Evolution of predator and prey movement in heterogenous environments

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Introduction

- Predator-prey systems:

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  - if I go, where should I go? patch selection

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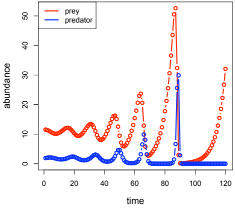
Nicholson-Bailey dynamics:



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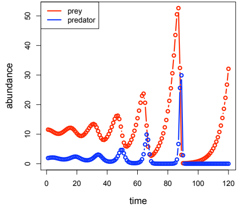
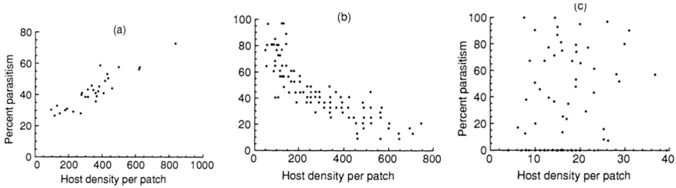


Spatial variation in predator attacks stabilizing: Hassell & May (1974,1988), May (1978), Hassell (1984), Chesson & Murdoch (1986), Hassell, May, Pacala & Chesson (1991)



The model

- N_t prey abundance in generation t

N_t

The model

- N_t prey abundance in generation t
- x_i fraction in patch i

$$x_i N_t$$

The model

- N_t prey abundance in generation t
- x_i fraction in patch i
- λ_i intrinsic fitness in patch i

$$x_i N_t \lambda_i$$

The model

- N_t, P_t prey, predator abundance in generation t
- x_i, y_i fraction in patch i
- λ_i intrinsic fitness in patch i
- a_i attack rate in patch i

$$x_i N_t \lambda_i \exp(-a_i y_i P_t)$$

The model

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$$N_{t+1} = \sum_i x_i N_t \lambda_i \exp(-a_i y_i P_t)$$

$$x_i N_t \left(1 - \exp(-a_i y_i P_t)\right)$$

The model

- N_t, P_t prey, predator abundance in generation t
- x_i, y_i fraction in patch i
- λ_i intrinsic fitness in patch i
- a_i, θ_i attack rate, conversion efficiency in patch i

$$N_{t+1} = \sum_i x_i N_t \lambda_i \exp(-a_i y_i P_t)$$

$$\theta_i x_i N_t \left(1 - \exp(-a_i y_i P_t)\right)$$

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How do x and y evolve?

ESA

“unbeatable” strategy (Hamilton 1967) “In the foregoing analysis a gamelike element...was present and made necessary the use of the word unbeatable to describe the [strategy] finally established. This word was applied in just the same sense in which it could be applied to the ‘minimax’ strategy of a zero-sum two-person game. Such a strategy should not, without qualification be called optimum because it is not optimum against - although unbeaten by - any strategy differing from itself.”

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Evolutionarily stable strategy (ESS) (Maynard Smith and Price 1973, Maynard Smith 1982) - a strategy if adopted by most members of the population resists all invasions by small populations playing a different strategy.

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Evolutionarily stable strategy (ESS) (Maynard Smith and Price 1973, Maynard Smith 1982) - a strategy if adopted by most members of the population resists all invasions by small populations playing a different strategy.

Evolutionarily stable attractor (ESA) (Rand et al. 1994) - an ecological attractor for a strategy that resists invasion attempts from “mutant” populations playing a different strategy.

"Mutant" prey

$$N_{t+1} = \sum_i x_i N_t \lambda_i \exp(-a_i y_i P_t)$$

$$P_{t+1} = \sum_i \left(x_i N_t \qquad\qquad \right) \theta_i \left(1 - \exp(-a_i y_i P_t)\right)$$

"Mutant" prey

- M_t mutant prey abundance in generation t

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$$M_t$$

$$P_{t+1} = \sum_i (x_i N_t \qquad) \, \theta_i \, (1 - \exp(-a_i y_i P_t))$$

"Mutant" prey

- M_t mutant prey abundance in generation t
- $\widetilde{x}_i$ fraction in patch i

$$N_{t+1} = \sum_i x_i N_t \lambda_i \exp(-a_i y_i P_t)$$

$$\widetilde{x}_i M_t$$

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P_{t+1} &= \sum_i \left(x_i N_t \qquad\qquad \right) \theta_i \left(1 - \exp(-a_i y_i P_t)\right)
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P_{t+1} &= \sum_i \left(x_i N_t + \widetilde{x}_i M_t\right) \theta_i \left(1 - \exp(-a_i y_i P_t)\right)
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- M_t mutant prey abundance in generation t
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$$\begin{aligned} N_{t+1} &= \sum_i x_i N_t \lambda_i \exp(-a_i y_i P_t) \\ M_{t+1} &= \sum_i \widetilde{x}_i M_t \lambda_i \exp(-a_i y_i P_t) \\ P_{t+1} &= \sum_i (x_i N_t + \widetilde{x}_i M_t)\, \theta_i \,(1 - \exp(-a_i y_i P_t)) \end{aligned}$$

Mutant fitness

$$\mathcal{F}_N(x, y; \widetilde{x}) = \sum_i \widetilde{x}_i \lambda_i \exp(-a_i y_i P)$$

"Mutant" predators

$$N_{t+1} = N_t \sum_i x_i \lambda_i \exp(-a_i y_i P_t \qquad\qquad)$$

$$P_{t+1} = \sum_i x_i N_t \theta_i \left(1 - \exp(-a_i y_i P_t \qquad\qquad)\right)$$

"Mutant" predators

- Q_t mutant prey abundance in generation t

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"Mutant" predators

- Q_t mutant prey abundance in generation t
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$$N_{t+1} = N_t \sum_i x_i \lambda_i \exp(-a_i y_i P_t \qquad)$$

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"Mutant" predators

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$$N_{t+1} = N_t \sum_i x_i \lambda_i \exp(-a_i y_i P_t - a_i \tilde{y}_i Q_t)$$

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Q_{t+1} &= \sum_i x_i N_t \theta_i \left(1 - \exp(-a_i y_i P_t)\right) \frac{\tilde{y}_i Q_t}{y_i P_t + \tilde{y}_i Q_t}
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Mutant fitness

$$\mathcal{F}_P(x, y; \widetilde{y}) = \sum_i x_i N \theta_i \exp(-a_i y_i \widetilde{P}) \frac{\widetilde{y}_i}{y_i P}$$

the ESA

(N_i^*, P_i^*) – the NB equilibrium for patch i

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(N_i^*, P_i^*) – the NB equilibrium for patch i

$$x_i = \frac{N_i^*}{\sum_j N_j^*} \text{and } y_i = \frac{P_i^*}{\sum_j P_j^*}$$

$$N^* = \sum_j N_j^* \text{and } P^* = \sum_j P_j^*$$

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Then

- $\mathcal{F}_N(x, y; \widetilde{x}) \leq 1$, $\mathcal{F}_P(x, y; \widetilde{y}) \leq 1$ at equilibrium for all $\widetilde{x}, \widetilde{y}$

the ESA

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Then

- $\mathcal{F}_N(x, y; \tilde{x}) \leq 1$, $\mathcal{F}_P(x, y; \tilde{y}) \leq 1$ at equilibrium for all $\tilde{x}, \tilde{y}$
- stable with respect to spatial perturbations ($n = 2$) (Cressman 2003; Cressman et al. 2004)

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Then

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- stable with respect to spatial perturbations ($n = 2$) (Cressman 2003; Cressman et al. 2004)
- yields an ideal free distribution

the ESA

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Then

- $\mathcal{F}_N(x, y; \tilde{x}) \le 1$, $\mathcal{F}_P(x, y; \tilde{y}) \le 1$ at equilibrium for all $\tilde{x}, \tilde{y}$
- stable with respect to spatial perturbations ($n = 2$) (Cressman 2003; Cressman et al. 2004)
- yields an ideal free distribution
- yields ecological stability if $\sum_{i=1}^n \left[y_i \frac{\ln \lambda_i}{\lambda_i - 1} + x_i \ln \lambda_i \right] < 1$.

Outcomes

Environment	Behavior	Distribution	Stabilizing?
$\theta_1 > \cdots > \theta_n$ $\lambda_1 = \cdots = \lambda_n$	Predators no pref.	Density-independent	Never
$\theta_1 = \cdots = \theta_n$ $\lambda_1 > \cdots > \lambda_n$	Congruent choices	Density-dependence	Sometimes
$\theta_1 \gg \cdots \gg \theta_n$ $\lambda_1 > \cdots > \lambda_n$	Contrary choices	Inverse density-dependence	Sometimes
$0 \approx \theta_1 \ll \theta_2, \ldots, \theta_n$ $1 \approx \lambda_1 \ll \lambda_2, \ldots, \lambda_n$	Strong contrary choices	Inverse density dependence	Always

Evolutionary convergence

- two patch types

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- x,y fraction of N,P in patch type 1

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- $N_t(x)$,$P_t(x)$ density of type x at time t

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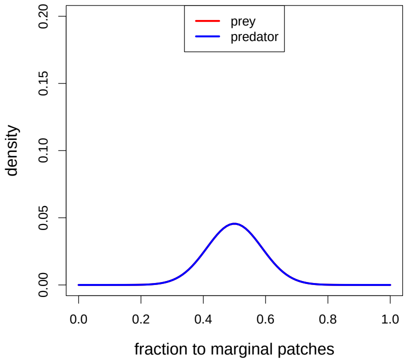
$$
\begin{aligned}
N_{t+1}(x) &= \int N_t(z) \sum_i z_i \lambda_i \exp(-a_i P_t^i) m_N(z,x)\, dz \\
P_{t+1}(y) &= \int \sum_i \theta_i N_t^i \left(1 - \exp(-a_i P_t^i)\right) \frac{z_i P_t(z)}{P_t^i} m_P(z,x)\, dz \\
N_t^i &= \int \eta_i N_t(\eta)\, d\eta \\
P_t^i &= \int \eta_i P_t(\eta)\, d\eta
\end{aligned}
$$

Evolutionary convergence



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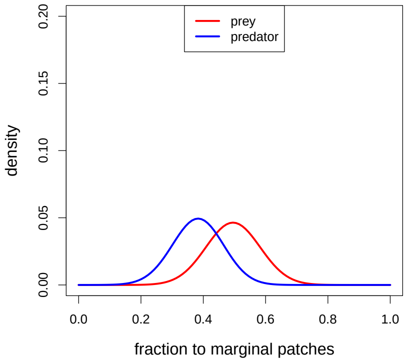

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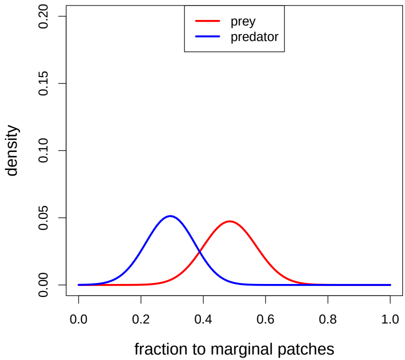
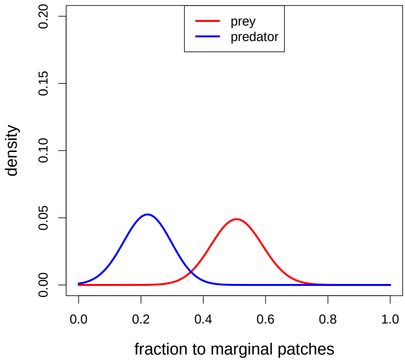
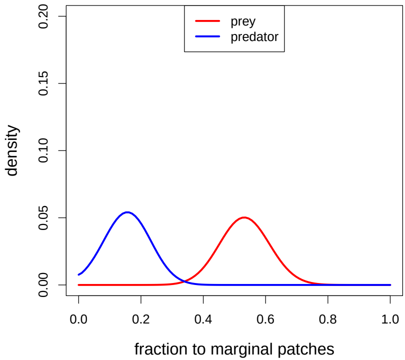


Evolutionary convergence



Evolutionary convergence



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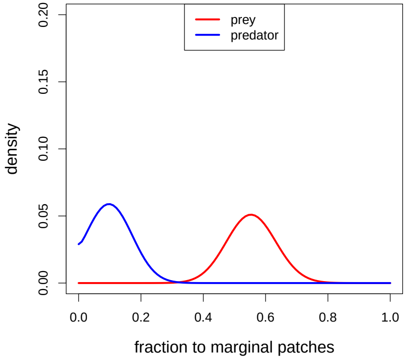

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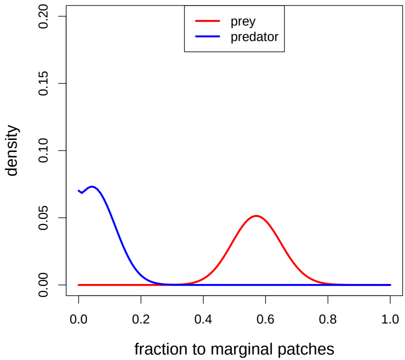

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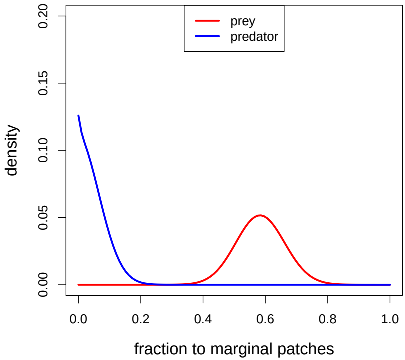

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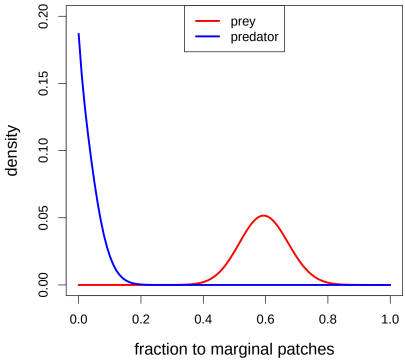

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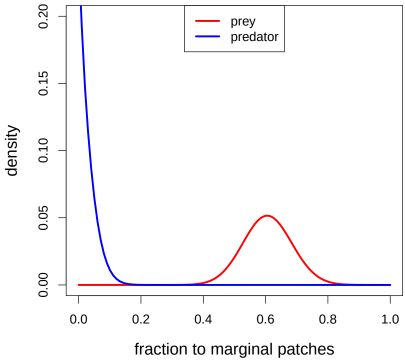

