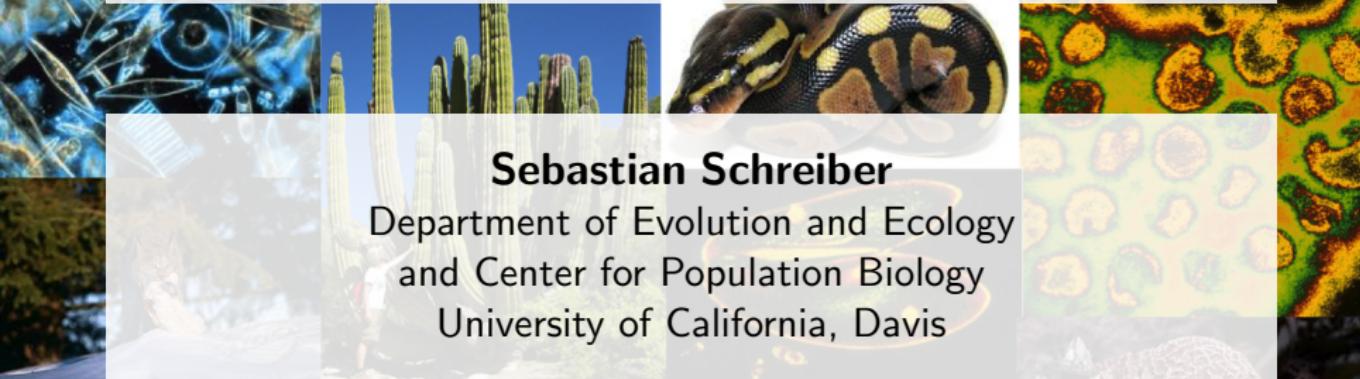




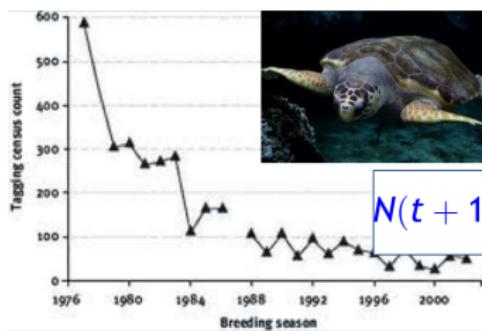
Population persistence & diversity maintenance in fluctuating environments

Sebastian Schreiber

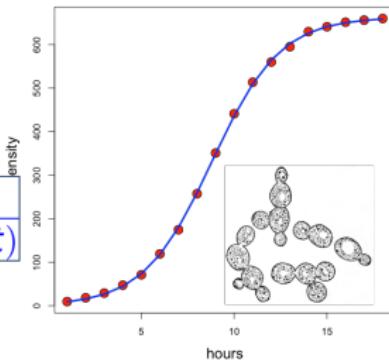
Department of Evolution and Ecology
and Center for Population Biology
University of California, Davis



Under what abiotic and biotic conditions does a population persist for a long time? When does it tend toward extinction?



$$N(t+1) = N(t) \frac{\lambda}{1 + aN(t)}$$

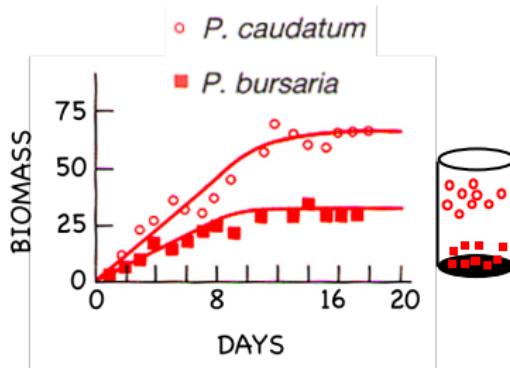
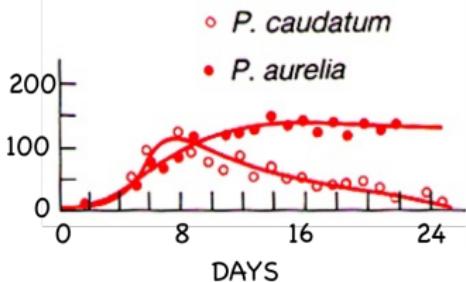


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When are interacting populations likely to coexist for extended periods of time? When does exclusion occur and why?

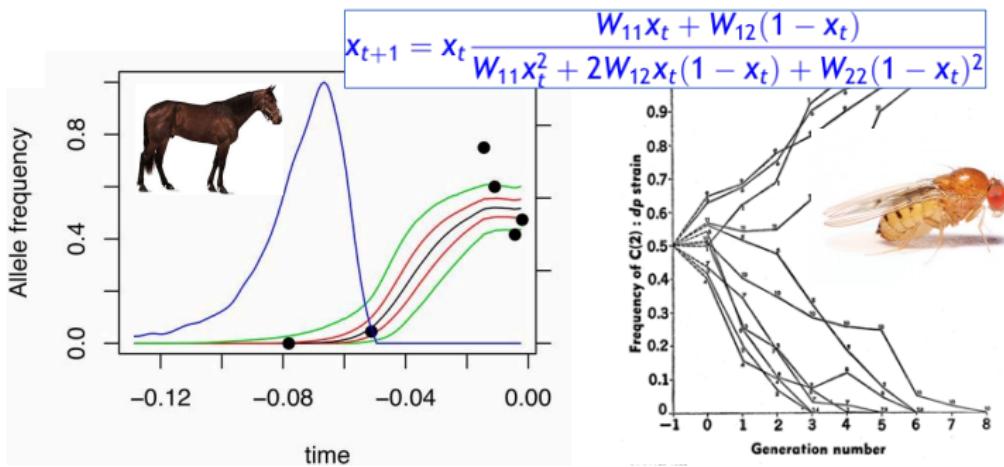
$$\frac{dN_1}{dt} = r_1 N_1 (1 - a_{11} N_1 - a_{12} N_2)$$

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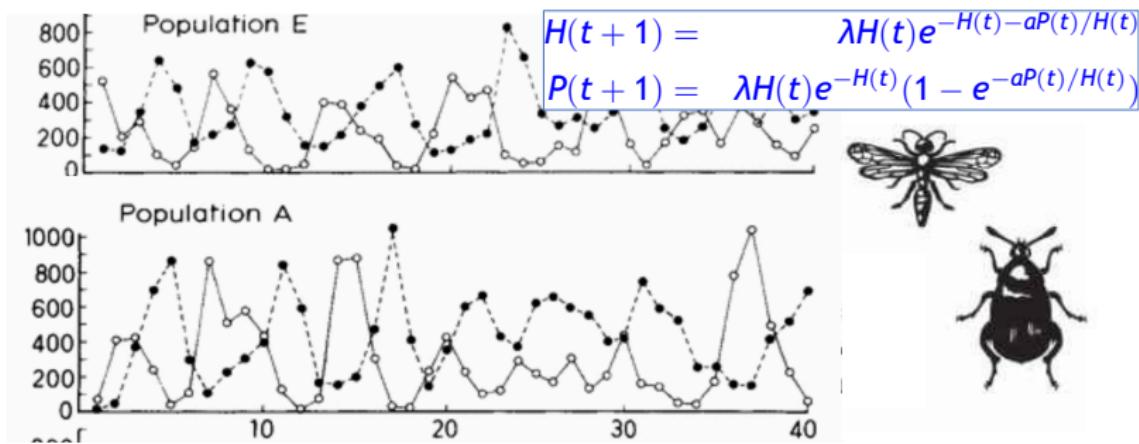
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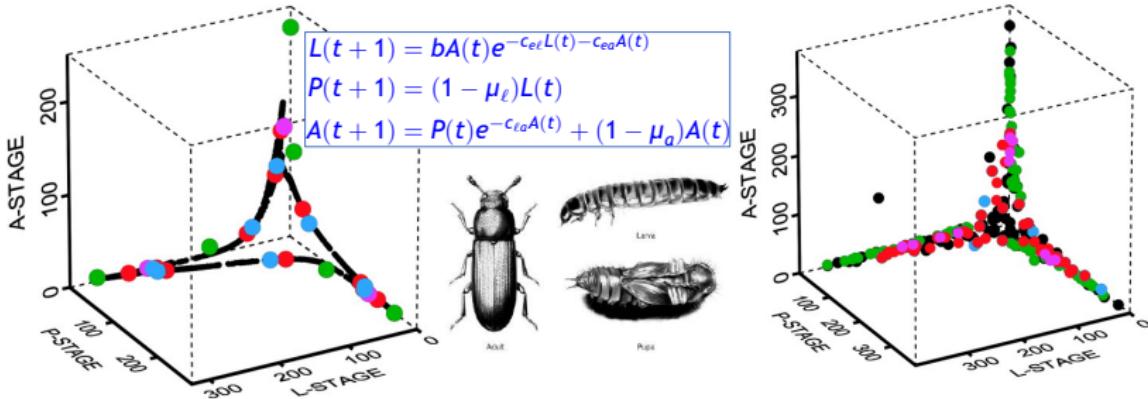
For persisting populations, when do they exhibit simple versus complex dynamical behaviors?



