Evolution of Complex Density-Dependent Dispersal Strategies

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Not examples of evolution

butterfly metamorphosis

cell differentiation: osteoclast
[Boyle et al, Nature 2003]

human development
The theory of evolution by natural selection assumes:

- individuals differ by their trait, different survival probability
- traits are heritable
- too many offspring, not all can survive
- struggle for existence
- Individuals that survive and reproduce before dying are on average, better suited to their local environment

Therefore...

- As time passes by the distribution of traits change.
- More fitted become more general: Adaptation
Some questions:

- Why nature is green?
- Why multicellular organism evolved?
- Why helping behavior evolved?
- Why we have two genders?
- Why senescence?
- Why dispersing evolved?
- Can we prevent evolution of drug resistance?
- Can we control cancer?

And so many more!
American pika - *Ochotona princeps*

- order: Lagomorpha
- small, diurnal herbivore
- native to cold climates
American pika - *Ochotona princeps*

talus - rocky slopes

hay pile for winter
Bodie metapopulation

ore dumps - patches
Dispersal is selected for, because of...

- Resource competition
- Fluctuating environment
- Kin competition

Density dependent dispersal

- Large patches: threshold strategy
  [Gyllenberg and Metz:2001]
- Larger patch models “dilute” the kin benefits

Our question:

- How density-dependent dispersal evolves in metapopulation with small local populations?
Strategy types

Examples of density dependent dispersal strategies

a) threshold for large patch-sizes

b) threshold

c) monotone

d) non-monotone
Emigration:
- Natal dispersal: probability that an individual born in a patch with $n$ inhabitants will emigrate immediately after birth
- Adult dispersal: rate to emigrate from a patch with $n$ inhabitants
  
- $e = (e_1, e_2, ..., e_K)$
- Natal dispersal: $0 \leq e_i \leq 1$
- Adult dispersal: $e_i \geq 0$

Immigration:
- Probability to stay in a patch when encountered
- $m = (m_0, m_1, ..., m_{K-1})$
- $0 \leq m_i \leq 1$
Local model

a) Adult dispersal, local dynamics

\[
\begin{array}{cccccccc}
0 & 1 & 2 & \cdots & k & \cdots & K \\
\text{Immigration} & \text{Birth or immigration} & \text{Birth or immigration} & \text{Birth or immigration} & \text{Birth or immigration} & \text{Birth or immigration} & \text{Birth or immigration} \\
\text{Death or emigration} & \text{Death or emigration} & \text{Death or emigration} & \text{Death or emigration} & \text{Death or emigration} & \text{Death or emigration} & \text{Death or emigration} \\
\text{Local extinction} & & & & & & \\
\end{array}
\]

b) Natal dispersal, local dynamics

\[
\begin{array}{cccccccc}
0 & 1 & 2 & \cdots & k & \cdots & K \\
\text{Immigration} & \text{Immigration or birth without emigration} & \text{Immigration or birth without emigration} & \text{Immigration or birth without emigration} & \text{Immigration or birth without emigration} & \text{Immigration or birth without emigration} & \text{Immigration or birth without emigration} \\
\text{Death} & \text{Death} & \text{Death} & \text{Death} & \text{Death} & \text{Death} & \text{Death} \\
\text{Local extinction} & & & & & & \\
\end{array}
\]
Metapopulation model

- Infinite number of patches
- Patches connected via global dispersal

Forward Kolmogorov equations for natal dispersal

\[
\begin{align*}
\frac{d}{dt} p_0 &= -\alpha m_0 D p_0 + d_1 p_1 + \mu (1 - p_0), \\
\frac{d}{dt} p_n &= [\alpha m_{n-1} D + (n - 1) b_{n-1} (1 - e_{n-1})] p_{n-1} \\
&\quad - [n (b_n (1 - e_n) + d_n) + \alpha m_n D + \mu] p_n \\
&\quad + (n + 1) d_{n+1} p_{n+1}, \\
\frac{d}{dt} p_K &= [\alpha m_{K-1} D + (K - 1) b_{K-1} (1 - e_{K-1})] p_{K-1} \\
&\quad - [K d_K + \mu] p_K \\
\frac{d}{dt} D &= -\alpha D \sum_{n=0}^{K-1} p_n m_n \\
&\quad + \sum_{n=1}^{K} n b_n e_n p_n + K b_K (1 - e_K) (1 - \eta) \sigma p_K - \nu D.
\end{align*}
\]
Assumptions

