Topics in evolutionary dynamics

Lecture 1:
Adaptation & the concept of fitness

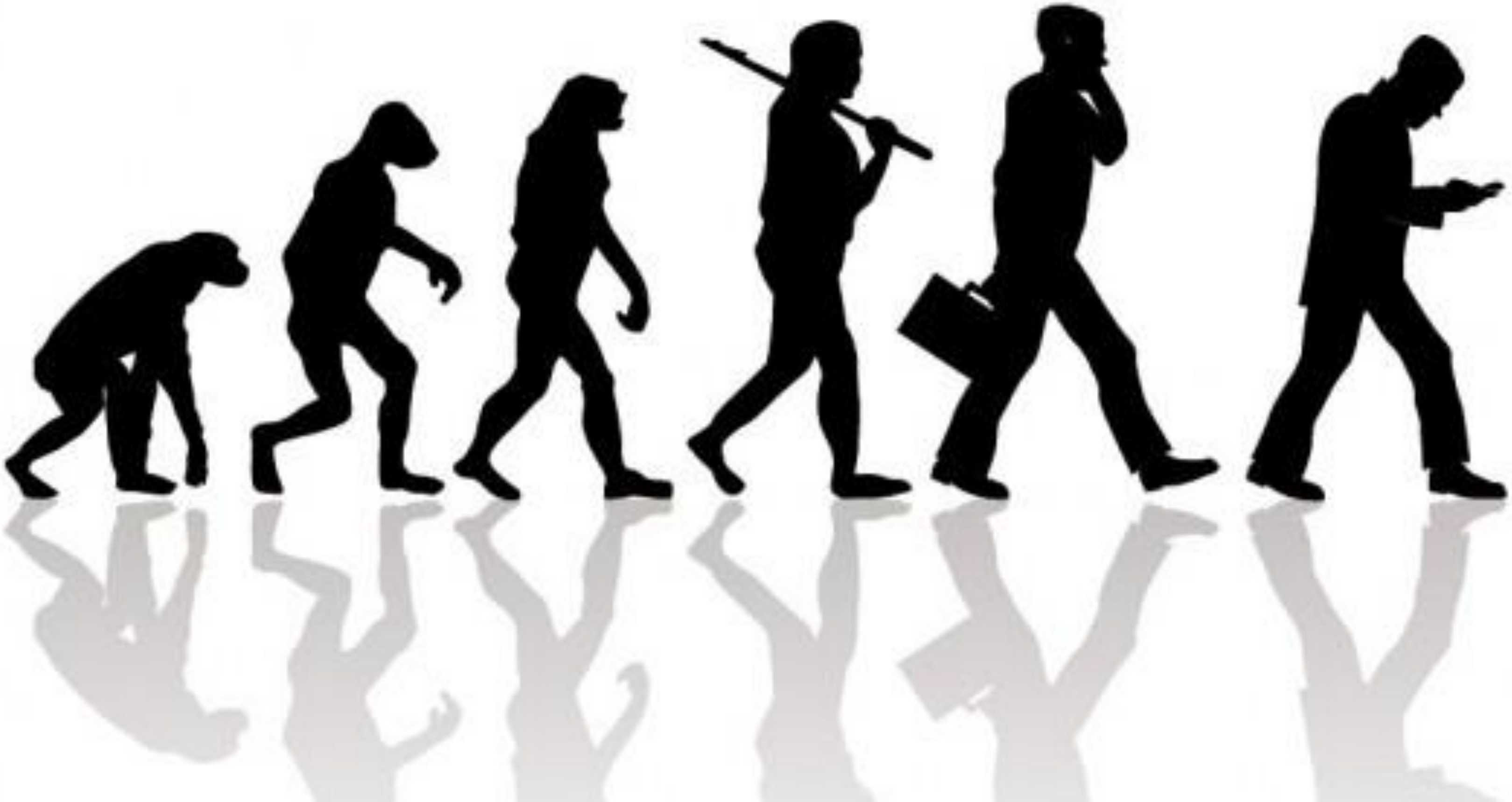
François Massol

3rd summer school on Mathematical Biology

São Paulo, February 2014

Lecture outline

1. Basics of evolution