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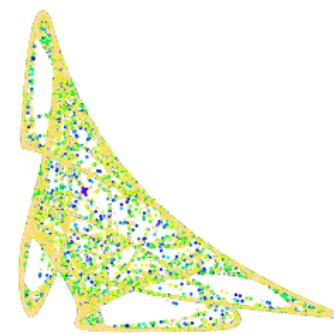
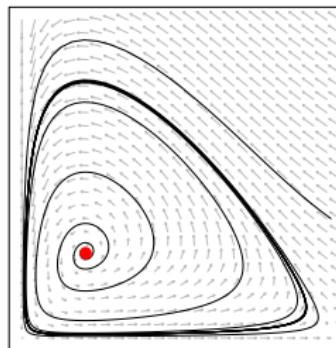
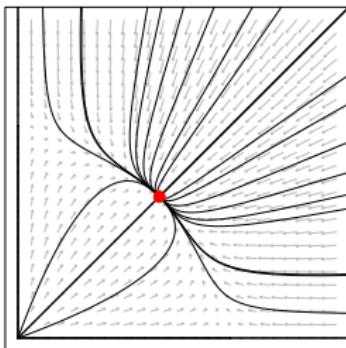
- ▶ differential equations: $\frac{dx}{dt} = f(x)$
- ▶ difference equations: $x_{t+1} = f(x_t)$
- ▶ on the non-negative orthant $\mathbb{R}_+^k = [0, \infty)^k$
- ▶ persistence = a positive attractor

Lotka 1925, Volterra 1926, Nicholson & Bailey 1935, Kermack & Mckendrick 1927

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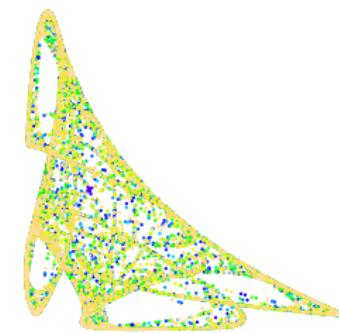
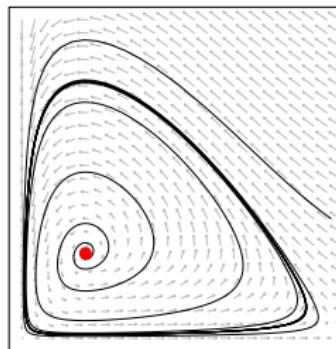
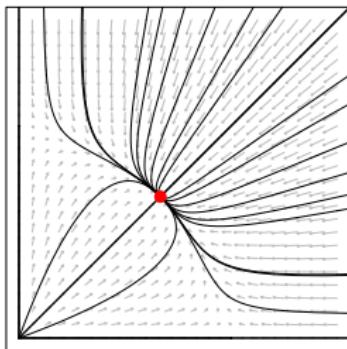
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Population geneticists (Wright, Fisher, Haldane) **were wiser from the beginning...**

Introduction

○○●

Single population

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Multiple populations

○○○○○○○○○○

Finale

○

Lest men suspect your tale untrue, Keep probability in view. –John Gay

Lest **biologists** suspect your **model** untrue, Keep probability in view.

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- ▶ finite number of individuals with uncorrelated fates

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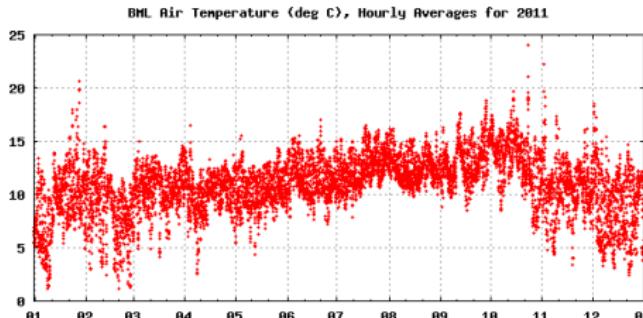
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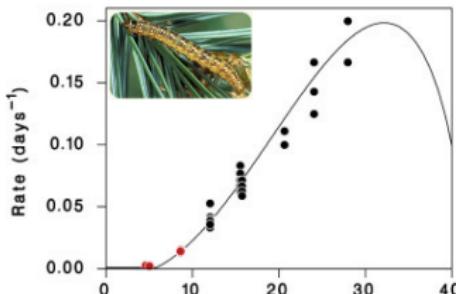
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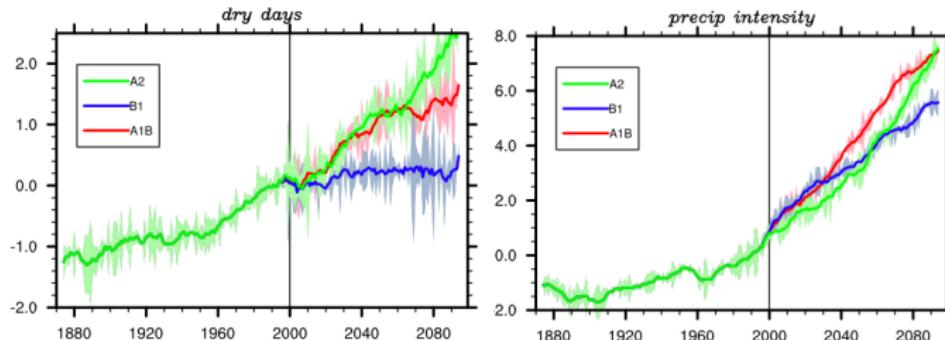
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Main question: How does environmental stochasticity influence population persistence and the maintenance of genetic diversity?

Single population

$X_{t+1} = X_t f(X_t, Y_t, \xi_{t+1})$ population density $[0, \infty)$

$Y_{t+1} = g(X_t, Y_t, \xi_{t+1})$ feedback variable \mathbb{R}^n

$\xi_1, \xi_2, \xi_3, \dots$ i.i.d.

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- Environmental forcing by a stationary process e.g.

$$Y_{t+1} = AY_t + \xi_{t+1}$$

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- ▶ Internal feedbacks due to evolving traits (e.g. Breeder's equation) or population structure (e.g. spatial distribution)

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$$\mathbb{P}\left[\lim_{t \rightarrow \infty} X_t = 0 \mid Z_0 = (x, y)\right] \rightarrow 1 \text{ as } x \rightarrow 0.$$

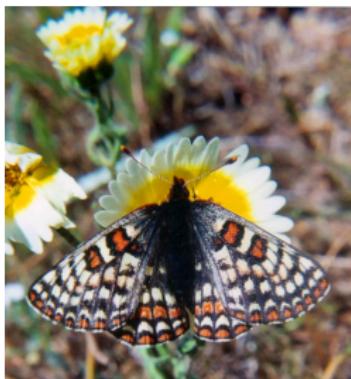
$X_{t+1} = X_t f(X_t, Y_t, \xi_{t+1})$ population density $Y_{t+1} = g(X_t, Y_t, \xi_{t+1})$ feedback variable $\xi_1, \xi_2, \xi_3, \dots$ i.i.d.realized per-capita growth rate $r(\mu) = \int \mathbb{E}[\log f(0, y, \xi_1)] \mu(dy)$ extinction set $M_0 = \{(0, y) \in M\}$ and persistent set $M_+ = M \setminus M_0$

Proposition Benaim & S. (in prep) If $r(\mu) < 0$ for all ergodic μ supported by M_0 , then

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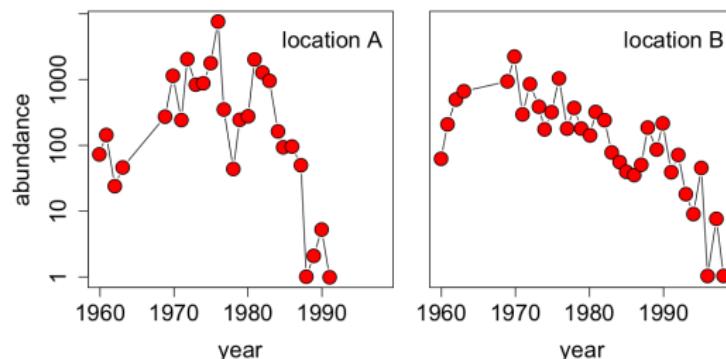
Moreover, if M_0 is “accessible” then $\lim_{t \rightarrow \infty} X_t = 0$ a.s. for all Z_0 .

