# The ideal free strategy with weak Allee effect

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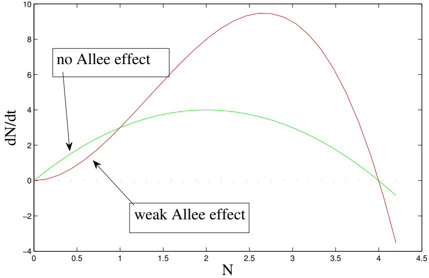
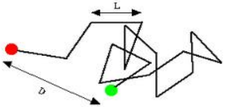


# Ecology and dispersal

Which patterns of dispersal provide an evolutionary advantage in a variable environment?

- Unbiased dispersal - independent of habitat, population density, etc.




- Biased dispersal - depends on one or more factors

# Generalized two species model

(Cantrell et al. 2010)

$$
\begin{aligned}
u_t &= \mu\nabla\cdot[\nabla u - u\nabla P(x)] + u[m(x)-u-v] \quad \text{in } \Omega\times(0,\infty),\\
v_t &= \nu\nabla\cdot[\nabla v - v\nabla Q(x)] + v[m(x)-u-v] \quad \text{in } \Omega\times(0,\infty),\\
&[\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = 0 \text{ on } \partial\Omega\times(0,\infty)
\end{aligned}
\tag{1}
$$

- Species have same population dynamics but different movement strategies
- $m(x) > 0$ is nonconstant (spatially inhomogeneous)
- Semi-trivial steady states: $(u^*, 0)$ and $(0, v^*)$
- Is there a strategy $P(x)$ which cannot be invaded?

# Single species distribution

- Diffusion creates a mismatch between population density at steady state and habitat quality $m(x)$ (Cantrell et al. 2010)

$$\mu\nabla\cdot[\nabla u - u\nabla P(x)] + u[m(x) - u] = 0 \quad \text{in} \quad \Omega,$$
$$[\nabla u - u\nabla P(x)]\cdot n = 0 \quad \text{on} \quad \partial\Omega.$$

- If $P(x) = \ln m(x)$, $u \equiv m$ is a positive steady state.
- No net movement:

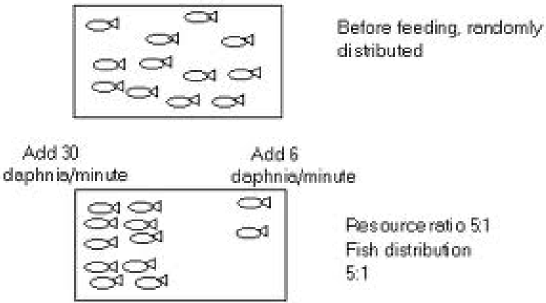
$$\nabla u - u\nabla P(x) = \nabla m - m\nabla \ln m = \nabla m - \nabla m = 0$$

- Fitness equilibrated throughout the habitat: $\frac{m}{u} \equiv 1$.
- We call $P = \ln m$ an Ideal Free Strategy (IFS).

Habitat Selection Theory (Fretwell and Lucas 1970):

1. Choose most suitable habitat (ideal)
2. Can move into any desired region (free)

Ideal Free Distribution: A species will aggregate in a location proportionately to the amount of available resources in that location



# Evolutionary stable strategy

- Cantrell et al. showed that $P = \ln m$ is a local evolutionary stable strategy (ESS) and no other strategy can be a local ESS.

**Theorem**

*(Averill et al.) Suppose that $P = \ln m$ and $Q - \ln m$ is nonconstant. Then $(0, v^*)$ is unstable and $(u^*, 0)$ is globally asymptotically stable.*

- Biologically, $P = \ln m$ is a global ESS.
- Main Question: Does this result still hold when $u(m - u - v)$ is replaced by $u^2(m - u - v)$ in model (1)?

# Modified model (Munther, JDE 2013)

$$\begin{aligned} u_t &= \mu\nabla\cdot[\nabla u - u\nabla\ln(m)] + u^2(m-u-v) && \text{in } \Omega\times(0,\infty), \\ v_t &= \nu\nabla\cdot[\nabla v - \beta v\nabla\ln(m)] + v(m-u-v) && \text{in } \Omega\times(0,\infty), \quad (2) \\ [\nabla u - u\nabla\ln(m)]\cdot n &= [\nabla v - \beta v\nabla\ln(m)]\cdot n = 0 && \text{on } \partial\Omega\times(0,\infty). \end{aligned}$$

Why is this interesting?

- $u$ is subject to weak Allee effect (species no longer have the same population dynamics)
- Interplay between IFS and weak Allee effect
- Invasion dynamics not useful for any $\beta \in [0,\infty)$

# $\beta = 0$ case

**Theorem (1)**

*Suppose* $m \in C^2(\bar{\Omega})$ *is positive and non-constant. Then for* $\beta = 0$ *and any* $\mu$, $\nu > 0$, *any solution* $(u, v)$ *of* (2) *with nonnegative, not identically zero initial data converges to* $(m, 0)$ *in* $L^\infty(\Omega)$ *as* $t \to \infty$.