2. Defining adaptation
3. The concept(s) of fitness
4. Fitness in different guises



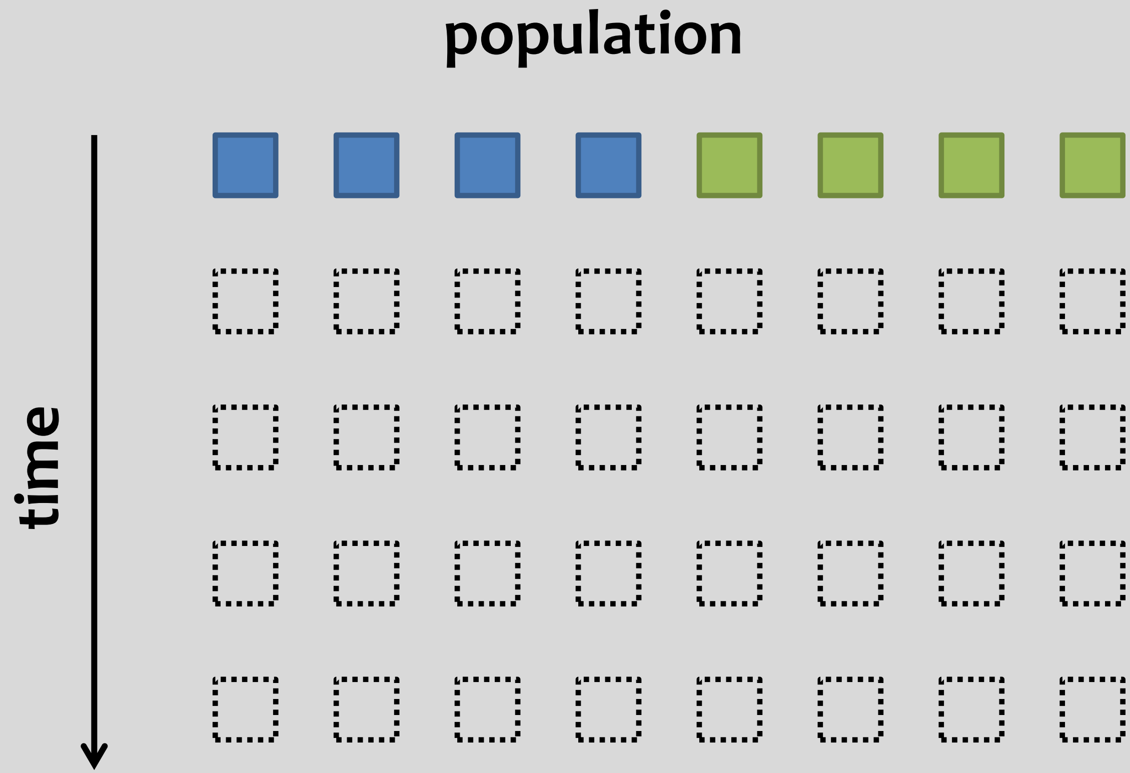
BASICS OF EVOLUTION

Basics of evolution

What are the forces shaping the evolution of organisms?