Climate induced extinction?

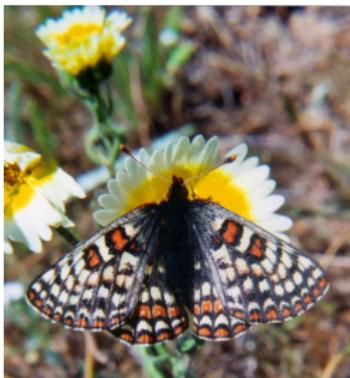


Bay checkerspot

2 checkerspot populations went extinct in 1990s

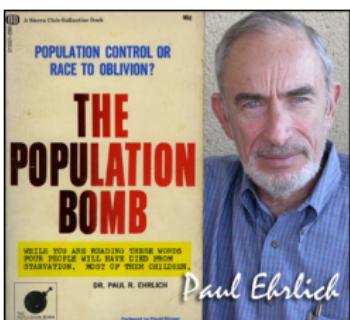
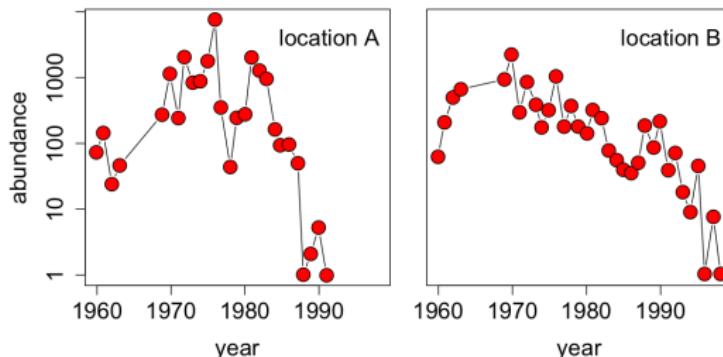


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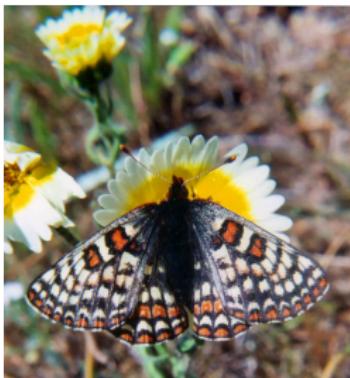
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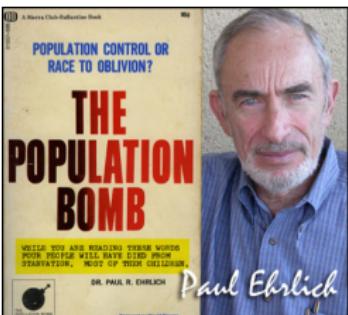


Paul Ehrlich

Climate induced extinction?

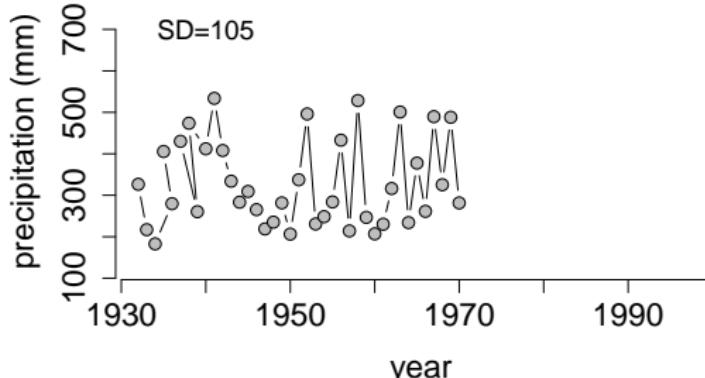
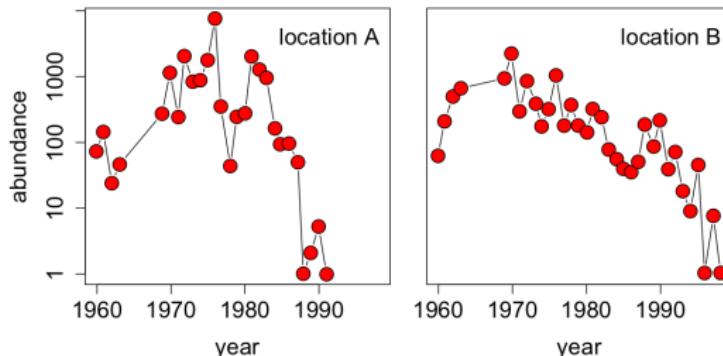


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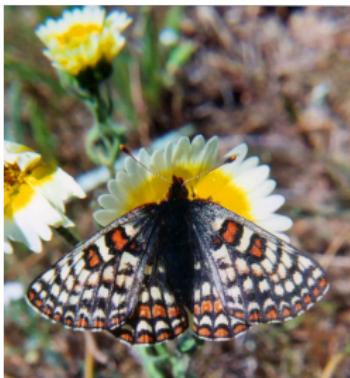


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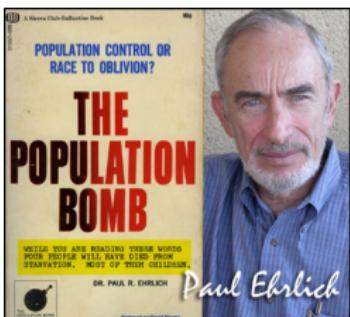
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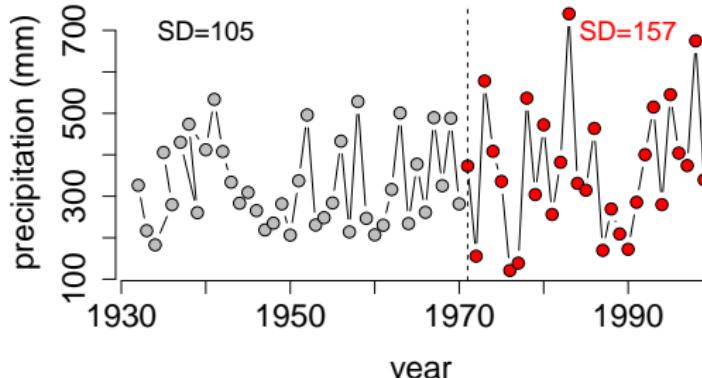
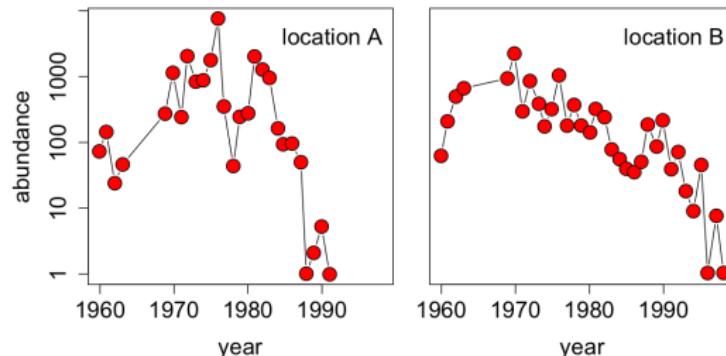


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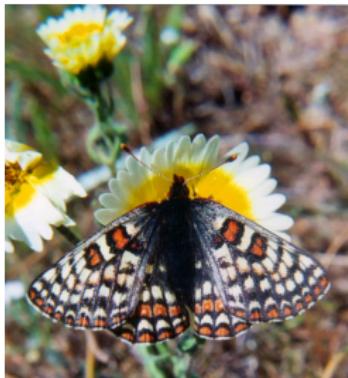


