year Program

# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects

# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects
- Workshop 1: Mathematical Modeling of Plant Development

# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects
- Workshop 1: Mathematical Modeling of Plant Development
- Workshop 2: Circadian Clocks in Plants and Fungi



# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects
- Workshop 1: Mathematical Modeling of Plant Development
- Workshop 2: Circadian Clocks in Plants and Fungi
- Workshop 3: Insect Self-organization and Swarming

# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects
- Workshop 1: Mathematical Modeling of Plant Development
- Workshop 2: Circadian Clocks in Plants and Fungi
- Workshop 3: Insect Self-organization and Swarming
- Workshop 4: Ecology and Control of Invasive Species, Including Insects

# MBI 2010-2011 Emphasis Year Program

- Evolution, Synchronization, and Environmental Interactions: Insights from Plants and Insects
- Workshop 1: Mathematical Modeling of Plant Development
- Workshop 2: Circadian Clocks in Plants and Fungi
- Workshop 3: Insect Self-organization and Swarming
- Workshop 4: Ecology and Control of Invasive Species, Including Insects
- Workshop 5: Coevolution and the Ecological Structure of Plant-insect Communities

Thank you