Counterintuitive patterns of dispersal evolution in a simple trophic metacommunity

Pradeep Pillai,
Marine Science Center,
Northeastern University

Everything Disperses to Miami,
University of Miami Coral Gables
Dec. 14-16, 2012
Evolution of dispersal in metapopulation

- Ecologically: Dispersal important for maintaining a species in a spatially subdivided population.
- Evolutionarily: Dispersal comes at a cost of decreasing local fitness.
Evolution of dispersal in a metacommunity

- What selection pressures exist on species dispersal rates at the metacommunity level?
- Dispersal repeatedly shown to increase with local extinction rate in metapopulations
Evolution of dispersal

Research Question

- Want to measure how evolutionary stable (ESS) dispersal will change with increasing extinction rates caused by unstable interaction between a prey and predator
Evolution of dispersal

Background theory: Importance of dispersal

- Eg. Huffaker, 1958

T. occidantelis

E. sexmaculatus
Evolution of dispersal

Background theory: Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory: Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory:
Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory: Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory:
Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory: Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory:
Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Background theory: Importance of dispersal

- Huffaker, 1958
Evolution of dispersal

Metacommunity framework for studying dispersal evolution

- Use a patch-dynamic metacommunity approach to model spatially structured populations of interacting predator and prey species.
Evolution of dispersal

Metapopulation dynamics

"population of populations which go extinct locally and recolonize." (Levins 1970)
Evolution of dispersal

Metapopulation dynamics
Evolution of dispersal

Metapopulation dynamics
Evolution of dispersal

Metapopulation dynamics
Evolution of dispersal

Metapopulation dynamics

\[
\frac{dp}{dt} = \text{Colonization of new patches} - \text{local Extinction in occupied patches}
\]
Evolution of dispersal

Metapopulation dynamics

\[ \frac{dp}{dt} = \text{Colonization of new patches} - \text{local Extinction in occupied patches} \]

\[ \frac{dp}{dt} = cp(h - p) - ep \]
Evolution of dispersal
Predator-prey metacommunity dynamics
Evolution of dispersal
Predator-prey metacommunity dynamics
Evolution of dispersal

Metacommunity dynamics

Predator-prey metacommunity

\[
\frac{dR}{dt} = c_R R (h - R) - e_R R - \mu P \quad \text{(prey)}
\]

\[
\frac{dP}{dt} = c_P P (R - P) - e_P P - (e_R + \mu) P \quad \text{(predator)}
\]
Evolution of dispersal

Model framework and assumptions

- Model based on Jansen and Vitalis (2007)
- Increased dispersal between patches comes at cost of decreasing local fitness
- Need to have a link between local within-patch dynamics (i.e., fitness) and regional metacommunity-level processes (colonization-extinction)
Evolution of dispersal

Model framework and assumptions

Regional metacommunity scale

\[
\frac{dR}{dt} = c_R R(h - R) - e_R R - \mu P \quad \text{(prey)}
\]

\[
\frac{dP}{dt} = c_P P(R - P) - e_P P - (e_R + \mu) P \quad \text{(predator)}
\]

Local within-patch scale

\[
\dot{x} = rx \left(1 - \frac{x}{K}\right) - \gamma_x x - axy \quad \text{(prey equation)}
\]

\[
\dot{y} = axy - \gamma_y y - my \quad \text{(predator equation)}
\]
Evolution of dispersal

Local (within-patch) dynamics

\[ \dot{x} = rx \left(1 - \frac{x}{K}\right) - \gamma_x x - axy \]  \hspace{1cm} \text{(prey equation)}

\[ \dot{y} = aqxy - \gamma_y y - my \]  \hspace{1cm} \text{(predator equation)}
Evolution of dispersal

Local (within-patch) dynamics

\[ \dot{x} = rx \left(1 - \frac{x}{K}\right) - \gamma_x x - axy \]  
(prey equation)

\[ \dot{y} = aqx y - \gamma_y y - my \]  
(predator equation)

\[ \tilde{x}_0 = \frac{K}{r} (r - \gamma_x) \]  
(local prey density without predator)

\[ \tilde{x}_p = \frac{(m + \gamma_y)}{aq} \]  
(local prey density with predator)

\[ \tilde{y} = \frac{r}{a} \left(1 - \frac{m + \gamma_y}{aqK}\right) - \frac{\gamma_x}{a} \]  
(local predator density)
Evolution of dispersal