Basics of evolution

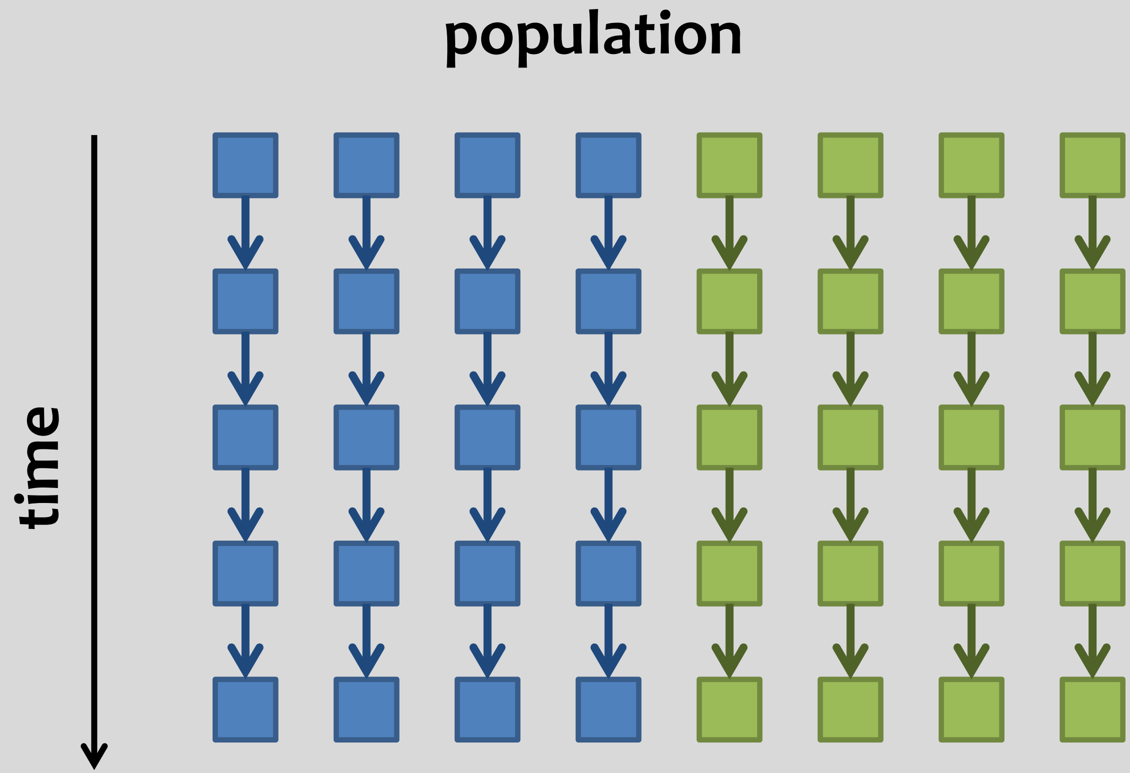
What are the forces shaping the evolution of organisms?



Basics of evolution

What are the forces shaping the evolution of organisms?

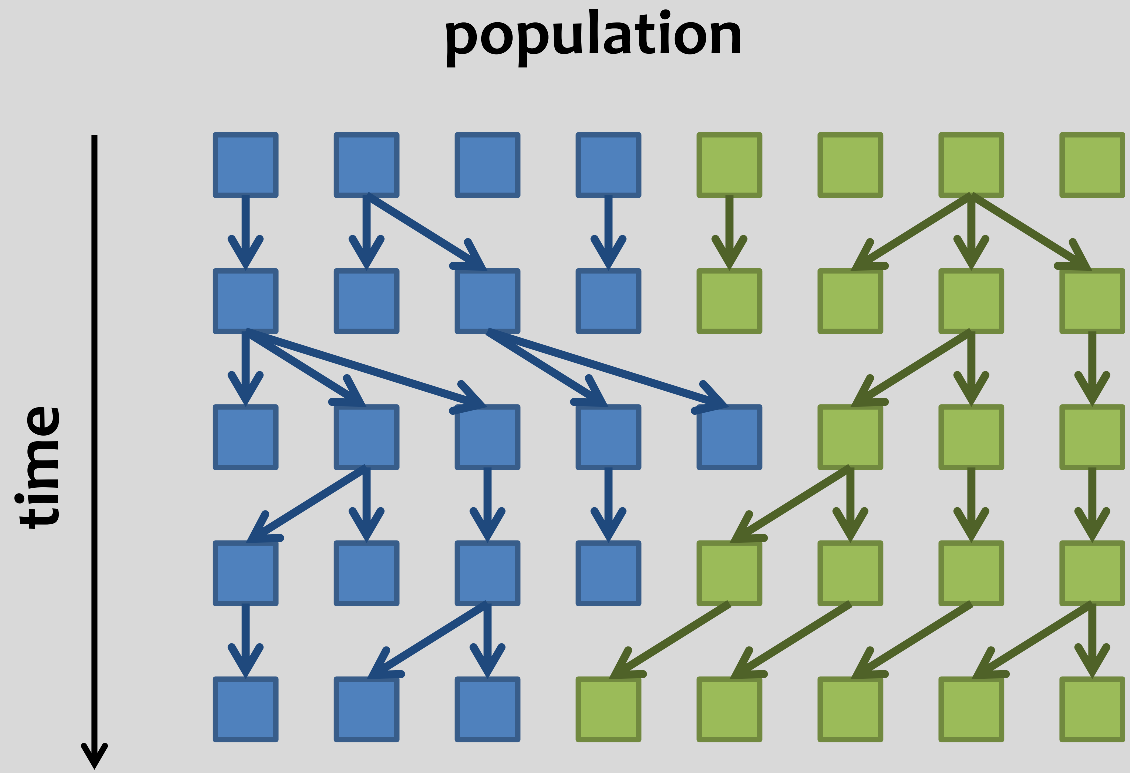
- ~~mutation~~
- ~~selection~~
- ~~migration~~
- ~~drift~~