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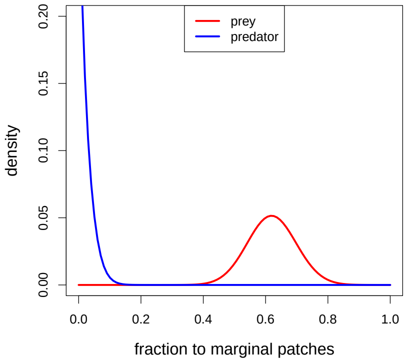

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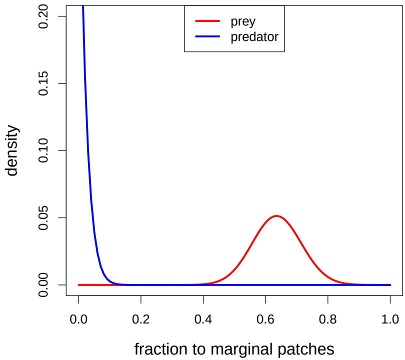

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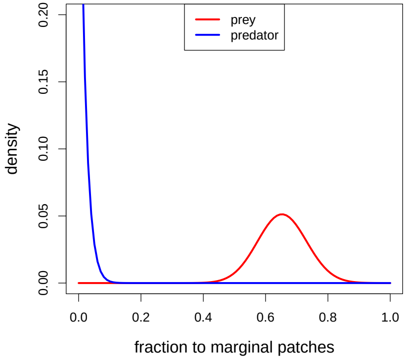

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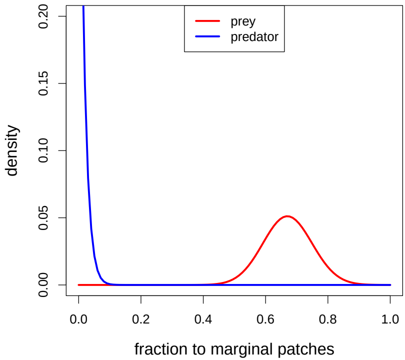

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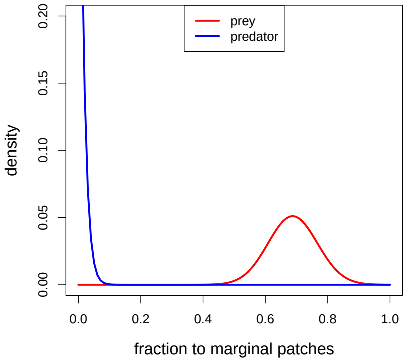

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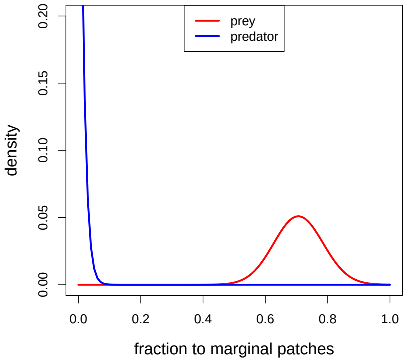

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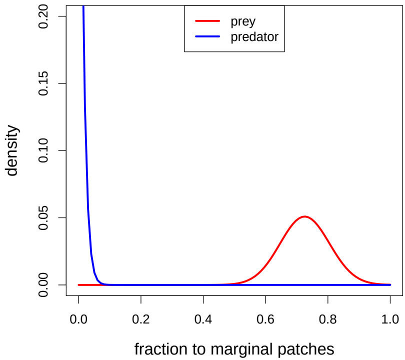

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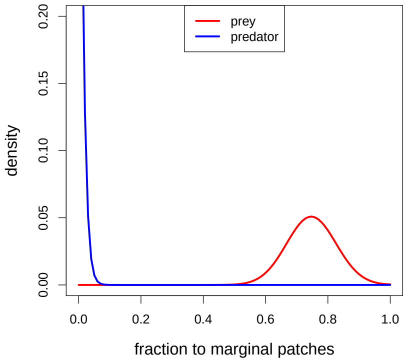

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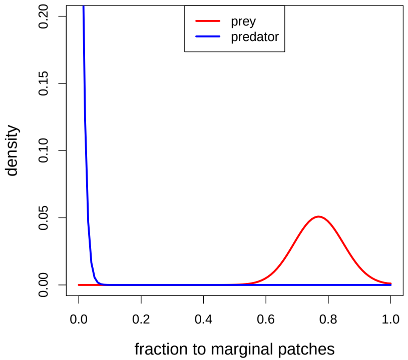

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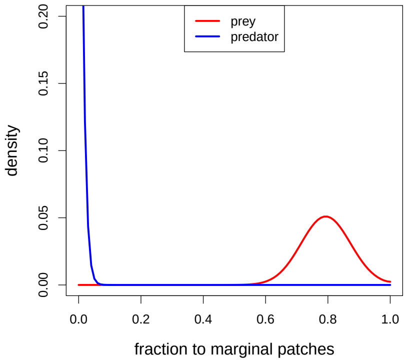

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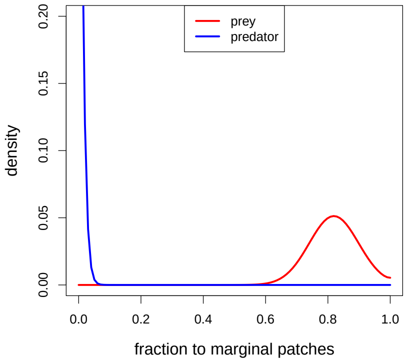

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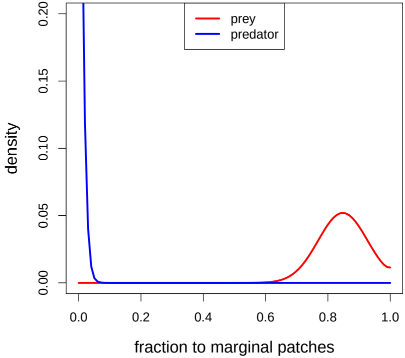

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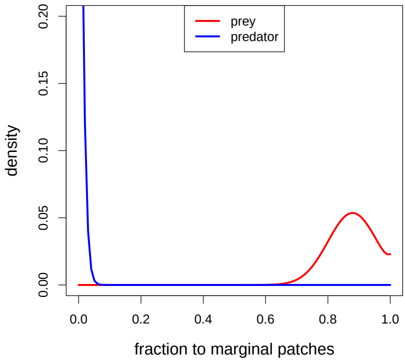

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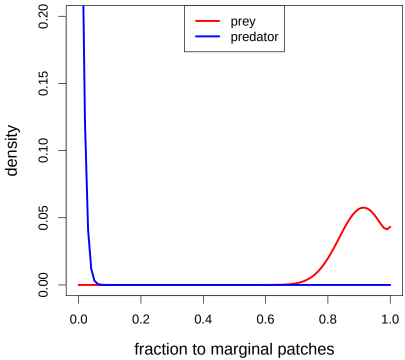

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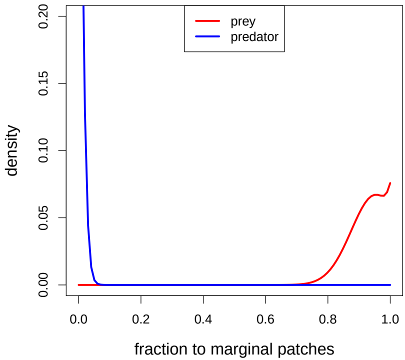

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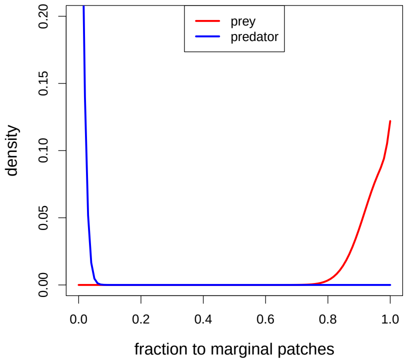

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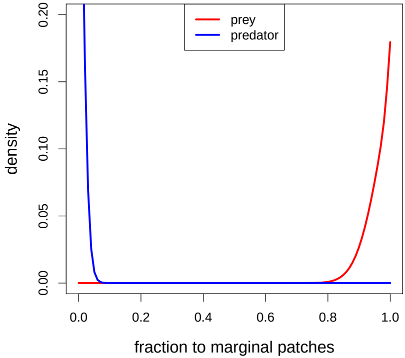

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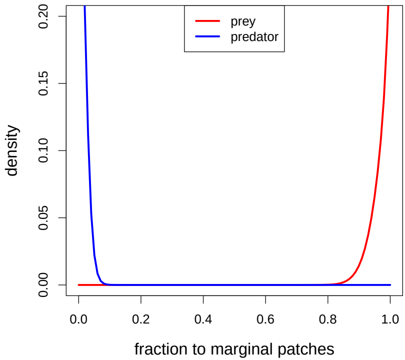

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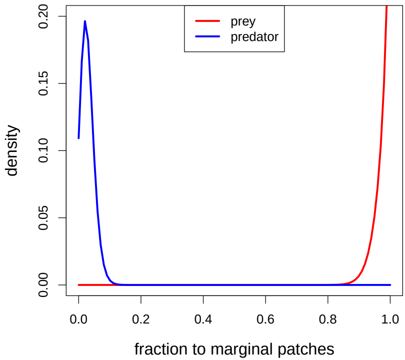

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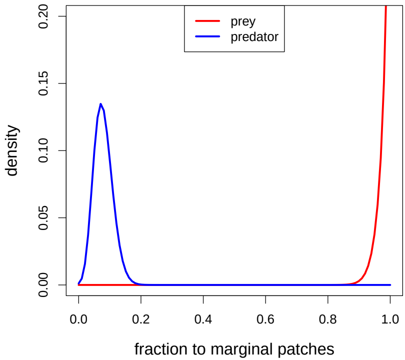

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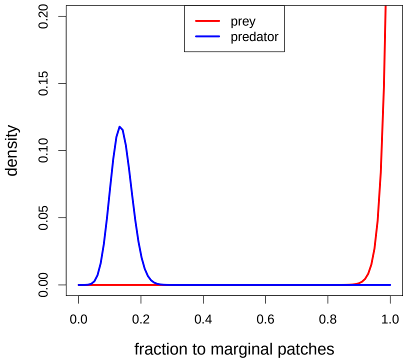

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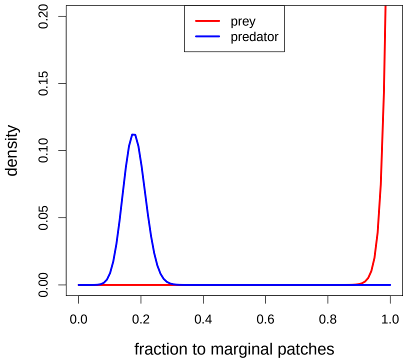

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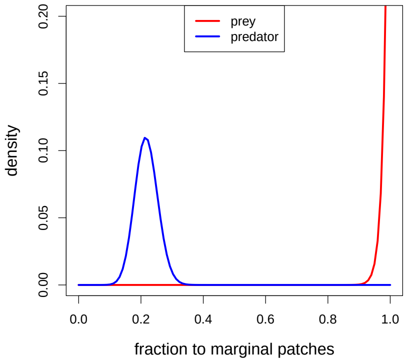

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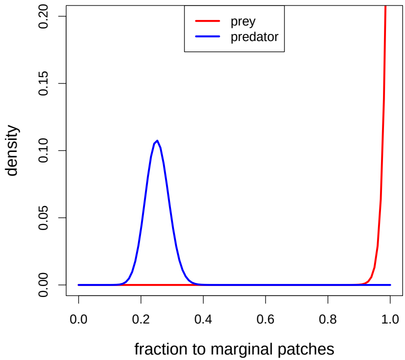

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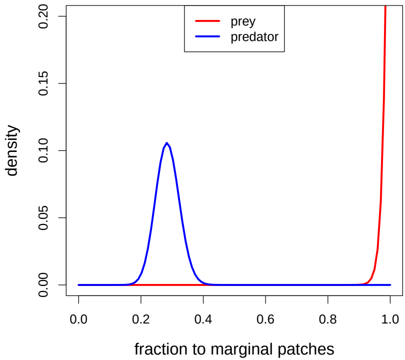

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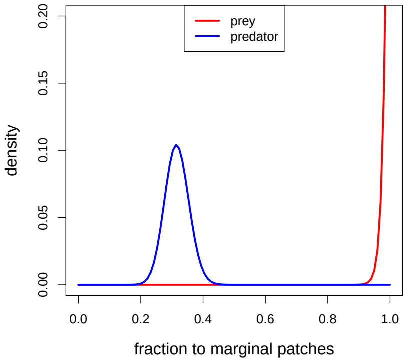

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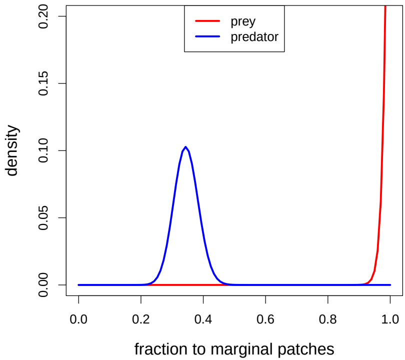

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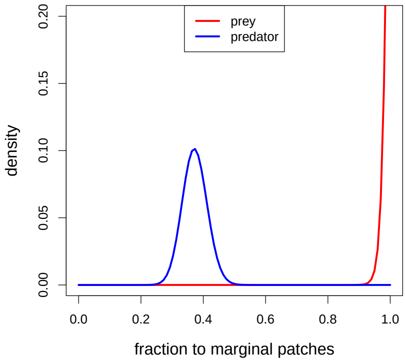

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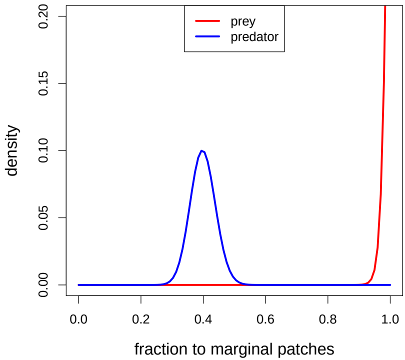