Model framework and assumptions

Regional metacommunity scale

\[
\frac{dR}{dt} = c_R R (h - R) - e_R R - \mu P \quad \text{(prey)}
\]

\[
\frac{dP}{dt} = c_P P (R - P) - e_P P - (e_R + \mu) P \quad \text{(predator)}
\]

When metacommunity is at equilibrium

\[
\tilde{R} = \frac{1}{2} \left[ 1 - \left( \frac{e_R + \mu}{c_{R_P}} \right) + \Gamma \right] + \frac{1}{2} \sqrt{1 - \left( \frac{e_R + \mu}{c_{R_P}} \right) + \Gamma}^2 + 4 \frac{\mu - \Delta c_R}{c_{R_P} c_P} (e_p + e_R + \mu),
\]

\[
\tilde{P} = \tilde{R} - \frac{(e_p + e_R + \mu)}{c_P}
\]
Evolution of dispersal
Scaling up from local (within-patch) dynamics to regional metacommunity dynamics

\[ e(x) = e_{x_{\text{max}}} \left( \frac{K}{\tilde{x}} \right)^z \]
Evolution of dispersal

Measuring fitness in a metacommunity

- Utilize this framework to study evolution of dispersal, $\gamma$, in a metacommunity.
Evolution of dispersal
Measuring fitness in a metacommunity

Follow the fate of a single single mutant invasive individual, with dispersal strategy $\gamma_{\text{mutant}}$, invading a metacommunity with a resident prey with dispersal rate, $\gamma_{\text{resident}}$, while both resident predator, $P$, and prey, $R$, patch-occupancies are at equilibrium.
Evolution of dispersal

Measuring fitness in a metacommunity

- Measure the total lifetime reproductive output of the focal invasive after it has landed in a patch, before going extinct, or being competitively displaced.

- Use $R_M$ as a measure of fitness (Metz and Gyllenberg, 2001; similar to $R_0$).
Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

\[ W = \]
Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

\[ W = \left( \text{prob. mutant landing on empty patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) \]
Measuring fitness in a metacommunity

State transition diagram for an invasive prey patch prior to extinction or reinvasion by a resident

State transition diagrams of a mutant invasive prey patch.

A, State transition diagram for an invasive patch before recolonization by a resident prey. The invasive prey patch exists in one of two states over time: in a patch without a predator or in a predator-occupied patch. It moves between these two states through extinction of local predators in a predator-occupied patch (at frequency $P$) or by colonization of a prey-only patch by predator colonizers (at frequency $e$).

It ceases to be a strictly mutant invasive patch through either patch extinction (with frequencies $P$ or $e$) or by conversion to a mixed-strategy patch through recolonization by resident strategy colonizers (with frequency $R$).

B, State transition diagram for an invasive patch after recolonization by a resident prey. After recolonization by a resident prey, the patch will once again exist in one of two states: a mixed-strategy patch without a predator or a mixed-strategy patch with a predator. Transitions are similar to those described in A; see text for details.
Evolution of dispersal

Measuring fitness in a metacommunity
Evolution of dispersal
Measuring fitness in a metacommunity
Evolution of dispersal
Measuring fitness in a metacommunity
Evolution of dispersal
Measuring fitness in a metacommunity

\[ \gamma_{\text{mutant}} \]
Evolution of dispersal
Measuring fitness in a metacommunity

$\gamma_{\text{resident}}$
Evolution of dispersal

Measuring fitness in a metacommunity
Evolution of dispersal

Measuring fitness in a metacommunity

$\gamma_{\text{mutant}}$
Evolution of dispersal
Measuring fitness in a metacommunity

\[ \gamma_{\text{mutant}} \]
Evolution of dispersal

Measuring fitness in a metacommunity

$\gamma_{\text{mutant}}$
Evolution of dispersal

Measuring fitness in a metacommunity
Evolution of dispersal

Measuring fitness in a metacommunity

- Involves measuring the output of a mixed strategy patch (when both resident and invasive strategy are present).
Evolution of dispersal
Measuring fitness in a metacommunity