Basics of evolution

What are the forces shaping the evolution of organisms?

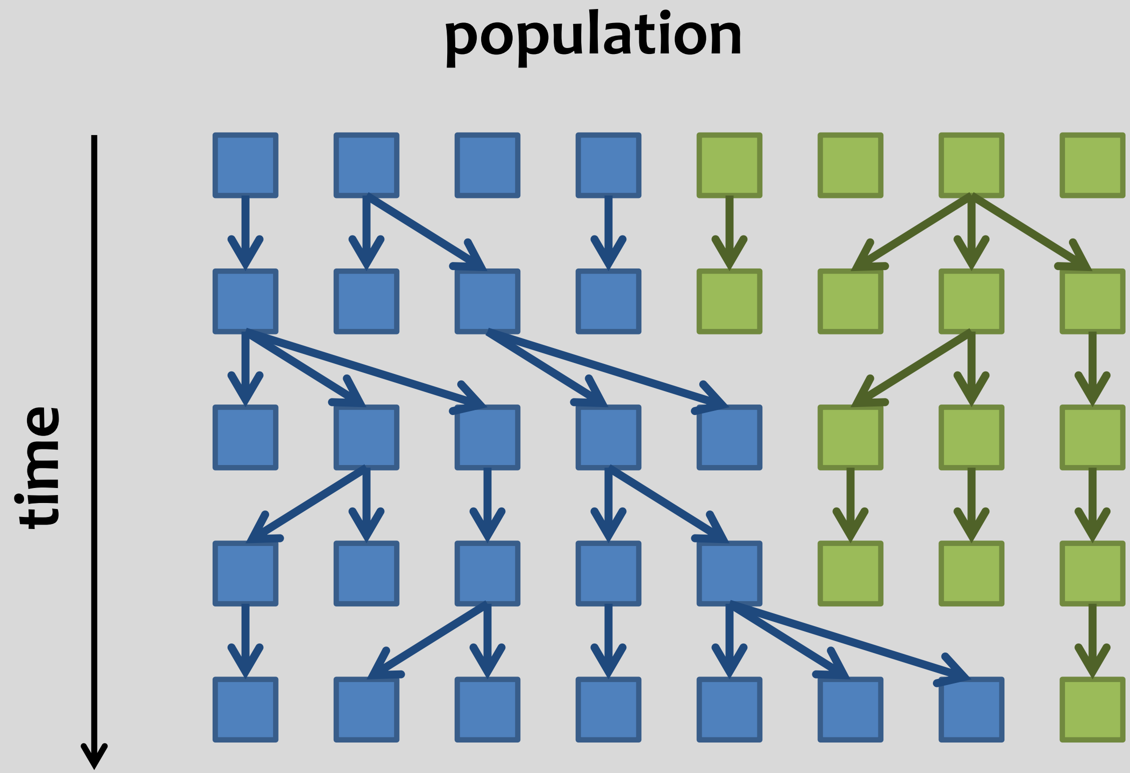
- ~~mutation~~
- ~~selection~~
- ~~migration~~
- **drift**



Basics of evolution

What are the forces shaping the evolution of organisms?