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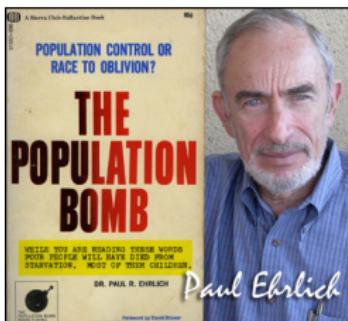
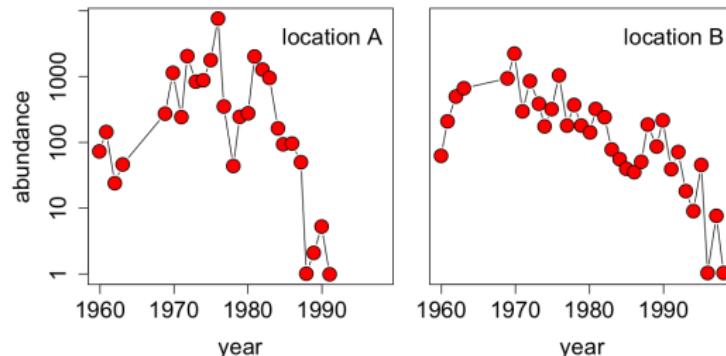


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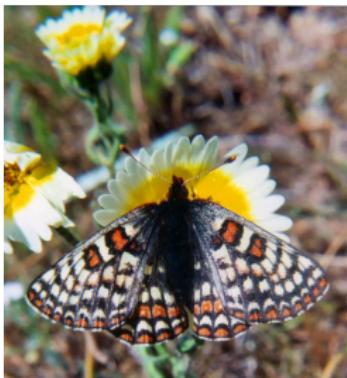
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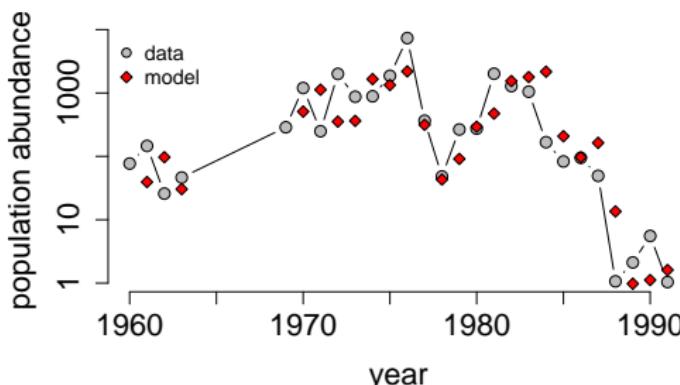
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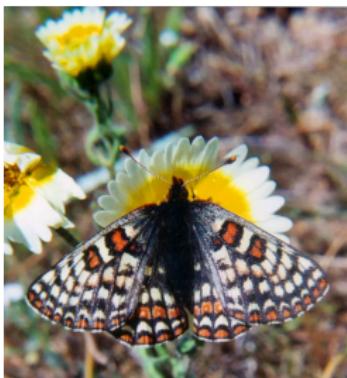
A simplified version of McLaughlin et al. (2002) PNAS:

$$X_{t+1} = X_t \exp(a_0 + a_1 X_t + a_2 Y_t)$$

where Y_t is precipitation.



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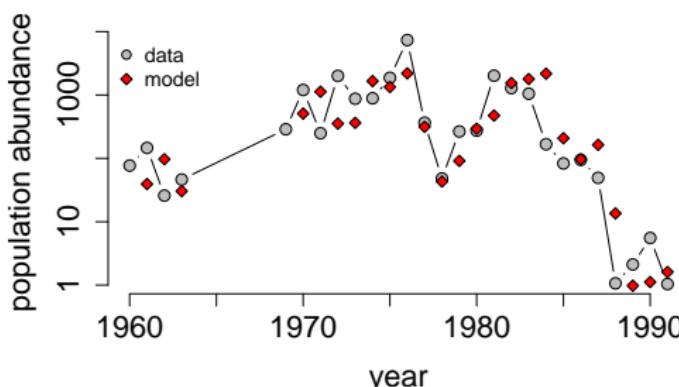
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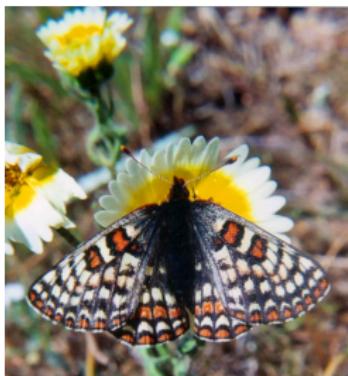
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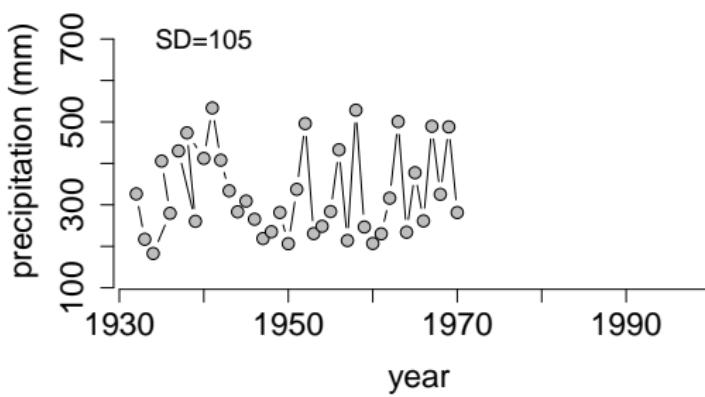
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Climate induced extinction?



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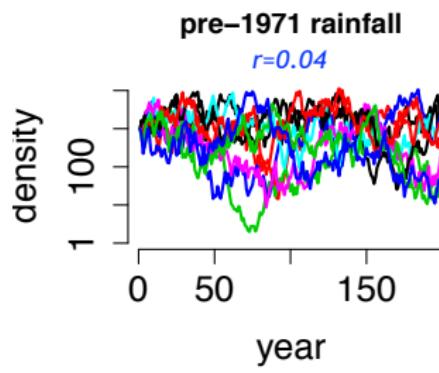


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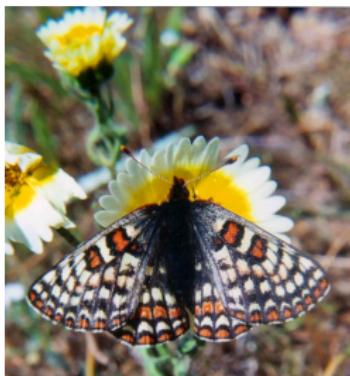
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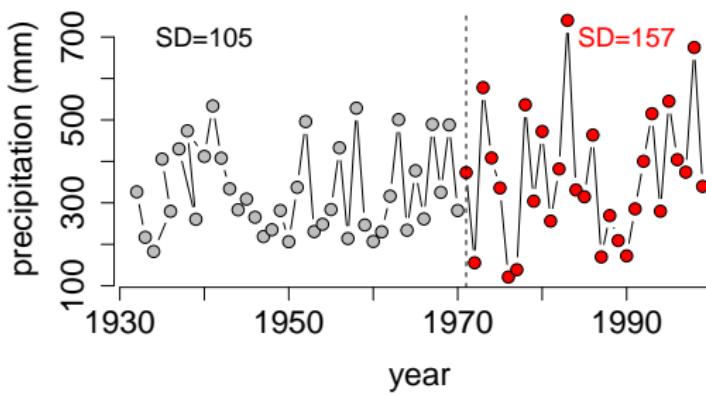
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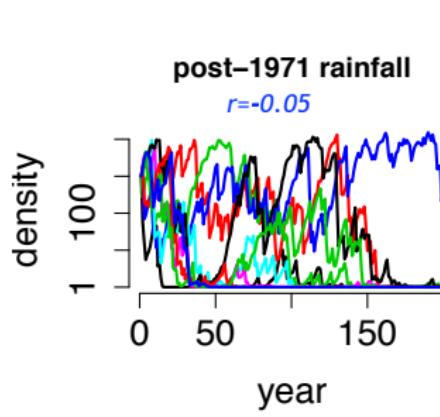