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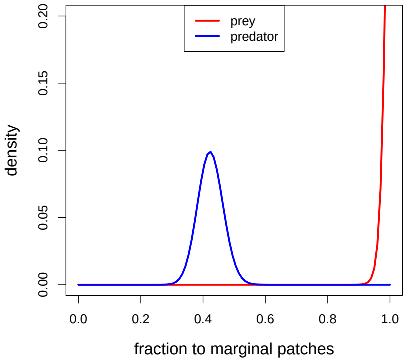

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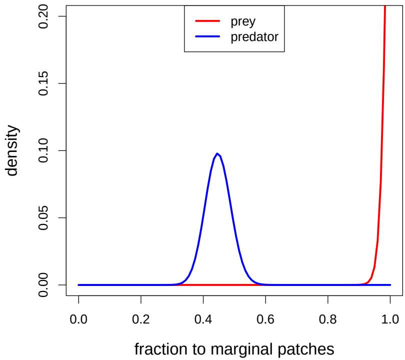

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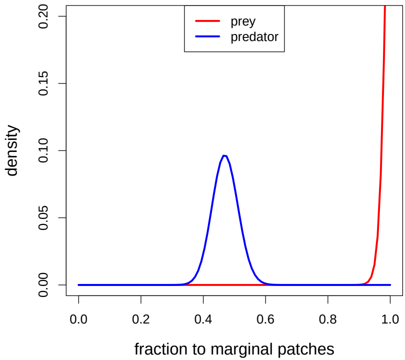

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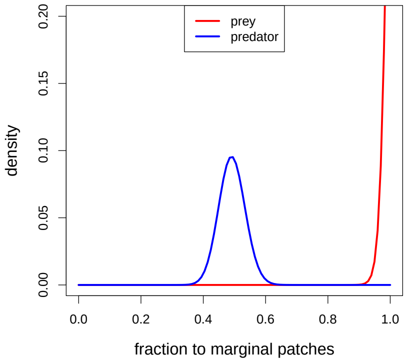

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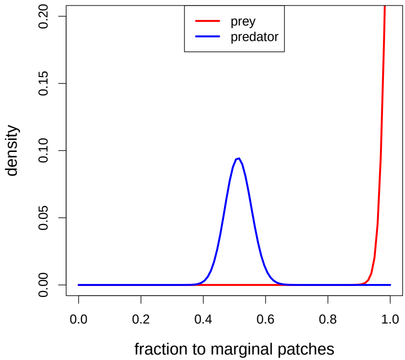

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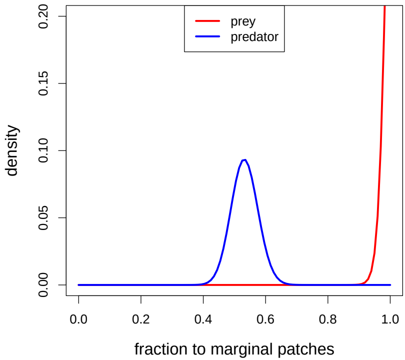

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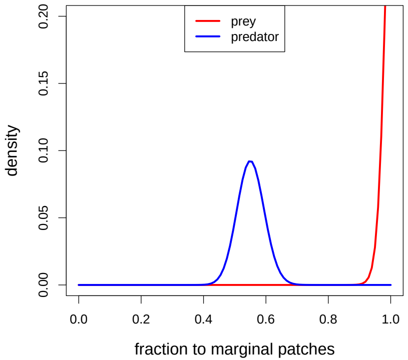

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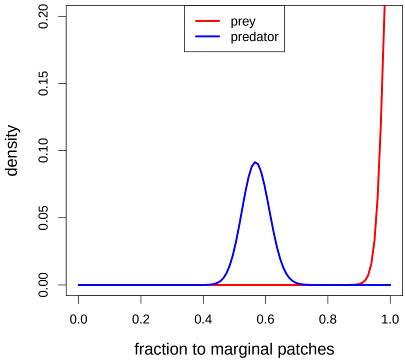

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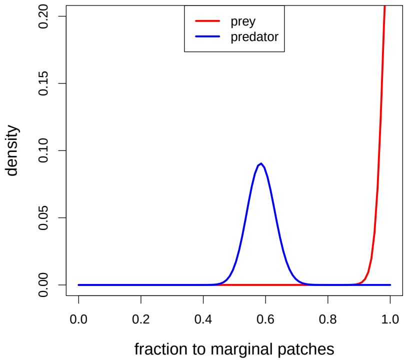

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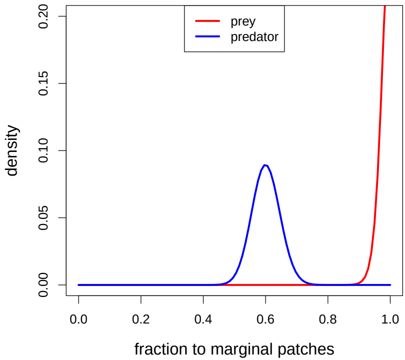

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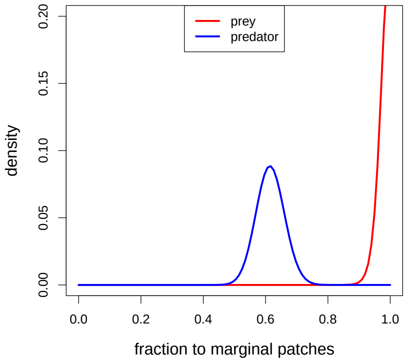

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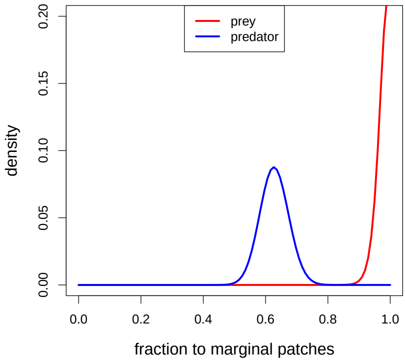

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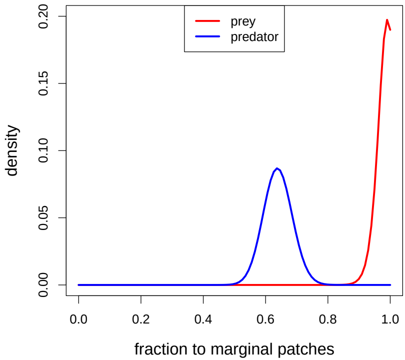

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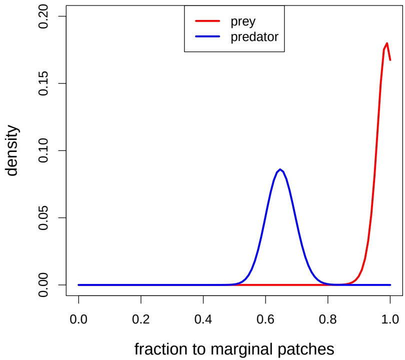

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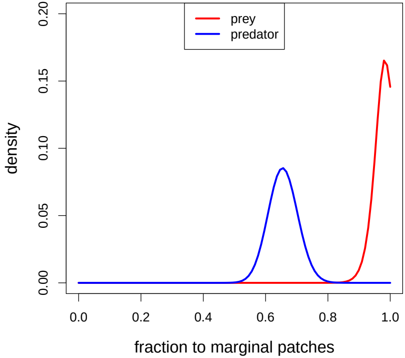

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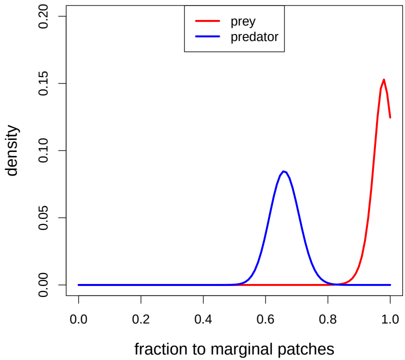

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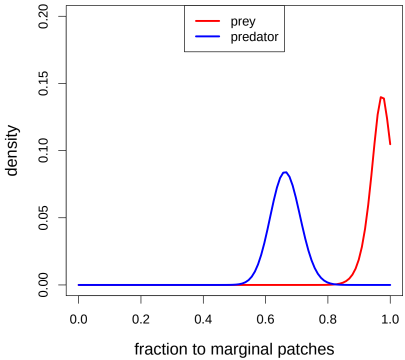

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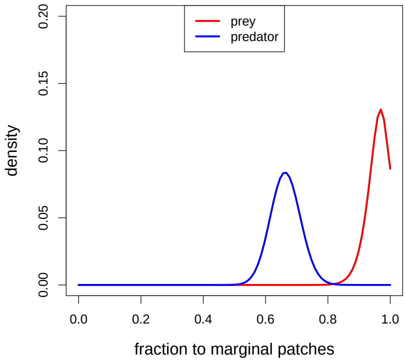

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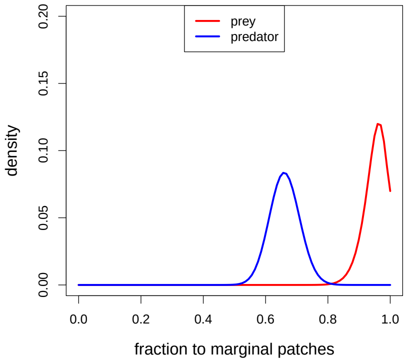

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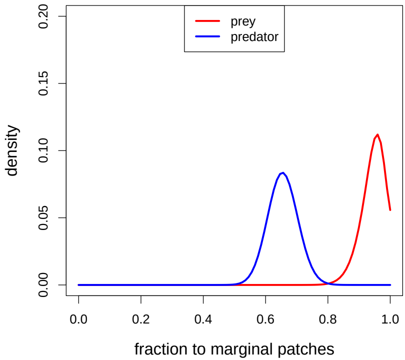

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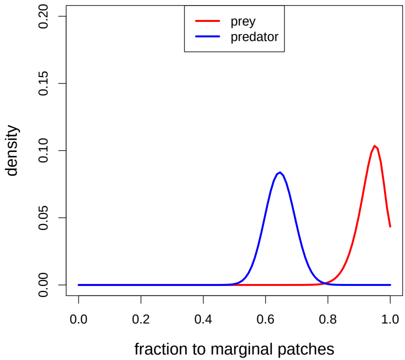

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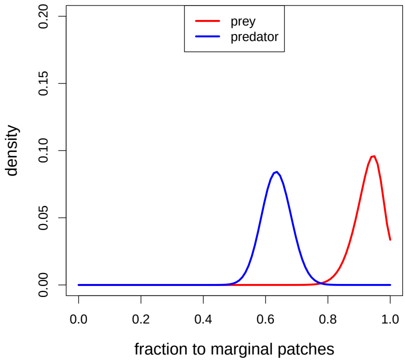

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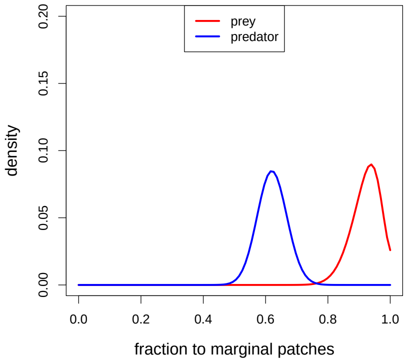

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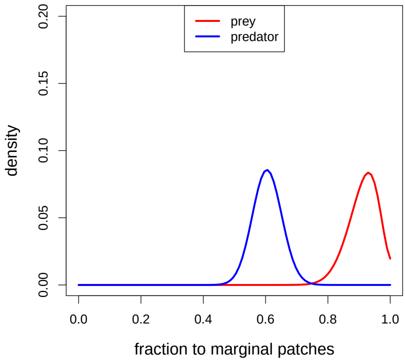

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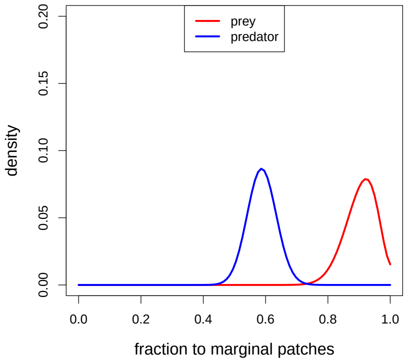

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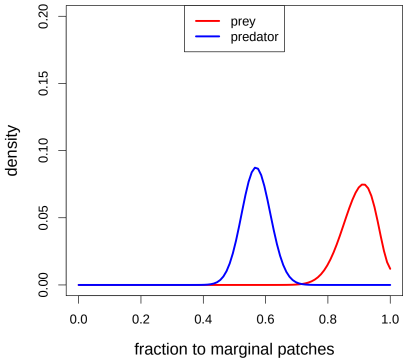

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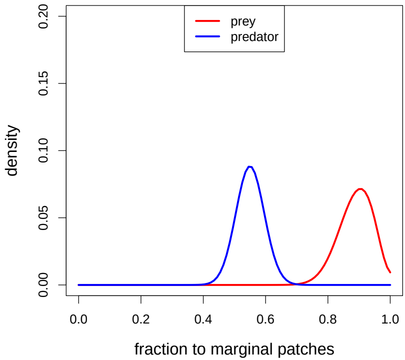

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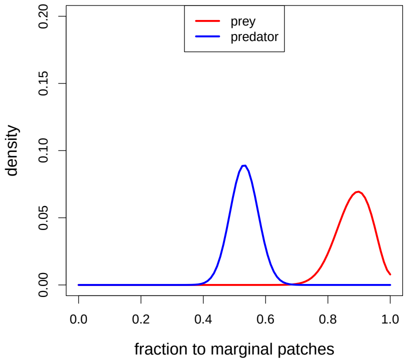

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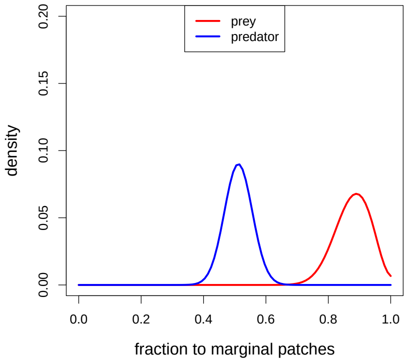

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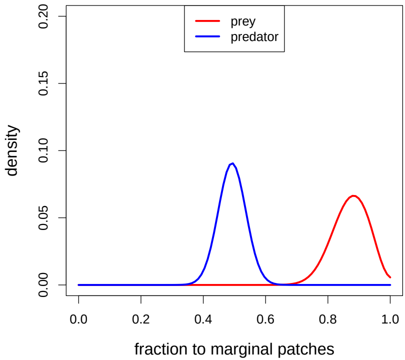