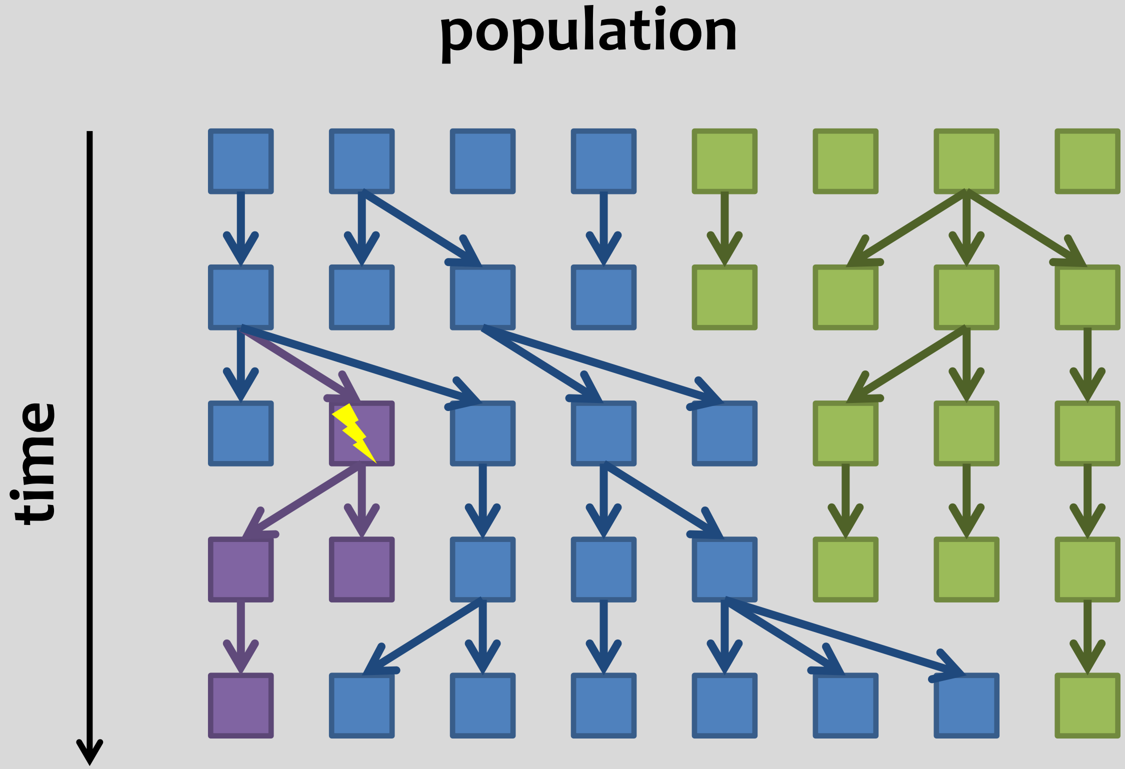
- ~~mutation~~
- **selection**
- ~~migration~~
- **drift**



Basics of evolution

What are the forces shaping the evolution of organisms?