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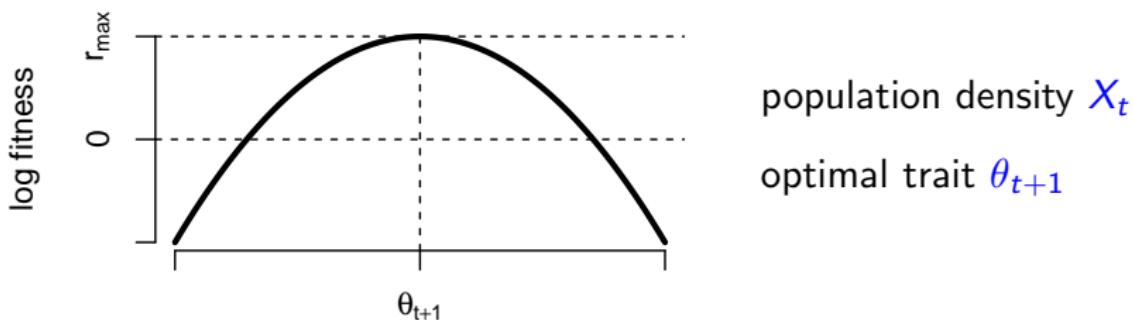
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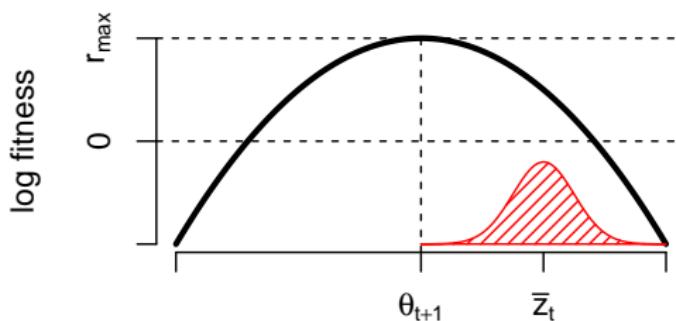
Evolution in a changing environment (cf. Lande & Shannon 1996)

population density X_t

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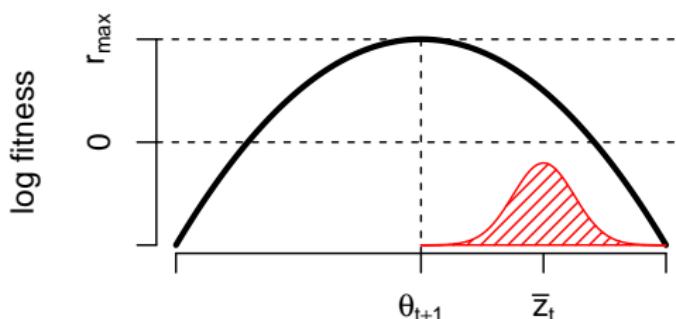


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optimal trait θ_{t+1}

mean trait \bar{z}_t w/ var. σ^2

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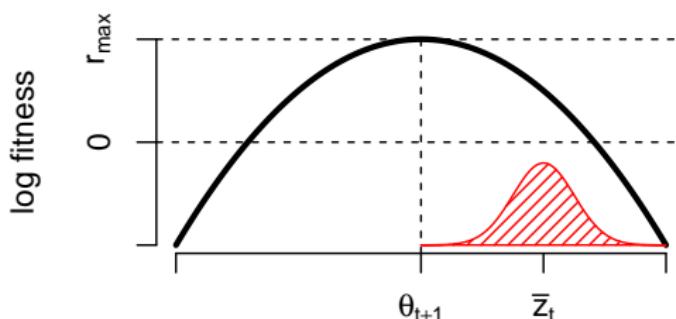
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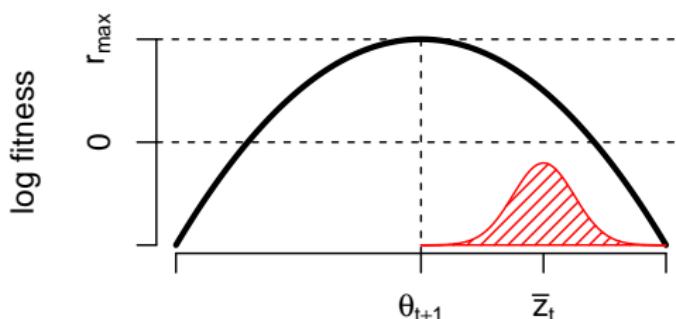
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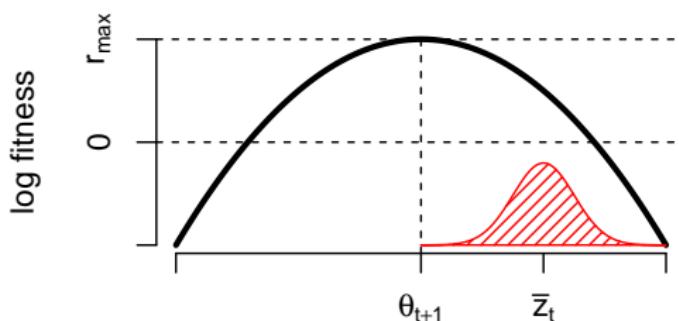
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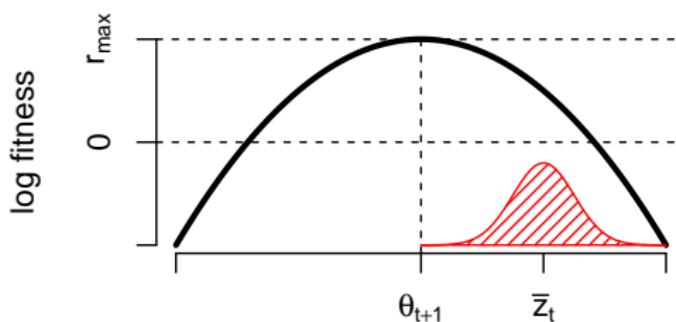
Breeder's equation for \bar{z}_t

(Lande 1976; Turelli & Barton 1994)

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ξ_t i.i.d. w/ mean 0, variance τ^2

ρ temporal autocorrelation

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$$\theta_{t+1} = \rho \theta_t + \sqrt{1 - \rho^2} \xi_{t+1}$$

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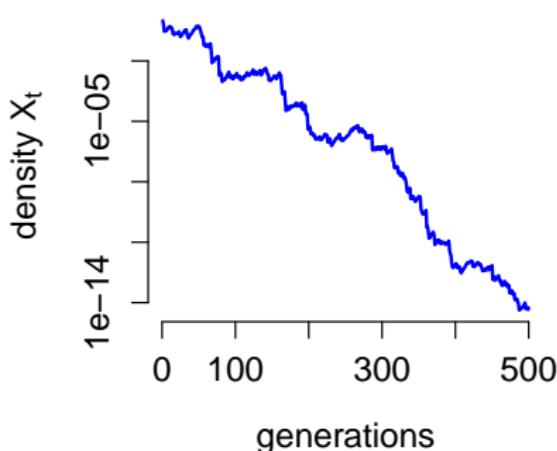
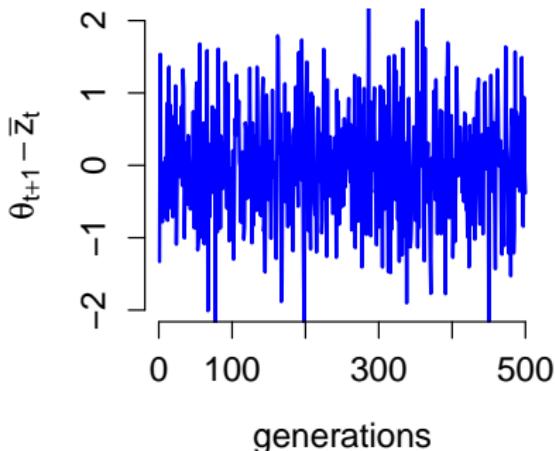
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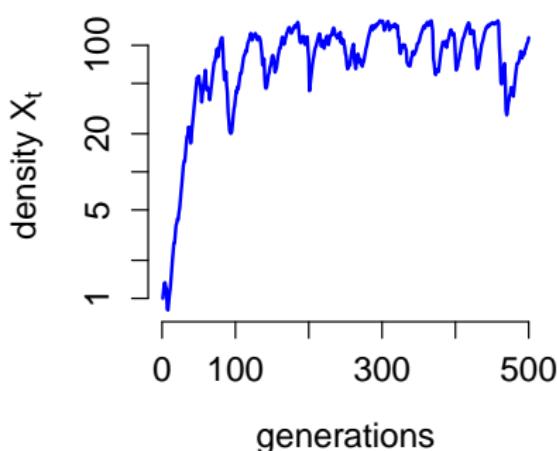
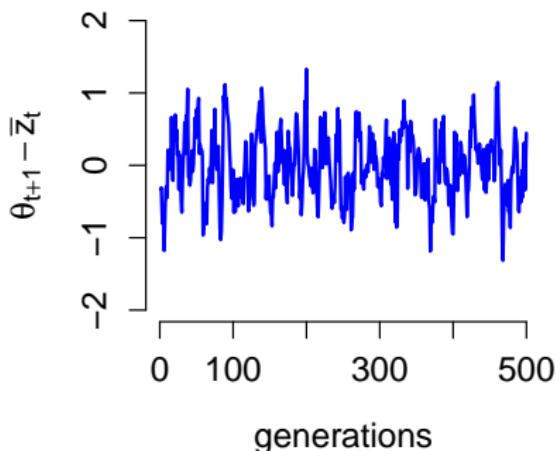