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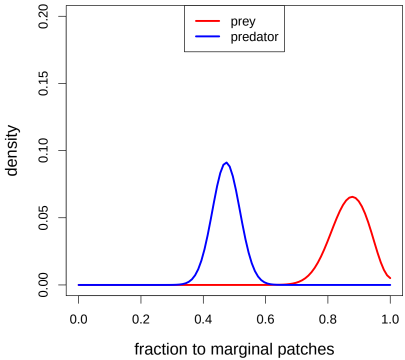

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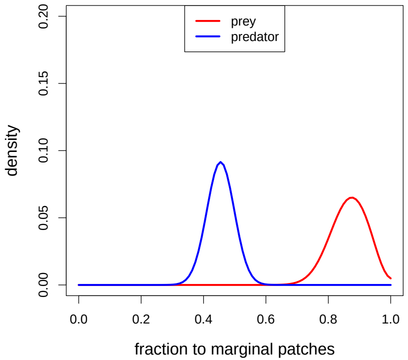

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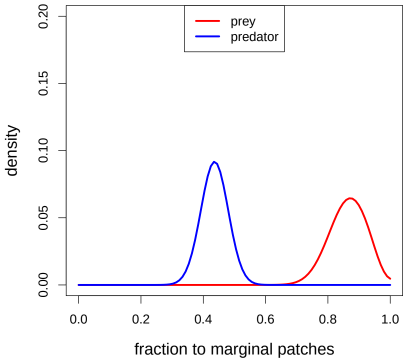

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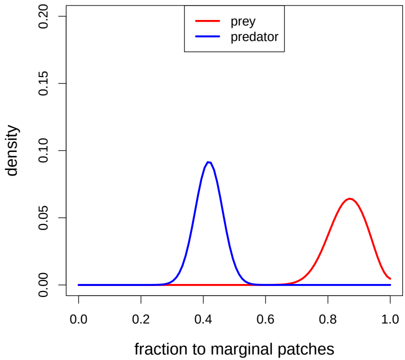

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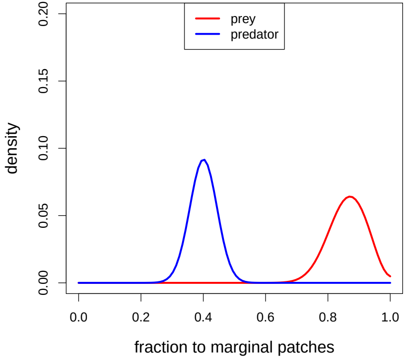

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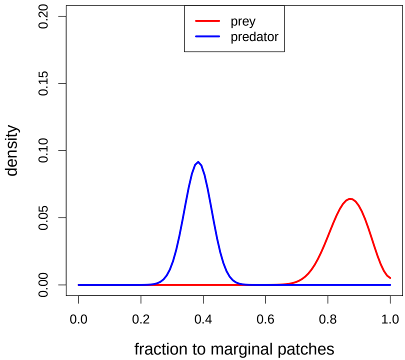

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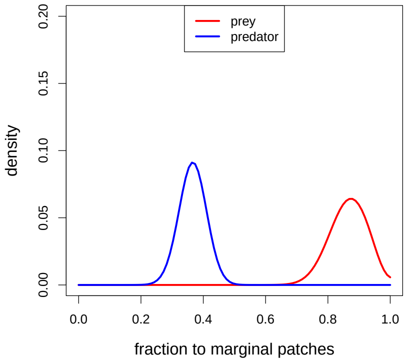

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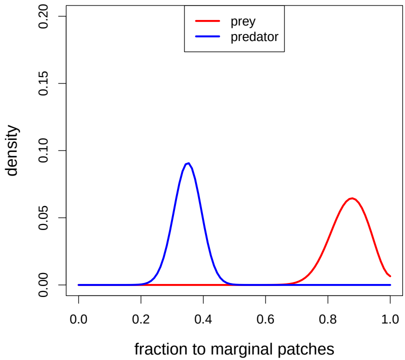
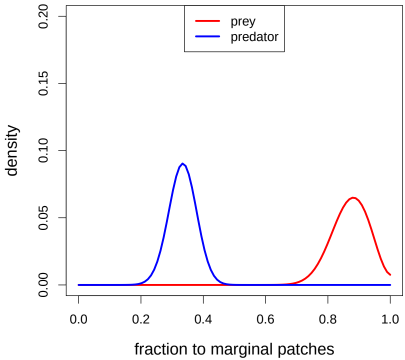


Evolutionary convergence



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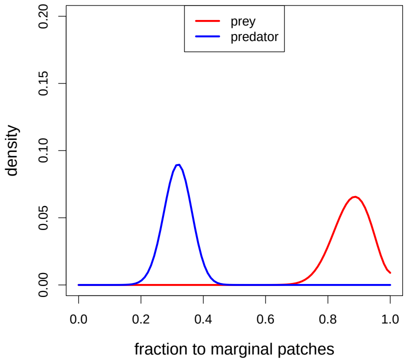

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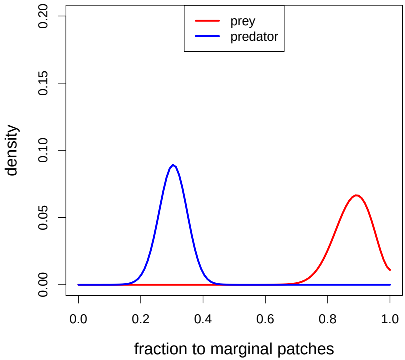

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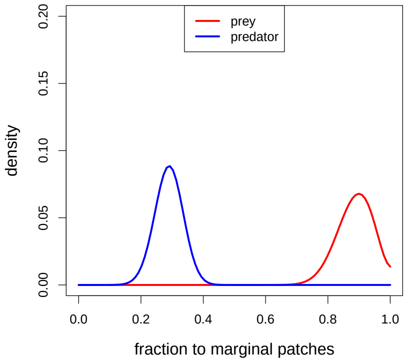

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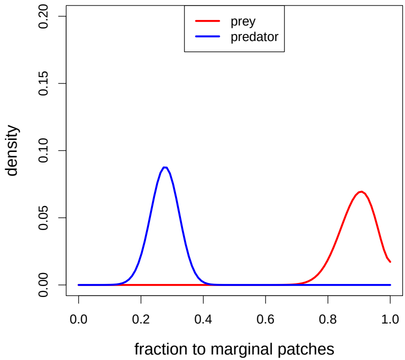

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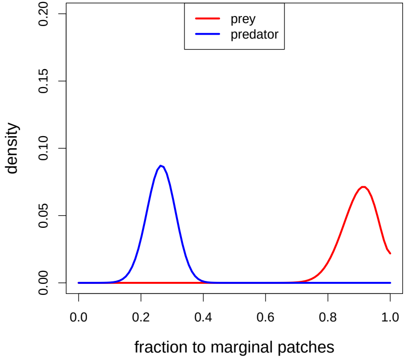

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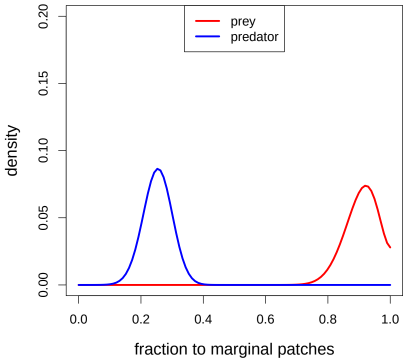

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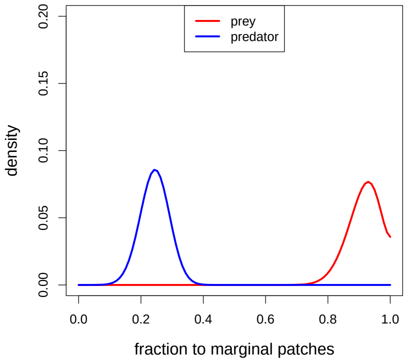

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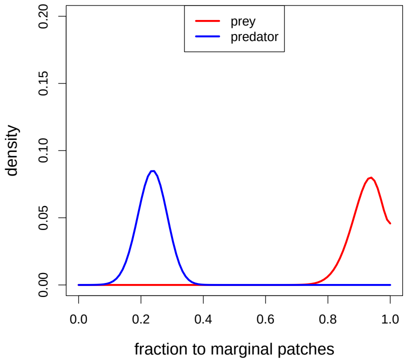

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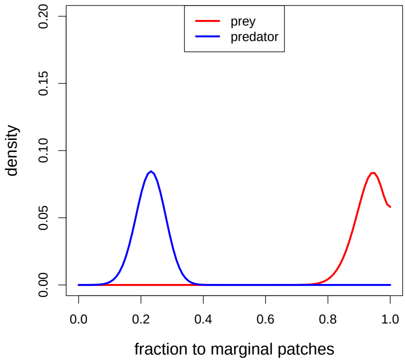

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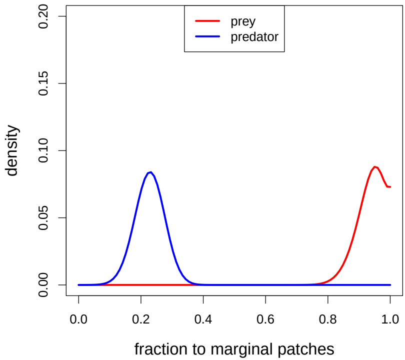

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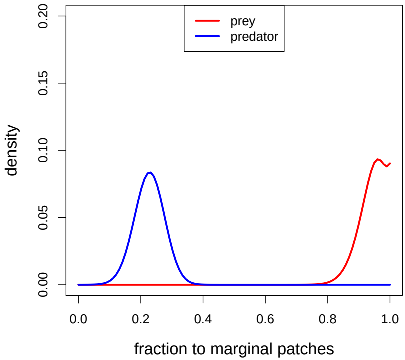

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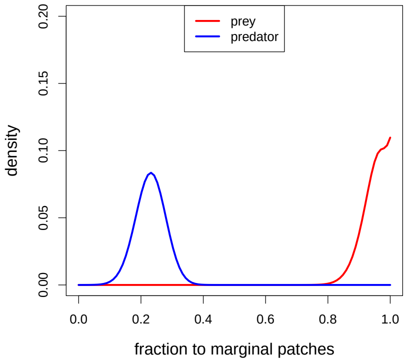

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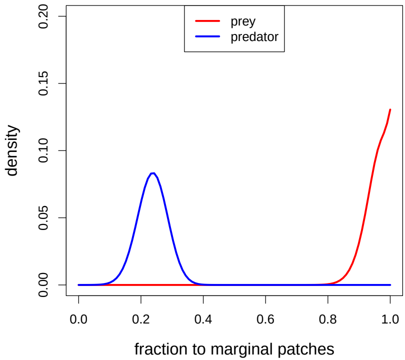

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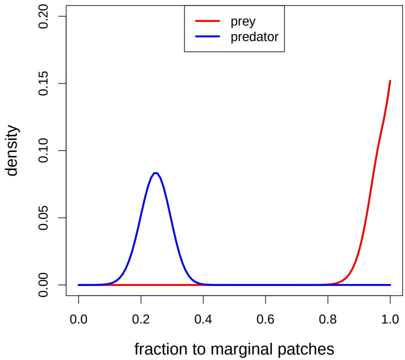

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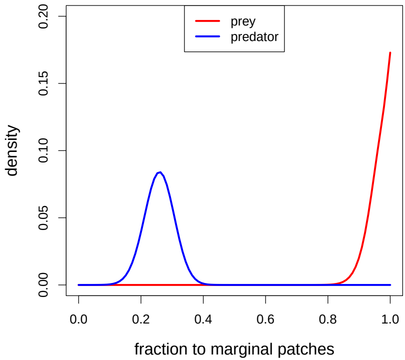

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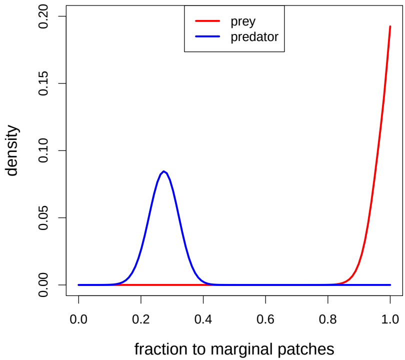

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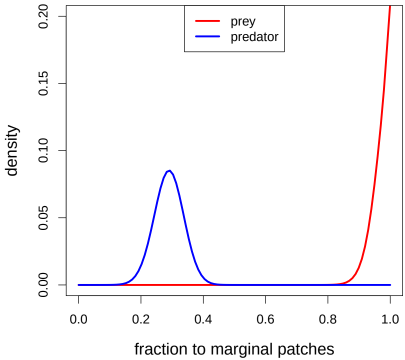

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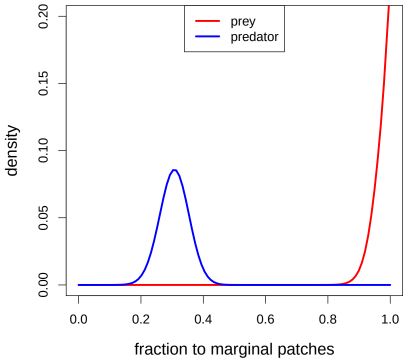

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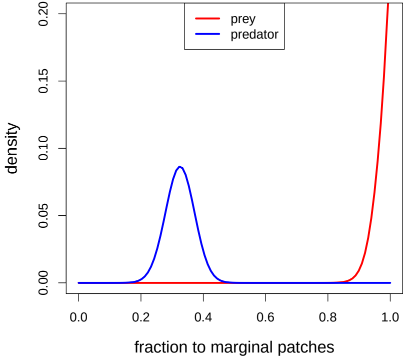

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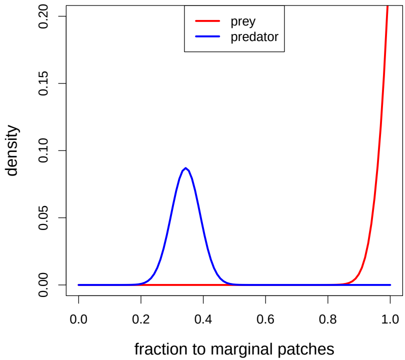