State transition diagram for an mixed-strategy prey patch prior to extinction

\[ \chi_0 \quad \xrightarrow{e_{R_0}} \quad \chi_P \]

- \[ e_P \]
- \[ c_p \tilde{p} \]
- \[ e_{R_P} (= e_{R_0} + \mu) \]
Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

\[ W = \]
Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

\[ W = \left( \text{prob. mutant landing on empty patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) \]
Fitness of single mutant invasive prey

Evolution of dispersal

Measuring fitness in a metacommunity

\[ W = \left( \text{prob. mutant landing on empty patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) + \left( \text{prob. invasive landing on resident prey-only patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) \]
Evolution of dispersal

Measuring fitness in a metacommunity

Fitness of single mutant invasive prey

\[
W = \left( \text{prob. mutant landing on empty patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) + \left( \text{prob. invasive landing on resident prey-only patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right) + \left( \text{prob. invasive landing on resident predator-prey patch} \right) \times \left( \text{Number of colonizers produced before extinction or complete competitive displacement} \right)
\]
Evolution of dispersal

Gradient of selection and evolutionarily singular strategy

\[ G = \left. \frac{\partial W}{\partial \gamma_m} \right|_{\gamma_{\text{mutant}} = \gamma_{\text{resident}}} = 0 \]

Evolutionary singular strategy: \( \gamma^* \) (Critical value of dispersal)
Evolution of dispersal

Condition ESS and CSS

If $\frac{dG}{d\gamma} \bigg|_{\gamma=\gamma^*} < 0$ then $\gamma^*$ is an evolutionary attractor

If $\frac{\partial^2 W}{\partial \gamma_m^2} \bigg|_{\gamma_{\text{mutant}}=\gamma_{\text{resident}}} < 0$ then $\gamma^*$ is ESS stable (not a potential evolutionary branching point)

If both of the above, then **Continuously Stable Strategy**
Evolution of dispersal

Research Question

- Want to measure how evolutionary stable (ESS) dispersal will change with increasing extinction rates caused by unstable interaction with predator
Evolution of dispersal

Results: **predator** ESS dispersal with increasing top-down extinction

Pillai, Gonzalez and Loreau American Naturalist, 2012
Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction.
Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction

![Graph showing the evolution of dispersal with increasing top-down extinction rate. The graph plots metacommunity occupancy against the top-down extinction rate. The lines represent the dispersal strategies of prey and predator species.]
Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction
Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction

\[ e(x) = e_{\text{max}} \left( \frac{K}{\bar{x}} \right)^z \]
Evolution of dispersal

Results: prey ESS dispersal with increasing top-down extinction

For very low $z_x$ values.

Curves shown for:
- $z_x = 0.01$ (circles)
- $z_x = 0.08$ (triangles)
- $z_x = 0.10$ (squares)
- $z_x = 0.15$ (dots)

Pillai, Gonzalez and Loreau, American Naturalist, 2012
Evolution of dispersal

Results: Coevolution of a predator and prey

Joint evolutionary stable strategy for coevolved predator and prey

$z_x = 0.4$ hashed
$z_x = 0.8$ solid
$z_x = 1.2$ dashed

Pillai, Gonzalez and Loreau, American Naturalist, 2012
Evolution of dispersal

Summary of results

- Extinctions are caused by interspecific (trophic) interactions
- Feedback between local and metacommunity scale processes: predator-prey interactions play out differently at local and regional scales
Some patterns and processes are emergent at the metacommunity scale.

Non-monotonic dispersal is an emergent property at the scale of the metacommunity arising from contradiction between local and metacommunity scale selection processes.
Acknowledgements

- Thanks to Andrew Gonzalez (McGill University) and Michel Loreau (Station d’Ecologie Expérimentale du CNRS à Moulis, France)
- Research funded by an FQRNT (Fonds québécois de la recherche sur la nature et les technologies) team grant