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Multiple populations

$X_{t+1}^i = X_t^i f_i(X_t, Y_t, \xi_{t+1})$ species/genotype #s w/ $X_t = (X_t^1, \dots, X_t^k)$
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Coexistence set $M_+ = M \setminus M_0$

Introduction
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Single population
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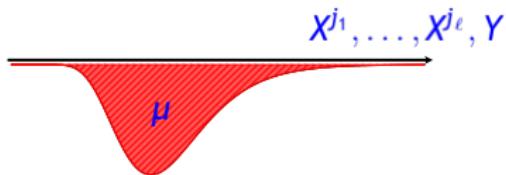
Multiple populations
○●○○○○○○○○

Finale
○

Suppose all but j_1, \dots, j_ℓ become infinitesimally rare

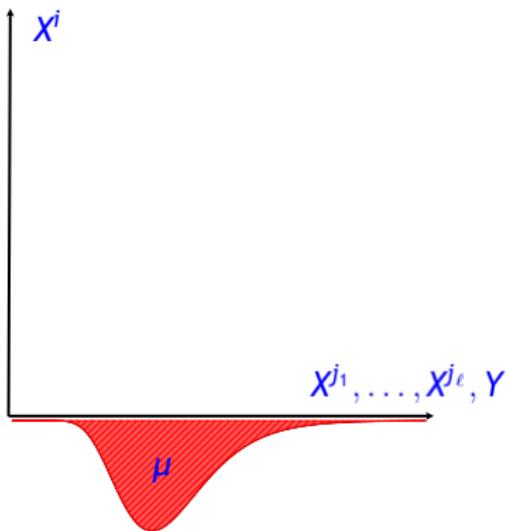
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$X_t^{j_1}, \dots, X_t^{j_\ell}$ & Y_t approach an ergodic stationary distribution with law μ



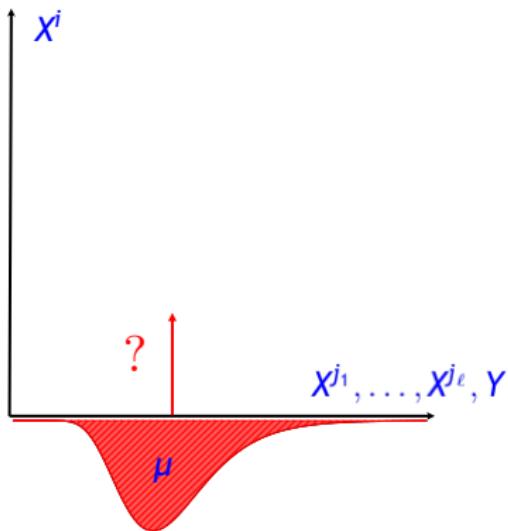
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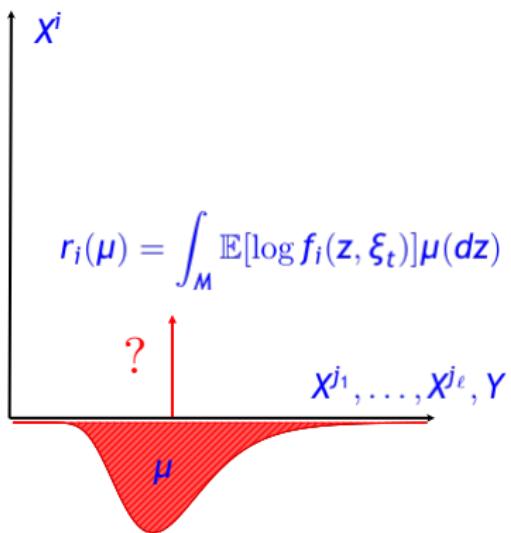
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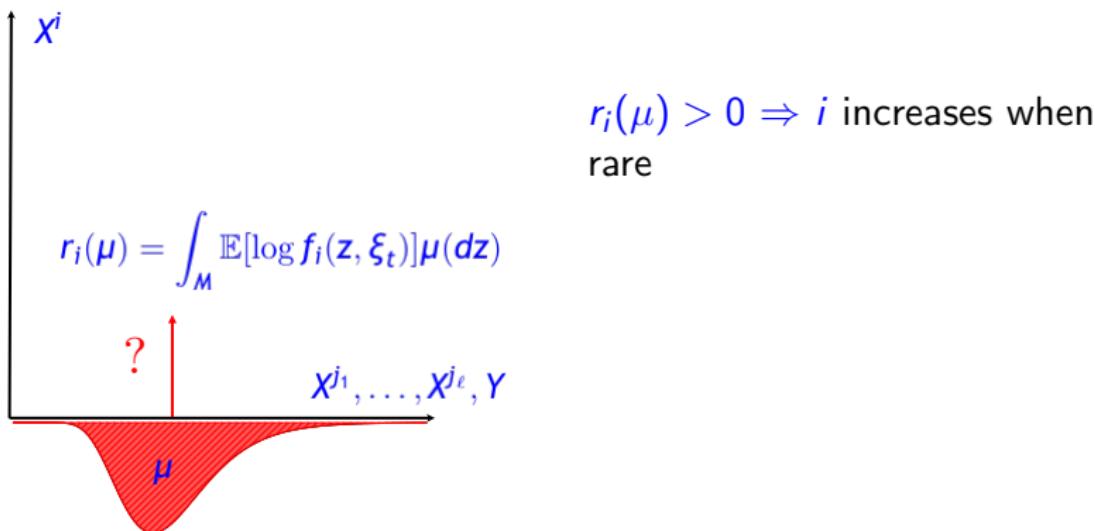
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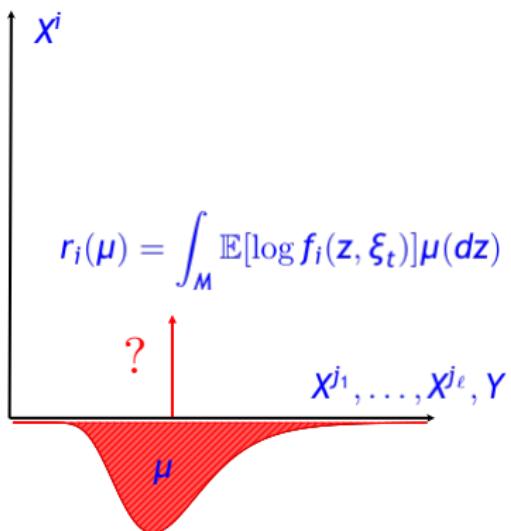
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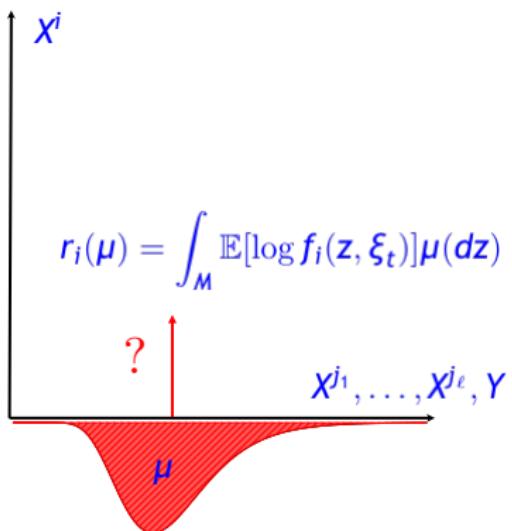


$r_i(\mu) > 0 \Rightarrow i$ increases when rare

$r_i(\mu) < 0 \Rightarrow i$ decreases when rare

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$X_t^{j_1}, \dots, X_t^{j_\ell}$ & Y_t approach an ergodic stationary distribution with law μ



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$r_j(\mu) = 0$ for any j “supported” by μ