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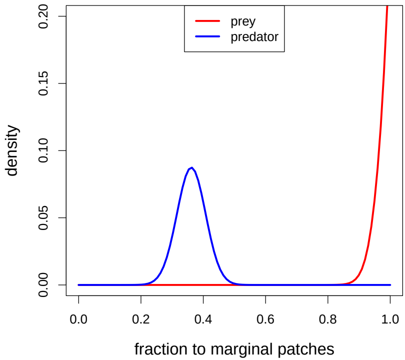

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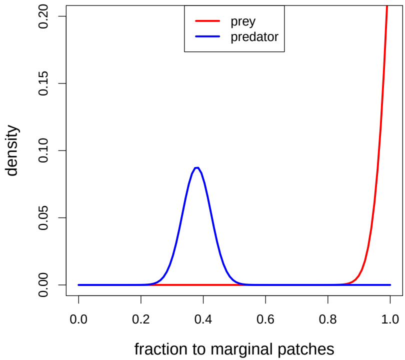

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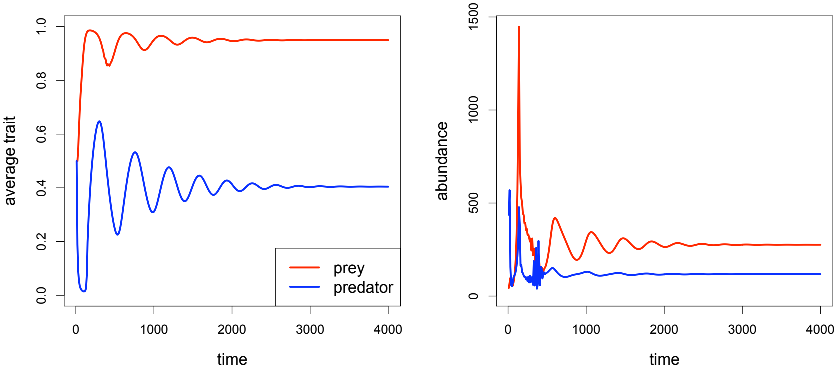
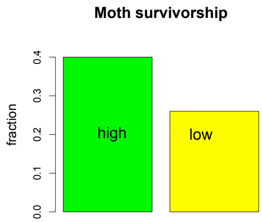


Fox & Eisenbach ’92

Line-up:
collards
diamond back moth
Diadegma insulare

Treatments:
High vs. low fertilized plants
Domesticated vs. wild

Fox & Eisenbach '92



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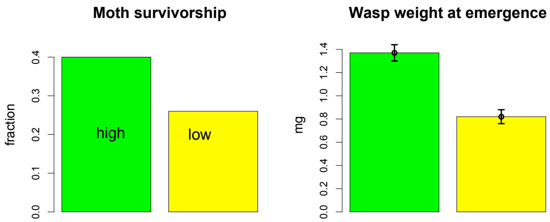

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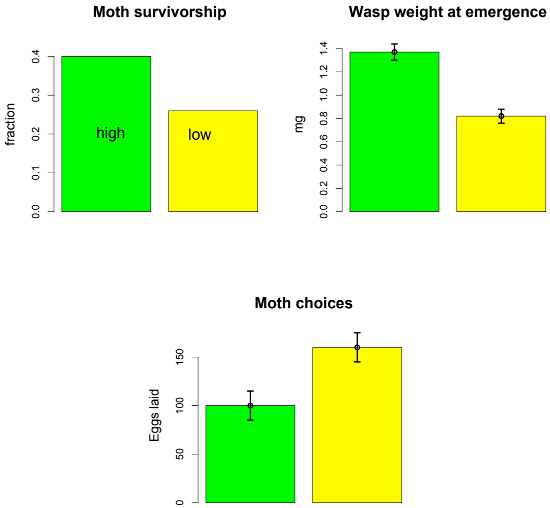

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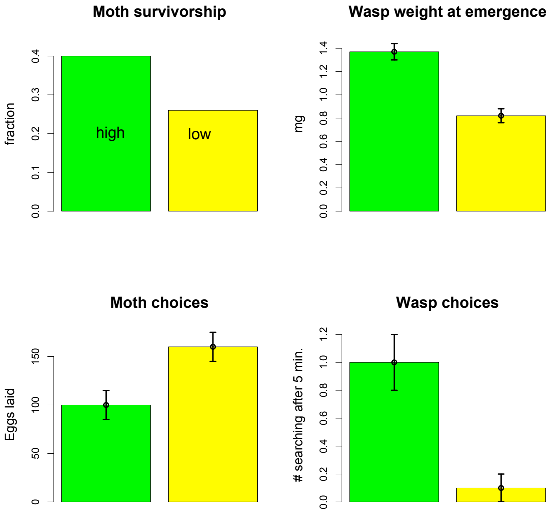

Biological ornamentations

Sex (allocation) strengthens contrary choices!
(S., Fox, & Getz '02, Fox et al. '96)

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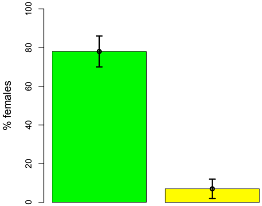

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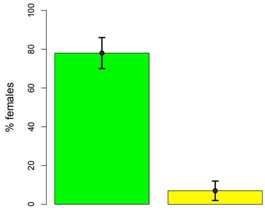

Predator satiation stabilizes predator-prey interactions!
(S. & Vejdani '06)

Outline

Introduction

- How do sink populations persist?

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Predator-prey interactions $\Rightarrow$ temporal heterogeneity
Do predator-prey interactions select for movement into sinks?

Should I stay or should I go now?
If I go there will be trouble
An if I stay it will be double
So come on and let me know – the Clash

A linear algebra interlude

- N_i abundance in patch i

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- D_{ij} fraction going from j to i

$$\frac{dN_i}{dt} = r_i N_i - x N_i + x \sum_j D_{ij} N_j$$

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Punchline: Selection against unconditional dispersal under equilibrium conditions.

General model

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$$
\begin{aligned}
\frac{\partial N_i}{\partial t}(x,t) &= b_i N_i\left(1 - \int N_i\,dx/S_i\right) - d_i N_i + x(N_j - N_i) \\
&\quad - \frac{a_i N_i \int P_i\,dy}{1 + a_i h \int N_i\,dx} \\
\frac{\partial P_i}{\partial t}(y,t) &= \frac{c a_i P_i \int N_i\,dx}{1 + ah \int N_i\,dx} - \delta_i P_i + y(P_j - P_i)
\end{aligned}
$$

General model

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- s,σ prey,predator mutation rates

$$
\begin{aligned}
\frac{\partial N_i}{\partial t}(x,t) &= (1+s\frac{\partial^2}{\partial x^2})b_iN_i(1-\int N_i\,dx/S_i) - d_iN_i + x(N_j - N_i)\\
&\quad - \frac{a_iN_i\int P_i\,dy}{1+a_ih\int N_i\,dx}\\
\frac{\partial P_i}{\partial t}(y,t) &= (1+\sigma\frac{\partial^2}{\partial y^2})\frac{ca_iP_i\int N_i\,dx}{1+ah\int N_i\,dx} - \delta_iP_i + y(P_j - P_i)
\end{aligned}
$$

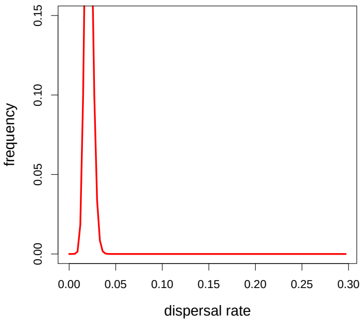
Prey evolution

- $N_i(x)$, $P_i(y)$ prey,predator density of type x,y in patch i
- b_i, d_i prey birth,death rates; S_i occupiable sites
- a_i, h_i, c_i, δ_i attack, handling, conversion, death rate
- s,σ prey,predator mutation rates

$$\begin{aligned}\frac{\partial N_i}{\partial t}(x,t) &= (1+s\frac{\partial^2}{\partial x^2})b_iN_i(1-\int N_i\,dx/K_i)-d_iN_i\\ &\quad -\frac{a_iN_i\int P_i\,dy}{1+a_ih\int N_i\,dx}+x(N_j-N_i)\\ \frac{\partial P_i}{\partial t}(y,t) &= (1+\sigma\frac{\partial^2}{\partial y^2})\frac{ca_iP_i\int N_i\,dx}{1+ah\int N_i\,dx}-\delta_iP_i+y(P_j-P_i)\end{aligned}$$

Assume: $y = P_2 = \sigma = 0$, $S_2 = \infty$, $b_2 < d_2$

To branch...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dispersal rate

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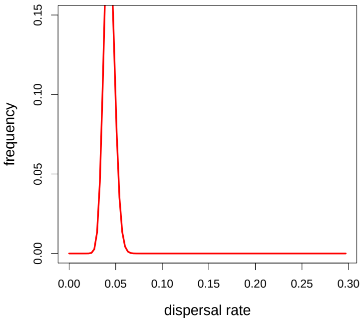
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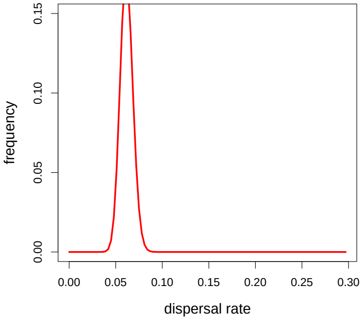
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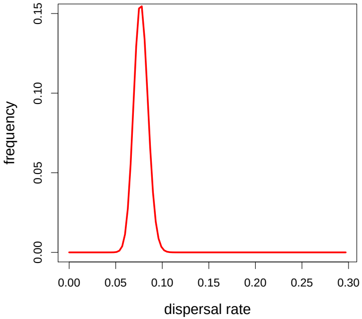
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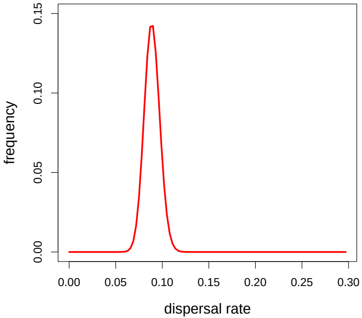
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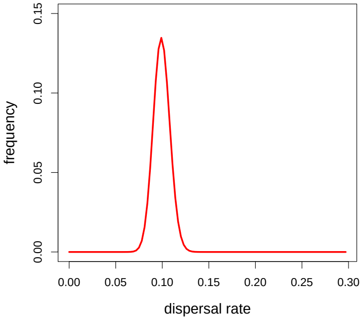
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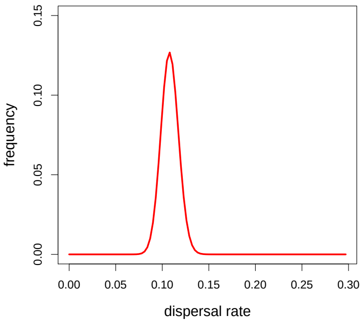
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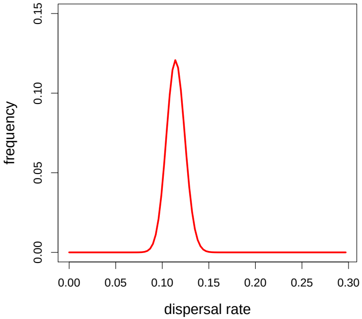
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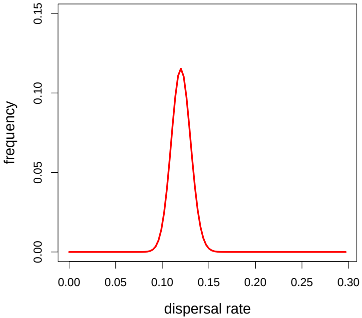
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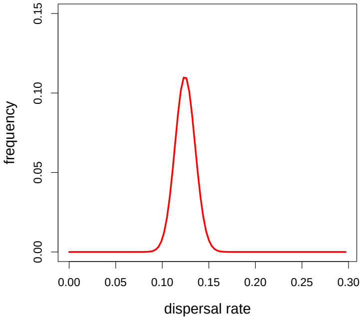
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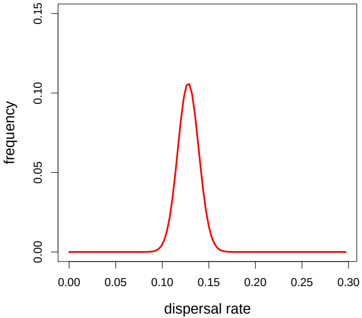
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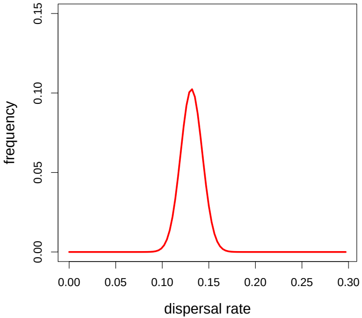
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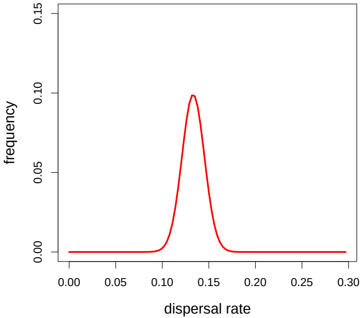
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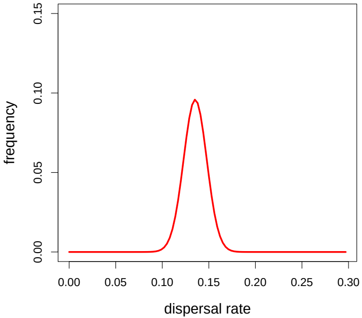
dispersal rate

To branch...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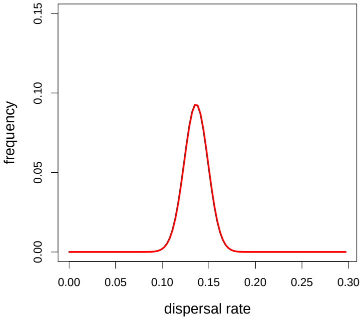
dispersal rate