Assume

- Separation of time scales:
  - fast ecological dynamics
  - slow evolutionary dynamics
- The resident is in its population dynamical attractor
- A mutant appears
  - rare
  - slightly different phenotype

What happens? Can the mutant invade?
Evolution of dispersal
Evolution of dispersal
Evolution of dispersal
Evolution

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Evolution of dispersal
Evolution of dispersal
Fitness

Invasion fitness $r$

- Exponential growth when rare.
- If $r > 0$ then invasion is possible.
- [Metz et al., 1992, 1996; Geritz et al., 1997, 1998]

$R_{\text{metapop}}$ - metapopulation reproduction ratio

- Operates on dispersal generations
- $\ln R_{\text{metapop}}$ and $r$ sign equivalent
Singular strategies

- Fitness gradient equals to 0.
- Attracting vs. repelling
- Unbeatable vs. beatable
Examples of density dependent dispersal strategies

a) threshold for large patch-sizes

![Graph showing a threshold for large patch-sizes]

b) threshold

![Graph showing a threshold]

c) monotone

![Graph showing a monotone pattern]

d) non-monotone

![Graph showing a non-monotone pattern]
Density-dependence vs. density-independence

\[ K = 10, \ k = 7 \]

Natal dispersal vs. Adult dispersal

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Evolution of dispersal
A Trait Substitution Sequence

\[ K = 10, \; k = 7, \; \nu = 0.08, \; \mu = 0.06 \]

\[ t = 0 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 1 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 2 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 3 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 4 \]

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Evolution of dispersal
A Trait Substitution Sequence

\[ K = 10, \, k = 7, \, \nu = 0.08, \, \mu = 0.06 \]

\[ t = 5 \]
A Trait Substitution Sequence

$$K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06$$

$$t = 6$$

pop.size

emigration
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 7 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 8 \]

pop.size

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Evolution of dispersal
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 9 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 10 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 20 \]

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Evolution of dispersal
A Trait Substitution Sequence

\[ K = 10, \, k = 7, \, \nu = 0.08, \, \mu = 0.06 \]

\[ t = 30 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 40 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 50 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 100 \]
$$K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06$$

$$t = 150$$
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 160 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 170 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 180 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 190 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 200 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 210 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 220 \]
A Trait Substitution Sequence

\[ K = 10, \, k = 7, \, \nu = 0.08, \, \mu = 0.06 \]

\[ t = 230 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 240 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 245 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 250 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 255 \]
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 258 \]

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Evolution of dispersal
A Trait Substitution Sequence

\[ K = 10, \ k = 7, \ \nu = 0.08, \ \mu = 0.06 \]

\[ t = 260 \]
Attracting vertices of the strategy space

a) $K = 10$
emigration only

b) $K = 8$
emigration only

c) $K = 8$ emigration and immigration

Expected threshold

$\tilde{n} = k \left(1 - \frac{\mu}{b}\right) < k$
Phase plane plot

a) $\mu = 0.048$

\begin{align*}
e_1 &= e_2 = e_3 = e_4 = 0 \\
e_7 &= e_8 = e_9 = e_{10} = 1
\end{align*}
Emigration and immigration are not always complements 
\( m_i \neq 1 - e_i \)

- Immigrant does not know his neighbors
- Newborn knows his mother is there

\[ K = 10, k = 7, \mu = 0.1 \]

\[ K = 10, k = 7, \mu = 0.07 \]
Adult dispersal

- Non-monotone density dependence?

a) \( t \in [0, 10], \mu = 0.25 \)

b) \( t \in [10, 80], \mu = 0.25 \)

c) \( t \in [80, 750], \mu = 0.25 \)

d) \( t \in [750, 10000], \mu = 0.25 \)
Nature is full of exciting questions.

Intuition is not always right.

Complex density dependent dispersal may evolve.

Adult dispersers may benefit more from conditional dispersal strategies.

Hypothesis: bang-bang type dispersal at Bodie.
Thank you!