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Theorem Benaïm & S. in prep If there exist weights $p_i > 0$ such that

$$\sum_i p_i r_i(\mu) > 0 \text{ for all } \mu \text{ supported by } M_0$$

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"arbitrarily little time at arbitrarily low densities"

Exclusion

$$X_{t+1}^i = X_t^i f_i(X_t, Y_t, \xi_{t+1}) \quad \text{species/genotype \#s w/ } X_t = (X_t^1, \dots, X_t^k)$$
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M_0 accessible $\Rightarrow \mathbb{P} \left[\lim_{t \rightarrow \infty} \text{dist}(Z_t, M_0) = 0 \mid Z_0 = z \right] = 1$

Introduction
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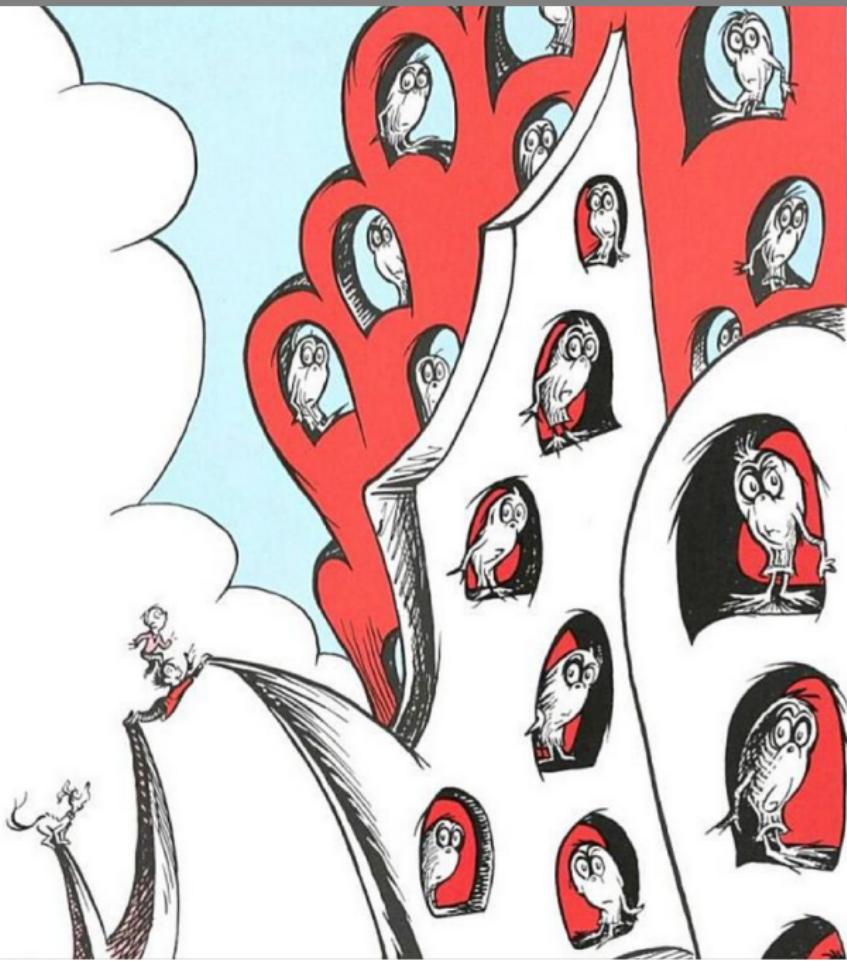
Single population
○○○○○○○

Multiple populations
○○○●○○○○

Finale
○



members of the same species, being very similar to each other, being machines for preserving genes in the same kind of place, with the same kind of way of life, are particularly direct competitors for all the resources necessary for life. - The Selfish Gene



“And NUH is the letter I use to spell Nuches,
Who live in small caves,
known as Niches, for hutches. These Nuches have troubles, the biggest of which is the fact there are many more Nuches than Niches. Each Nutch in a Nich knows that some other Nutch Would like to move into his Nich very much. So each Nutch in a Nich has to watch that small Nich or Nuches who haven't got Niches will snitch.”

Dr. Seuss

On Beyond the Zebra

Gillespie's SAS-CFF model with demography

k alleles at a single locus of a diploid population

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Define average fitness of allele i and average fitness of population

$$\overline{W}_{t+1}^i = \sum_j X_t^j (\xi_{t+1}^i + \xi_{t+1}^j)/2 \text{ and } \overline{W}_{t+1} = \sum_i X_t^i \overline{W}_{t+1}^i$$

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State space $\Delta \times [0, \infty)$ w/ $\Delta = \{(x^1, \dots, x^k) : x^i \geq 0, \sum_i x_i = 1\}$

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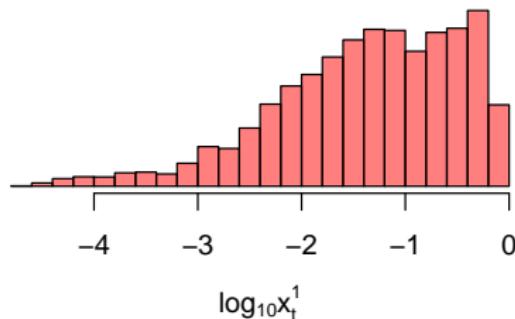
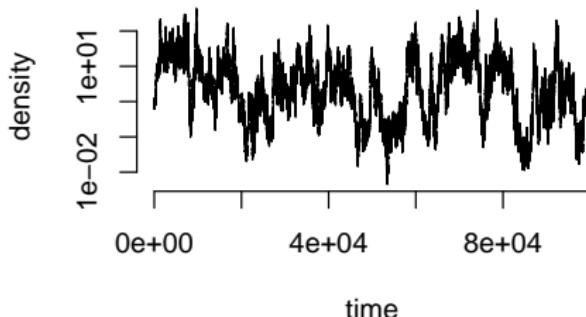
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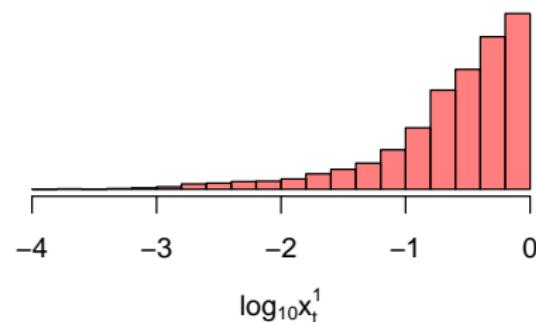
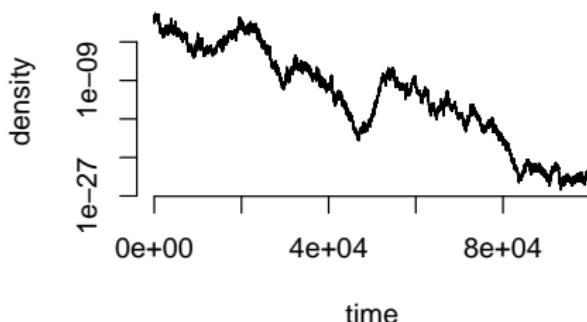
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Gillespie's SAS-CFF model with demography

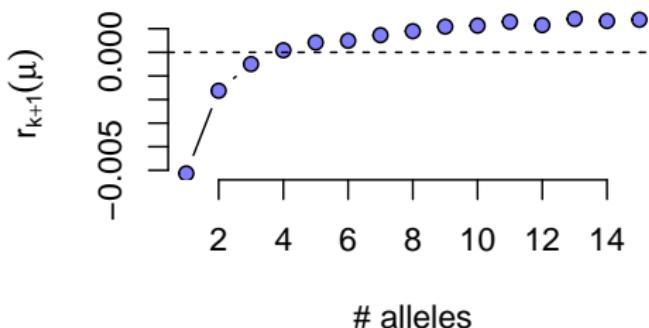
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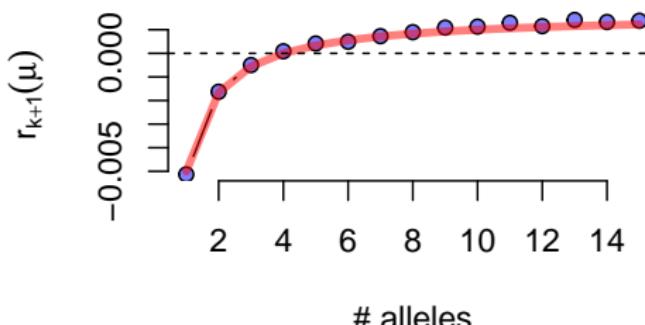
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Introduction