To branch...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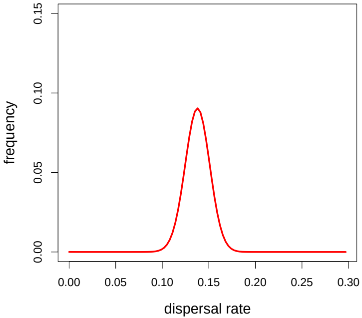
dispersal rate

To branch...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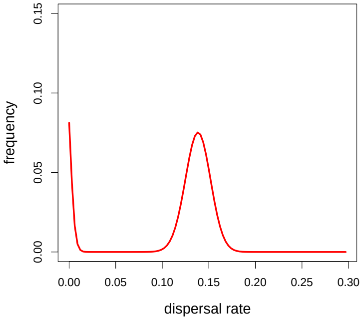
dispersal rate

To branch...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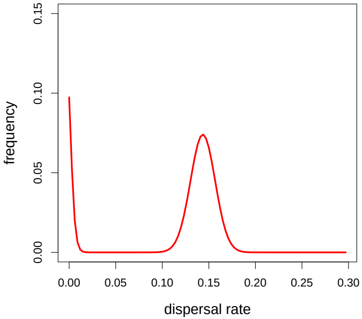
dispersal rate

To branch...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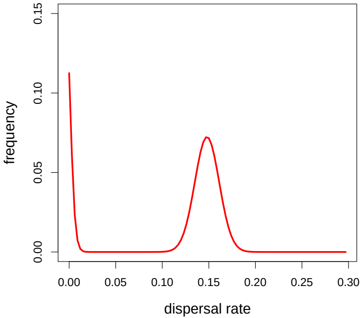
dispersal rate

To branch...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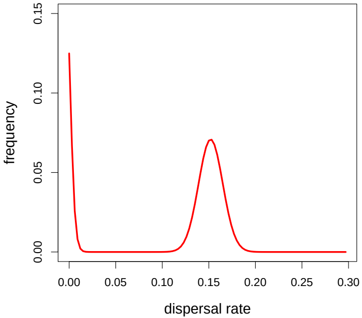
dispersal rate

To branch...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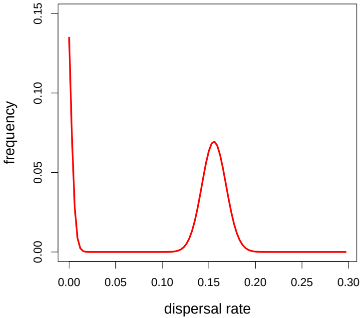
dispersal rate

To branch...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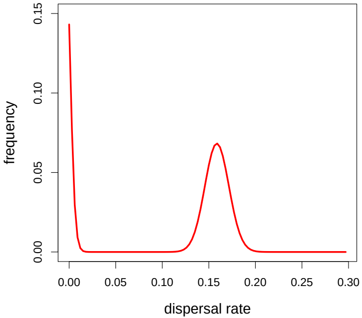
dispersal rate

To branch...



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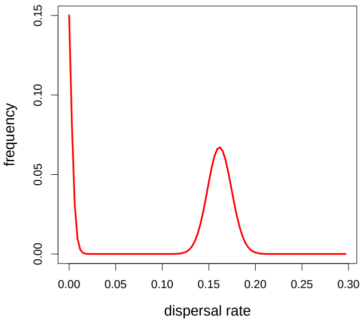
dispersal rate

To branch...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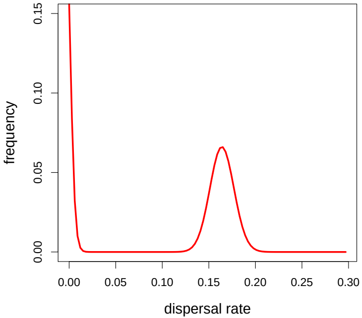
dispersal rate

To branch...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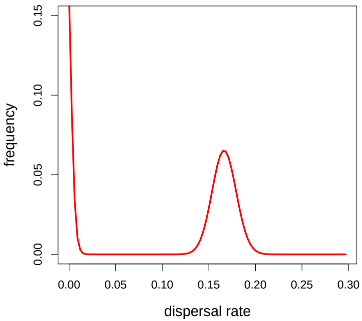
dispersal rate

To branch...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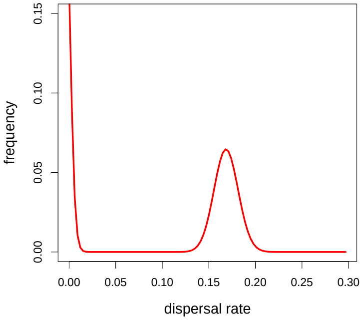
dispersal rate

To branch...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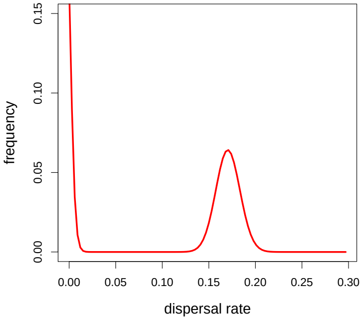
dispersal rate

To branch...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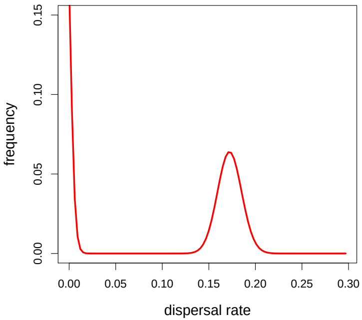
dispersal rate

To branch...


frequency
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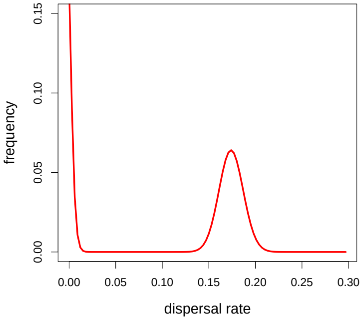
dispersal rate

To branch...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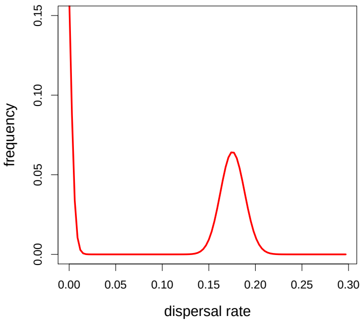
dispersal rate

To branch...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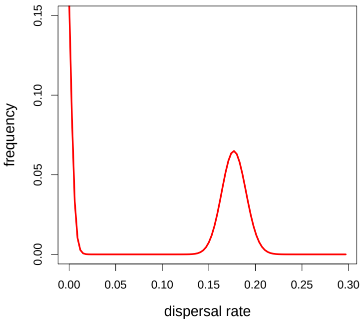
dispersal rate

To branch...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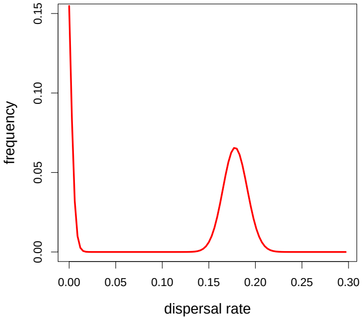
dispersal rate

To branch...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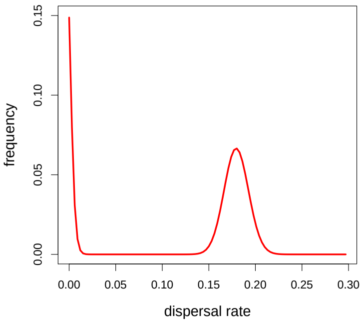
dispersal rate

To branch...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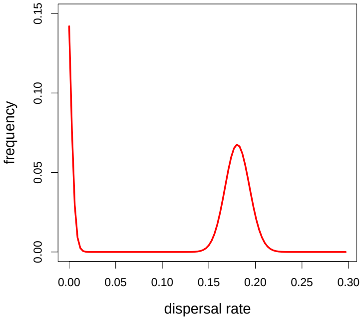
dispersal rate

To branch...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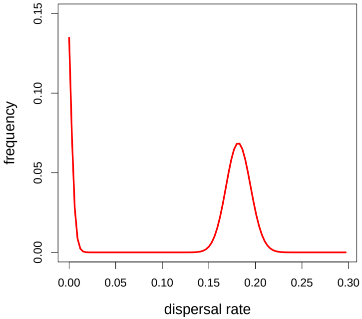
dispersal rate

To branch...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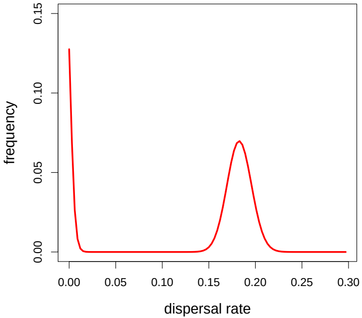
dispersal rate

To branch...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dispersal rate

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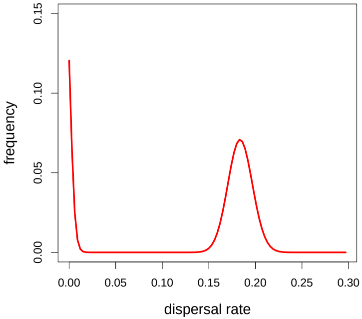
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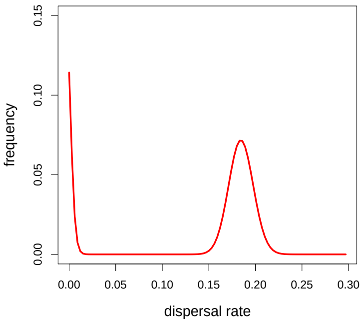
dispersal rate

To branch...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dispersal rate

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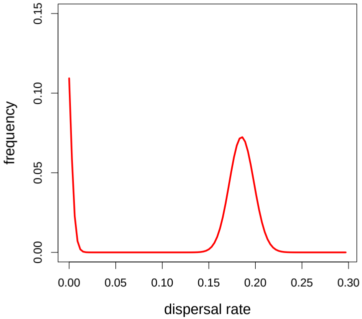
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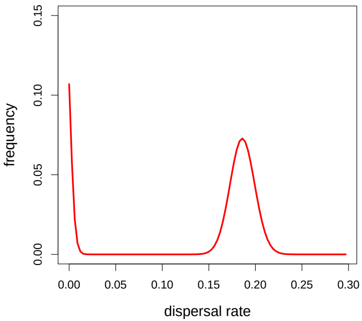
dispersal rate

To branch...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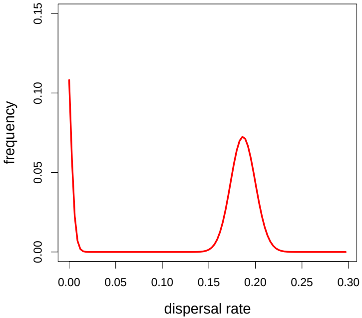
dispersal rate

To branch...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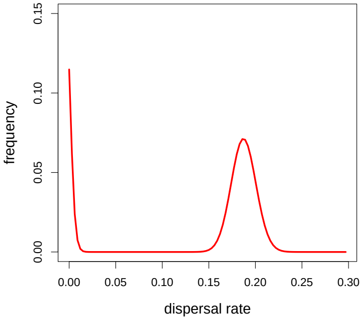
dispersal rate

To branch...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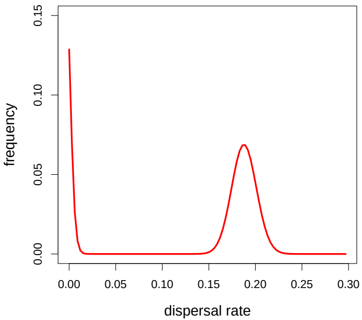
dispersal rate

To branch...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dispersal rate

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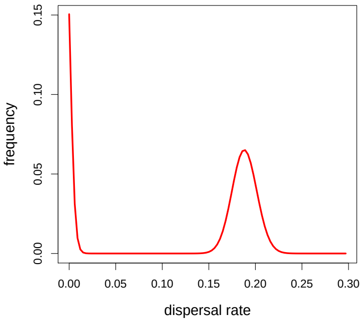
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dispersal rate

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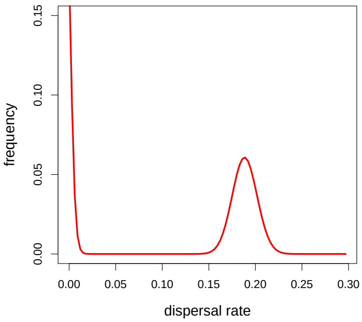
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dispersal rate

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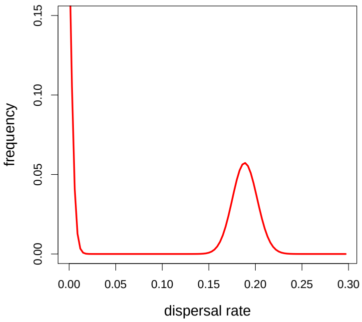
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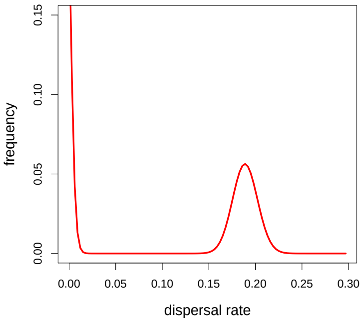
dispersal rate

To branch...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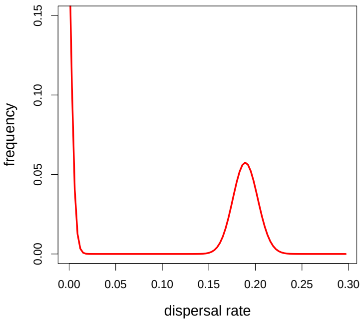
dispersal rate

To branch...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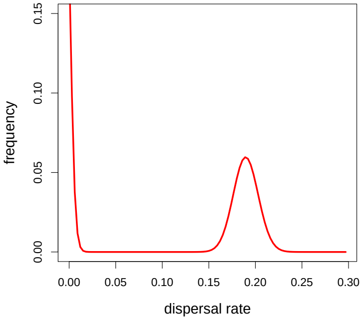
dispersal rate

To branch...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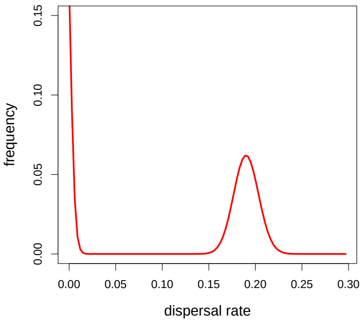
dispersal rate