- $u$ cannot only invade $v$, but it drives $v$ to extinction no matter its diffusion rate
- IFS offsets the weak Allee effect

# Proof of Theorem (1)

- Recast model as dynamical system $S[u, v]$ on $C(\bar{\Omega}) \times C(\bar{\Omega})$.
- The order interval $G = [(0, v^*), (m, 0)]$ is a basin of attraction.
- Define $E(u, v) = \int_\Omega \frac{m^2}{u} + 2m \ln u - u + \frac{v^2}{2}$.
- $\frac{dE}{dt} = -\mu \int_\Omega \frac{2m|\nabla(u/m)|^2(1-(u/m))}{(u/m)^3} - \nu \int_\Omega |\nabla v|^2$
  $- \int_\Omega ((m-u)^2 - v^2)(m - u - v) \leq 0$ on $G$.
- By LaSalle's invariance principal for infinite dimensions, $S[u, v] \to (m, 0)$.

# $\beta \ll 1$ case

**Theorem (2)**

*Suppose $m \in C^2(\bar{\Omega})$ is positive and non-constant. Then there exists $0 < \beta^* < 1$ such that for all $\beta \in (0, \beta^*)$ and any $\mu$, $\nu > 0$, any solution $(u, v)$ of (2) with nonnegative, not identically zero initial data converges to $(m, 0)$ in $L^\infty(\Omega)$ as $t \to \infty$.*

- Again, $u$ is sole winner as IFS is able to still offset the Allee effect.
- Proof for Theorem (2) is more tricky.

# Remarks

- Conjecture: Theorem (2) holds for all $\beta \in (0, 1)$.
  First, $(0, v^*)$ is unstable for $\beta \in (0, 1)$, since $\int_\Omega m^2(m - v^*) > 0$.
  Second, numerics indicate no positive steady states.

- For the $\beta = 1$ case, both species are playing IFS and hence coexist. System (2) has a continuum of positive steady states of the form $(sm, (1 - s)m)$ for $s \in (0, 1)$.

- For the $\beta >> 1$ case, we can show $(0, v^*)$ is unstable.
  Conjecture: $u$ (IFS) should be the sole winner as in Theorem (2).
  For $m$ with single max in $\Omega$, we can prove this (Adrian Lam).

# Intermediate $\beta \in (1, 1+\epsilon)$ case

Current work (with Adrian Lam):

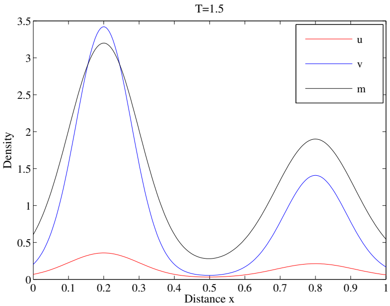
- We can show that $\int_\Omega m^2(m - v^*) < 0$.
- Using upper/lower solution argument, eliminate positive steady states near $(0, v^*)$.
- By monotonicity, we can show that $(0, v^*)$ is locally asymptotically stable.

Fundamentally different:

- The winning strategy is no longer a "resource matching" strategy.
- Biological explanation?

# Intermediate $\beta > 1$ case

Numerical example:



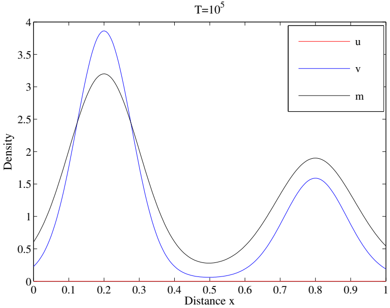




Figure: $m(x) = 3e^{-50(x-.2)^2} + 1.7e^{-40(x-.8)^2} + .2$ (black) and $u$ (red) and $v$ (blue), $\mu = 1000$, $\nu = 1000$, $\beta = 1.7$ a) two species at $T = 1.5$, b) $T = 10^5$.

- The growth rate for $u$ near $x = 0.8$ is $m(x) - v(x,t) > 0$ for all $t > T_0$.
- For $\beta$ in this range, $v$ can defeat $u$ even when $u$ has significant initial numbers.

Summary:

- For $\beta \in [0, 1)$ and $[\beta^*, \infty)$, the ideal free disperser dominates.
- For $\beta = 1$, coexistence as both species are ideal free dispersers
- For intermediate $\beta > 1$, the ideal free strategy cannot invade.

Future work:

- Prove global stability of $(0, v^*)$ for $\beta \in (1, 1 + \epsilon)$.
- $u$ subject to a strong Allee effect

# References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