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Single population

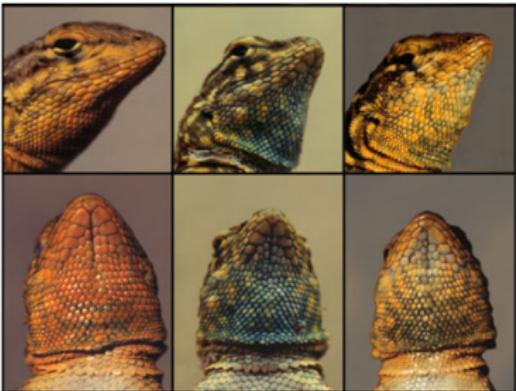
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Multiple populations

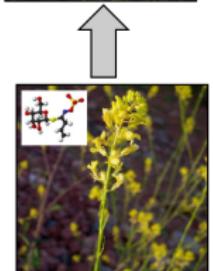
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Finale

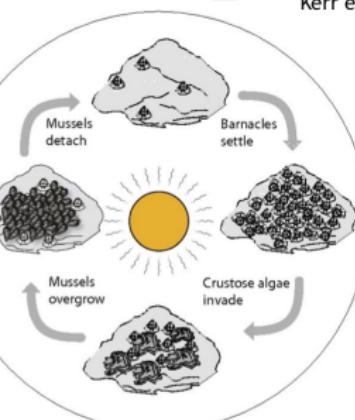
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Sinervo & Lively 1996 *Nature*



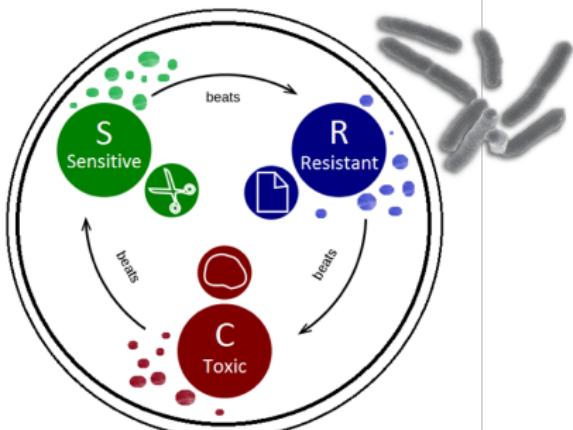
Lankau & Strauss 2007 *Science*



Beninica et al 2015 *PNAS*



Kerr et al. 2001 *Nature*



Rock (1), paper (2), scissors (0) mod 3

 $W_t^i > 1, 1, L_t^i < 1$ payoff to i when interacts w/ $i-1, i, i+1$

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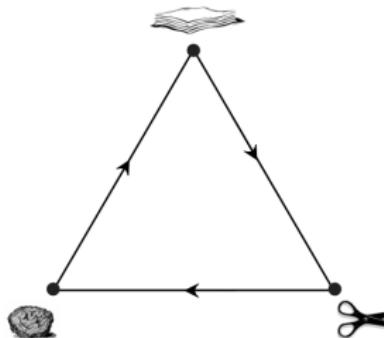
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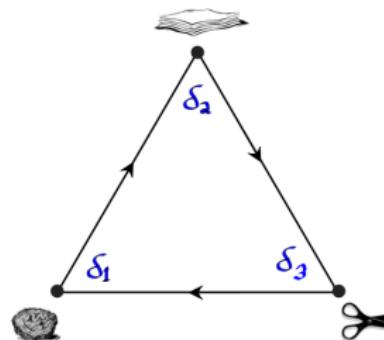
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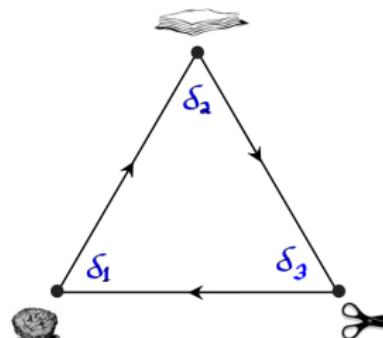


$$r_i(\delta_i) = 0, r_i(\delta_{i+1}) = \mathbb{E}[\log L_t^i], r_i(\delta_{i-1}) = \mathbb{E}[\log W_t^i]$$

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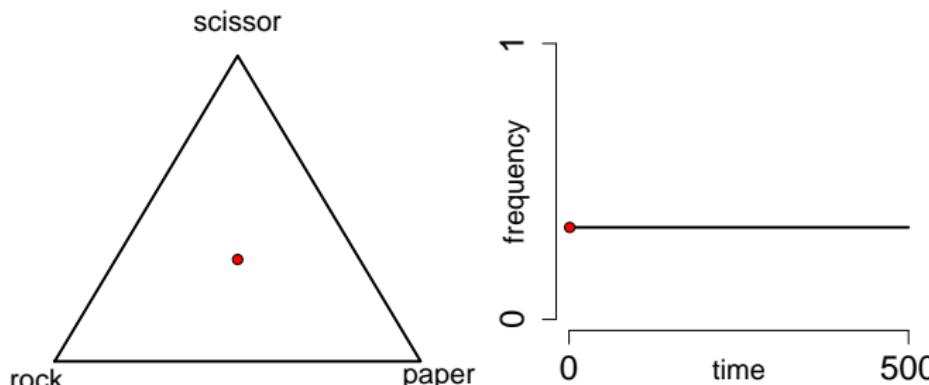
$$\mathbb{E}[\log W_t^i] + \mathbb{E}[\log L_t^i] > 0$$

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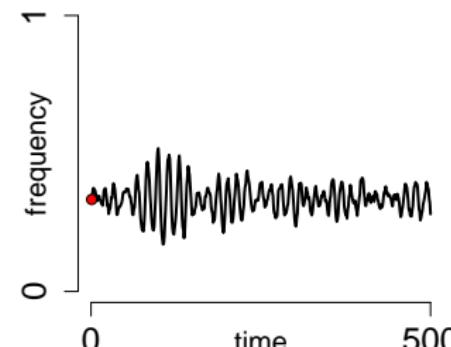
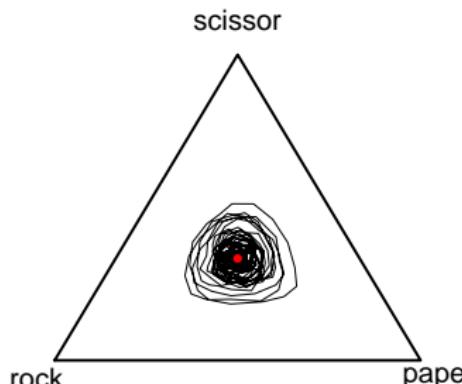


$$\mathbb{E}[\log W_t^i] + \mathbb{E}[\log L_t^i] > 0$$

Rock (1), paper (2), scissors (0) mod 3

 $W_t^i > 1, 1, L_t^i < 1$ payoff to i when interacts w/ $i-1, i, i+1$ W_t^i identically distributed, L_t^i identically distributed

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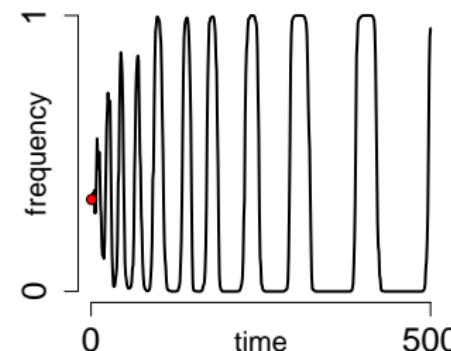
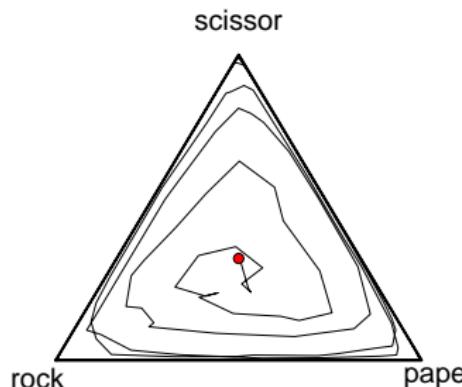


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$$\mathbb{E}[\log W_t^i] + \mathbb{E}[\log L_t^i] < 0$$

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Can inhibit or promote population persistence

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Can facilitate or disrupt genetic polymorphisms

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Persistence/extinction determined by $\sum_i p_i r_i(\mu)$

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Questions?