To branch...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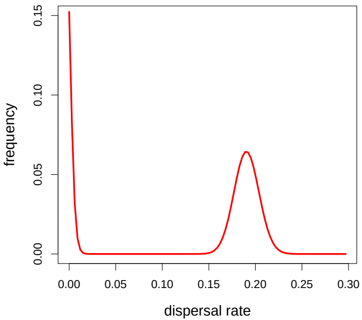
dispersal rate

To branch...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dispersal rate

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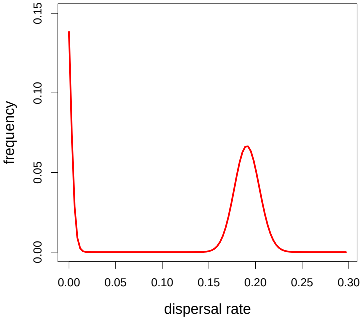
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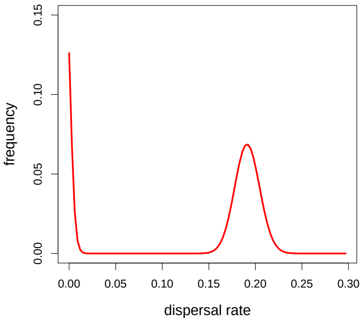
dispersal rate

To branch...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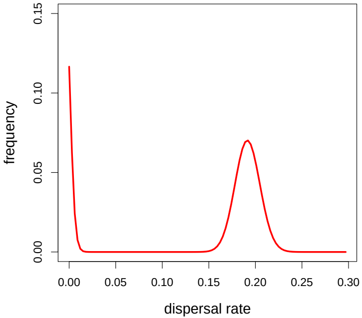
dispersal rate

To branch...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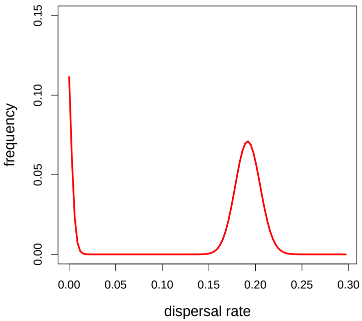
dispersal rate

To branch...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dispersal rate

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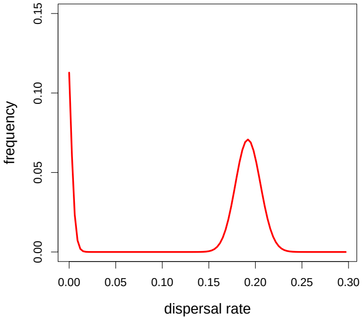

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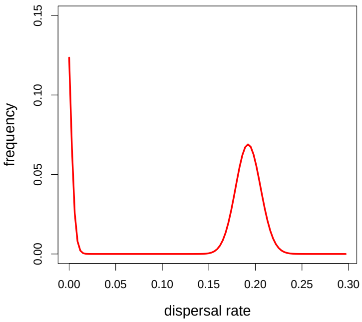
dispersal rate

To branch...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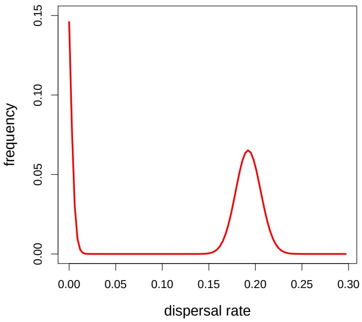
dispersal rate

To branch...



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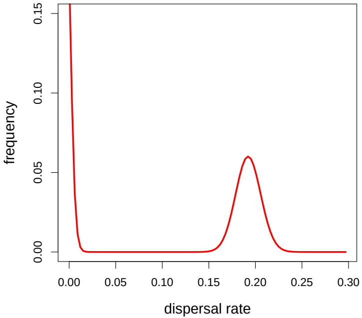
dispersal rate

To branch...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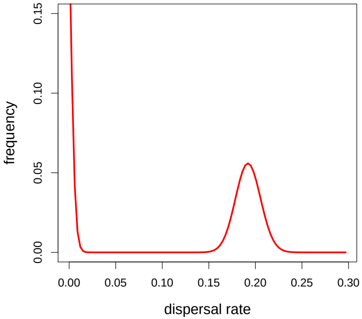
dispersal rate

To branch...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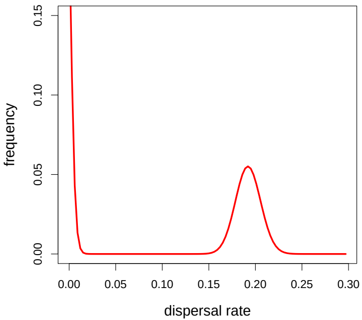
dispersal rate

To branch...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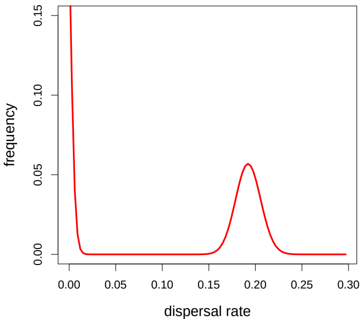
frequency
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...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0.00
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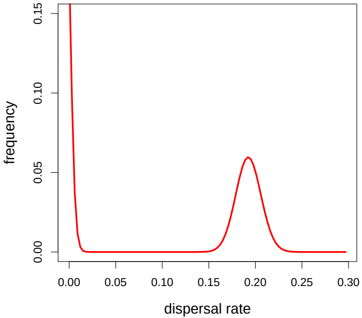
0.15
0.20
0.25
0.30
dispersal rate

To branch...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frequency
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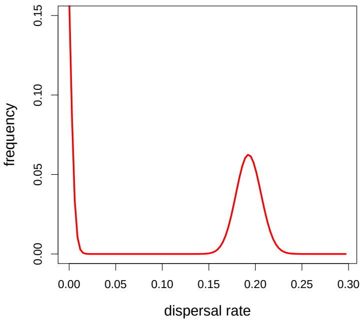
0.25
0.30
dispersal rate

To branch...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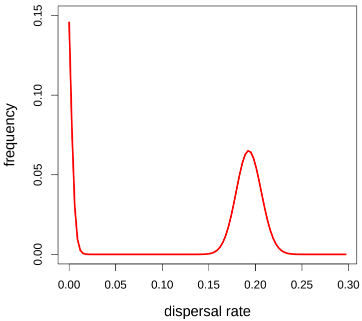
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...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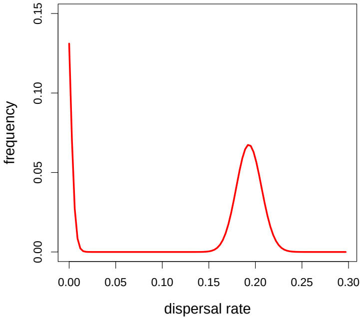
0.15
0.20
0.25
0.30
dispersal rate

To branch...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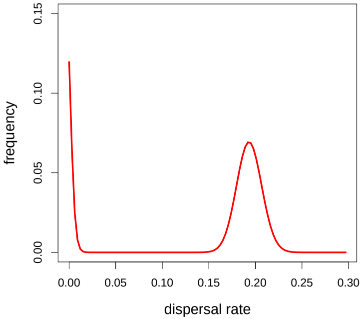
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
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0.15
0.20
0.25
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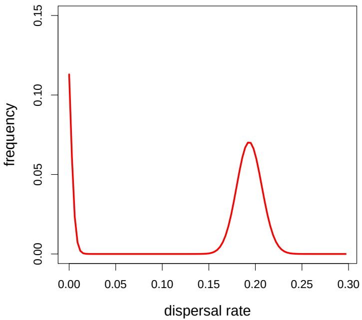
dispersal rate

To branch...


frequency
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0.05
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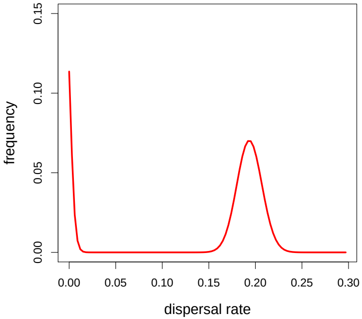
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
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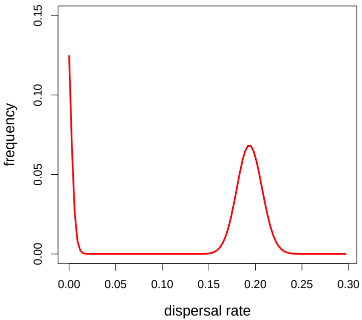
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
0.00
0.05
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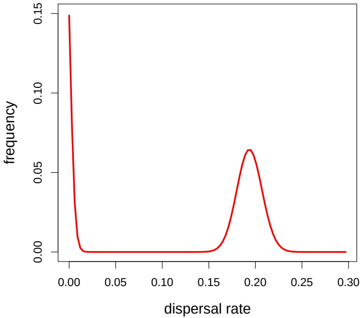
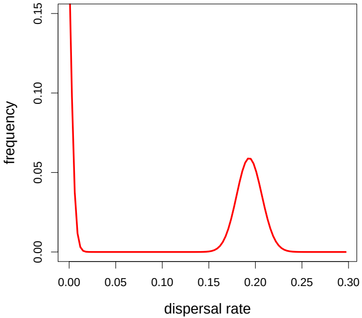
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

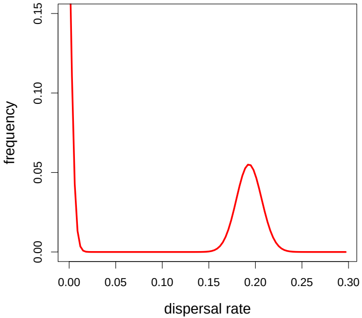
To branch...


frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

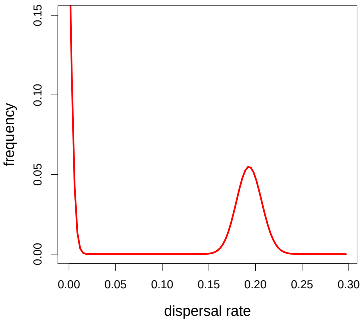
To branch...


0.15
0.10
0.05
0.00
frequency
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...



frequency
0.00
0.05
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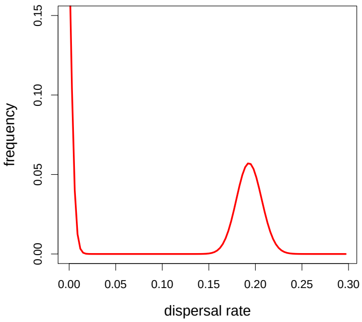
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
0.00
0.05
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0.05
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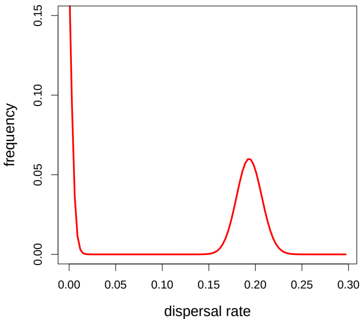
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
0.00
0.05
0.10
0.15
0.00
0.05
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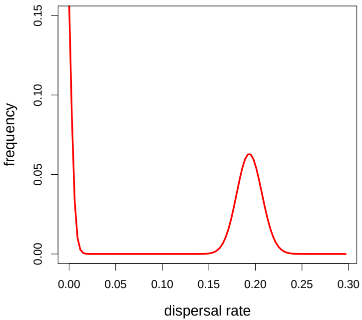
0.15
0.20
0.25
0.30
dispersal rate

To branch...


frequency
0.00
0.05
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0.05
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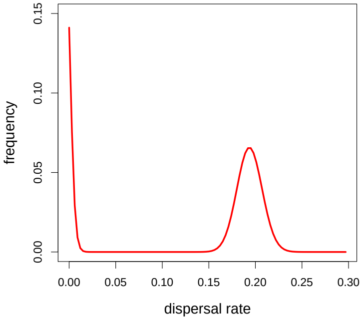
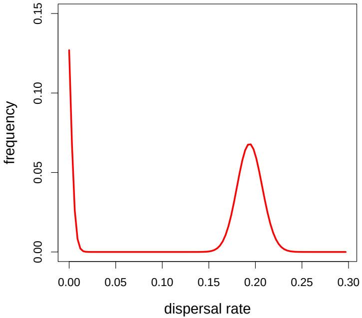
0.15
0.20
0.25
0.30
dispersal rate

To branch...

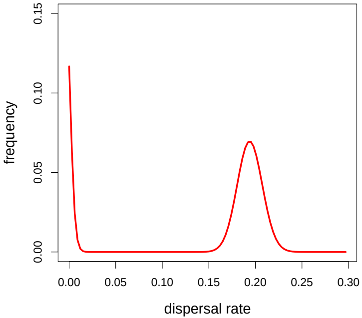

frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...

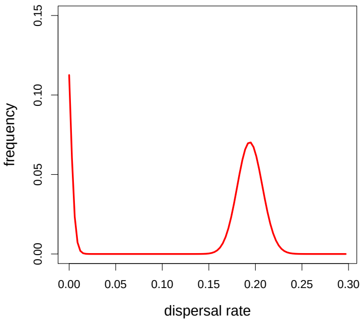


frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

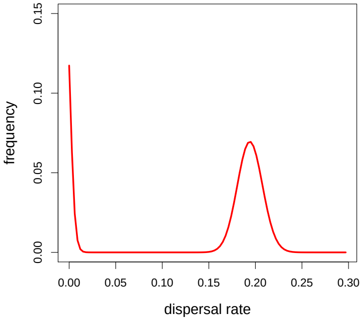
To branch...


frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

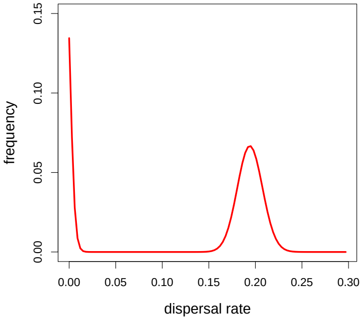
To branch...


frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

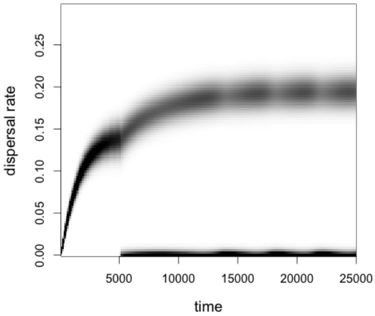
To branch...

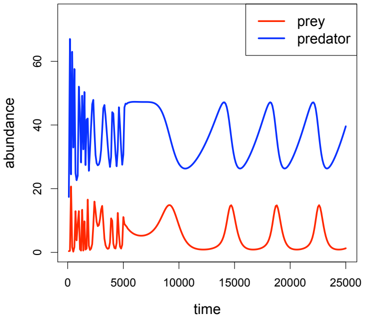

frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

To branch...

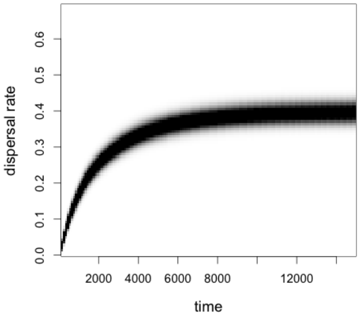

frequency
0.00
0.05
0.10
0.15
0.00
0.05
0.10
0.15
0.20
0.25
0.30
dispersal rate

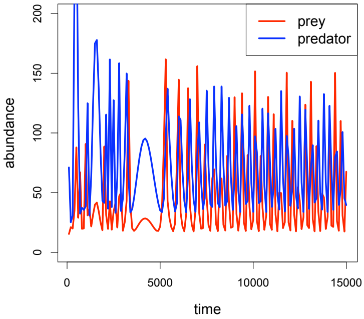
To branch...


dispersal rate
0.00
0.05
0.10
0.15
0.20
0.25
5000
10000
15000
20000
25000
time

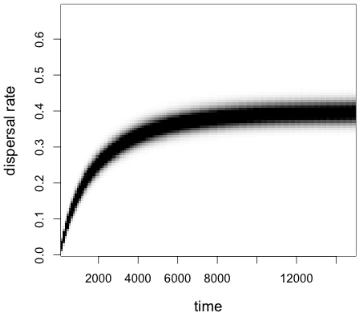

prey
predator
abundance
0
20
40
60
0
5000
10000
15000
20000
25000
time

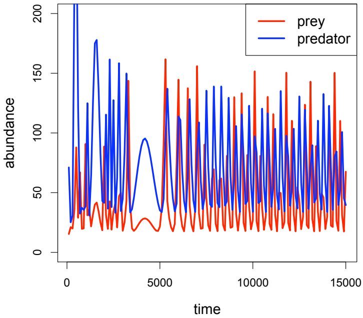
or not to branch?





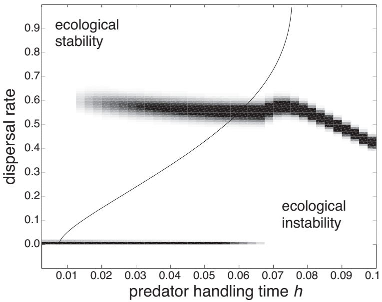
or not to branch?



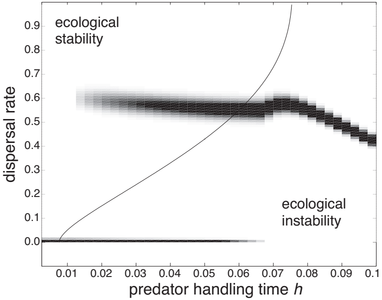


- monomorphisms: dispersive or sedentary

Three eco-evolutionary regimes

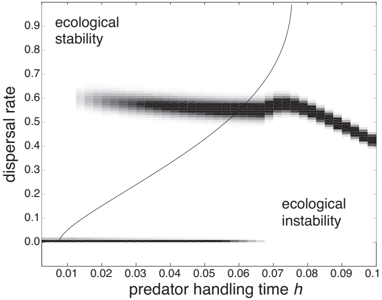


Three eco-evolutionary regimes



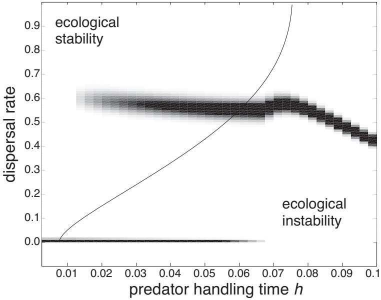
- stable source dynamics: selection against dispersal

Three eco-evolutionary regimes



- stable source dynamics: selection against dispersal
- dispersive prey do not stabilize: dispersive monomorphism

Three eco-evolutionary regimes



- stable source dynamics: selection against dispersal
- dispersive prey do not stabilize: dispersive monomorphism
- dispersive prey stabilize dynamics: dimorphisms

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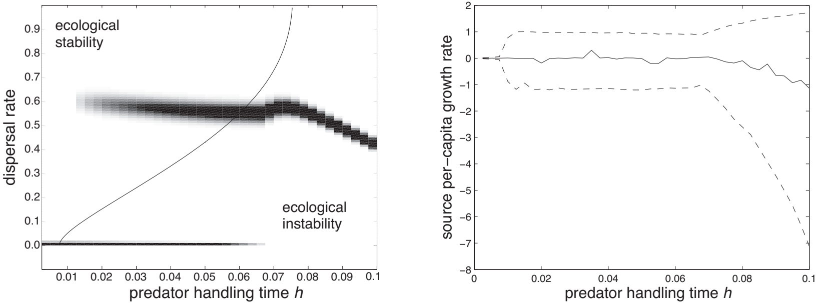

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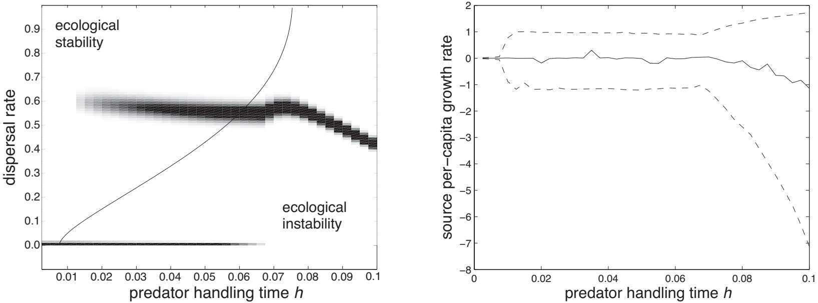
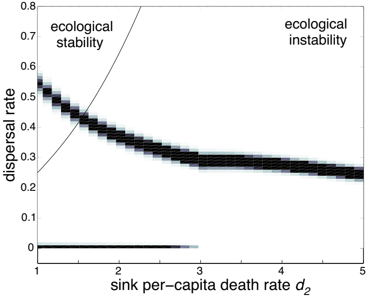
Three eco-evolutionary regimes

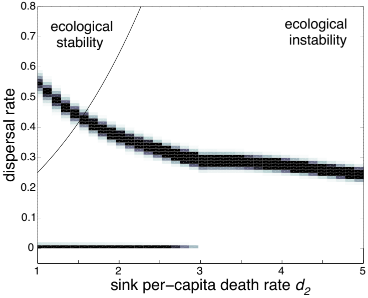


- stable source dynamics: selection against dispersal
- dispersive prey do not stabilize: dispersive monomorphism
- dispersive prey stabilize dynamics: dimorphisms
  - yields coupled sink populations!

Harvesting sinks vs. enriching sources

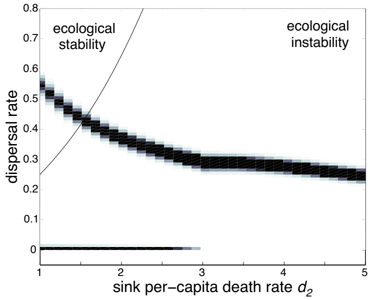


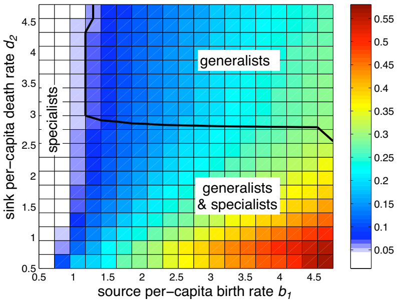
Harvesting sinks vs. enriching sources



- harvesting sinks can reduce phenotypic diversity

Harvesting sinks vs. enriching sources





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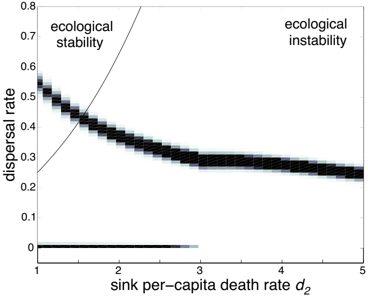
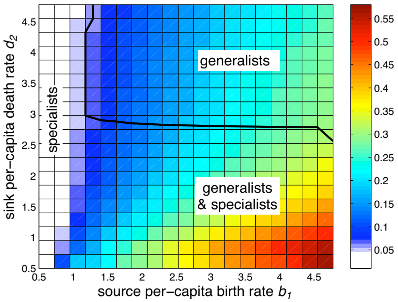
Harvesting sinks vs. enriching sources





- harvesting sinks can reduce phenotypic diversity
- maximal phenotypic diversity at intermediate enrichment

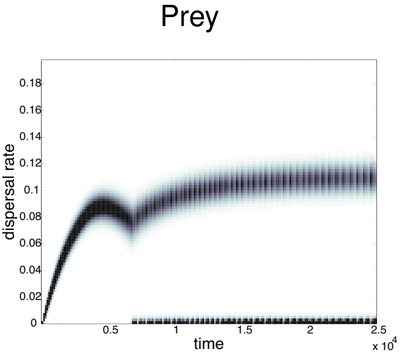
Predator-prey coevolution

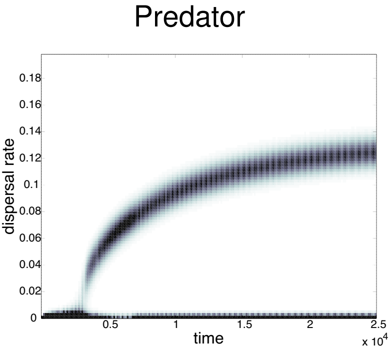
- $N_i(x)$, $P_i(y)$ prey,predator density of type x,y in patch i
- b_i, d_i prey birth,death rates; S_i occupiable sites
- a_i, h_i, c_i, δ_i attack, handling, conversion, death rate
- s,σ prey,predator mutation rates

$$
\begin{aligned}
\frac{\partial N_i}{\partial t}(x,t) &= (1+s\frac{\partial^2}{\partial x^2})b_iN_i(1-\int N_i\,dx/K_i) - d_iN_i \\
&\quad -\frac{a_iN_i\int P_i\,dy}{1+a_ih\int N_i\,dx} + x(N_j - N_i) \\
\frac{\partial P_i}{\partial t}(y,t) &= (1+\sigma\frac{\partial^2}{\partial y^2})\frac{ca_iP_i\int N_i\,dx}{1+ah\int N_i\,dx} - \delta_iP_i + y(P_j - P_i)
\end{aligned}
$$

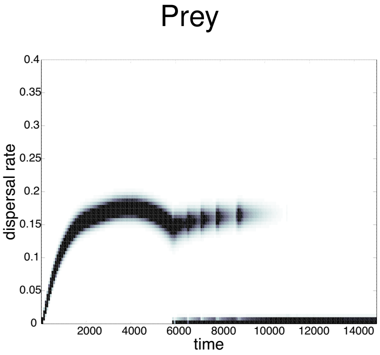
Assume: $\sigma > 0$, $S_2 = \infty$, $b_2 < d_2$

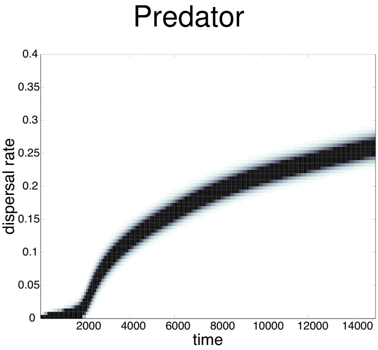
Double branching

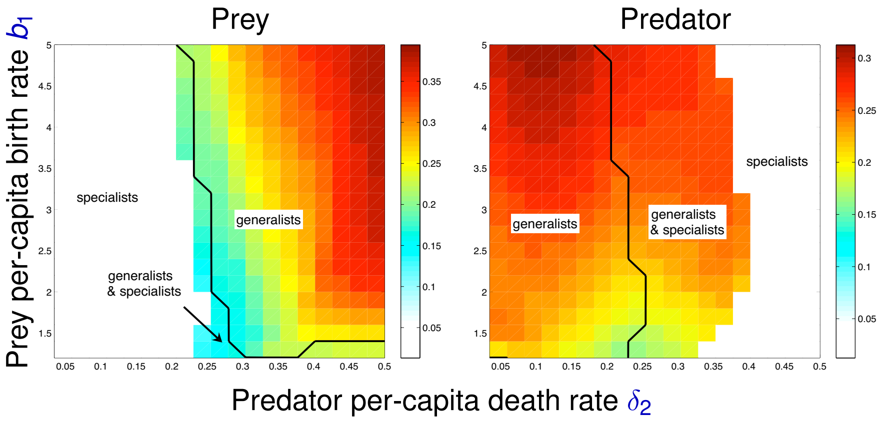




Evolution interuptus






Prey
Predator
Prey per-capita birth rate b_1
Predator per-capita death rate δ_2
specialists
generalists
generalists
& specialists
generalists
generalists
& specialists
specialists
5
4.5
4
3.5
3
2.5
2
1.5
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.35
0.3
0.25
0.2
0.15
0.1
0.05

Outline

Conclusions

- Evolution of patch selection

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- Evolution of patch selection
  - differential spatial distributions

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  - mechanisms of ecological instability become stabilizing

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  - no polymorphisms?

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- Evolution of random predator-prey movement

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  - polymophisms at multiple trophic levels

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Conclusions

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  - mechanisms of ecological instability become stabilizing
  - no polymorphisms?
- Evolution of random predator-prey movement
  - permanent sink populations
  - persistent sink-sink structures
  - polymophisms at multiple trophic levels
  - evolutionary paradox of enrichment
- what happens when there is conditional dispersal?