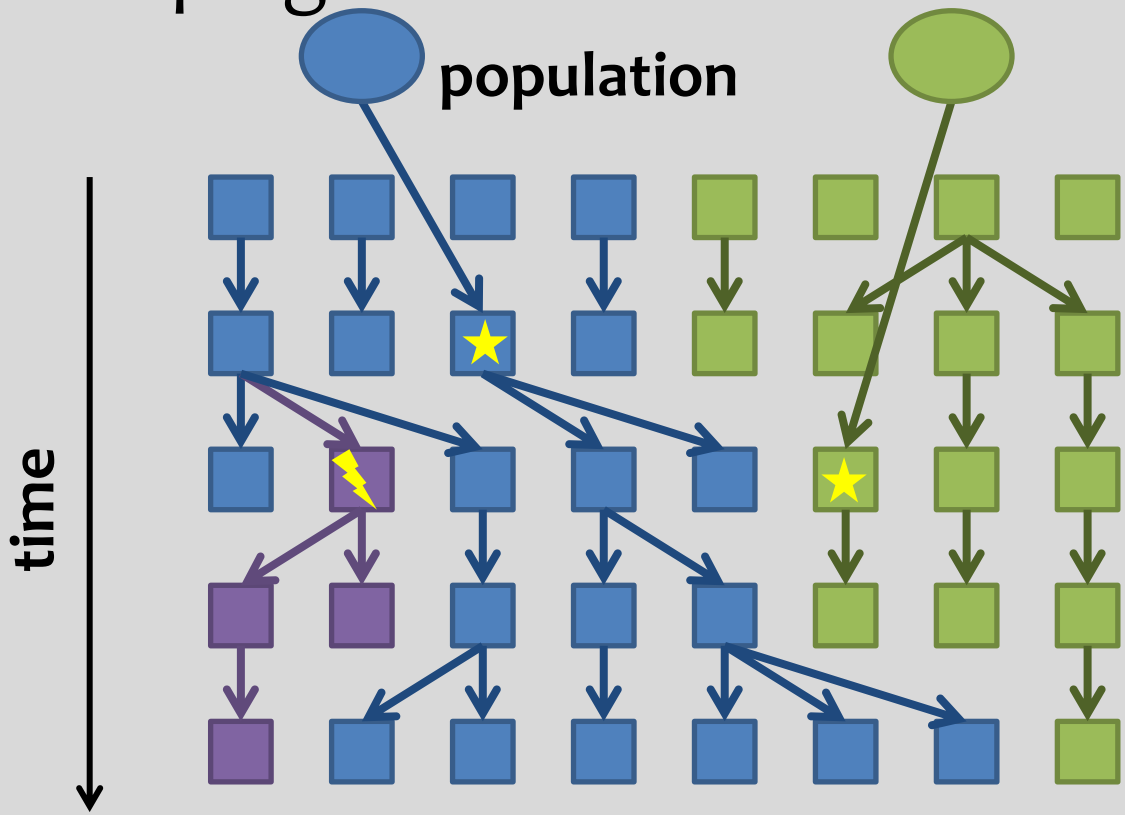
- **mutation**
- **selection**
- ~~**migration**~~
- **drift**



Basics of evolution

What are the forces shaping the evolution of organisms?

- **mutation**
- **selection**
- **migration**
- **drift**



Basics of evolution

What are the forces shaping the evolution of organisms?

- **mutation**: *new random variants*
- **selection**: *heterogeneous degrees of success*
- **migration**: *mixing with neighboring populations*
- **drift**: *randomness takes its toll*

Basics of evolution

What are the forces shaping the evolution of organisms?

- **mutation**: *new random variants*
- **selection**: *heterogeneous degrees of success*
- **migration**: *mixing with neighboring populations*
- **drift**: *randomness takes its toll*

Evolution shapes the distribution of **genotypes**

Genotype = set of **alleles** carried at different **loci**

Genotype × Environment = Phenotype

Basics of evolution

Population genetics formalism ($p + q = 1$)

Mutation

Selection

Migration

Drift

Basics of evolution

Population genetics formalism ($p + q = 1$)

Mutation $$p_{t+1} = \left(1 - \mu_{A \to a}\right) p_t + \mu_{a \to A} q_t$$

Selection

Migration

Drift

Basics of evolution

Population genetics formalism ($p + q = 1$)

Mutation $$p_{t+1} = \left(1 - \mu_{A \to a}\right) p_t + \mu_{a \to A} q_t$$

Selection $$p_{t+1} = w_A p_t / \bar{w}$$

Migration

Drift

Basics of evolution

Population genetics formalism ($p + q = 1$)

Mutation $$p_{t+1} = \left(1 - \mu_{A \to a}\right) p_t + \mu_{a \to A} q_t$$

Selection $$p_{t+1} = w_A p_t / \bar{w}$$

Migration $$p_{t+1} = \left(1 - m\right) p_t + m P_t$$

Drift

Basics of evolution

Population genetics formalism ($p + q = 1$)

Mutation $$p_{t+1} = \left(1 - \mu_{A\to a}\right) p_t + \mu_{a\to A} q_t$$

Selection $$p_{t+1} = w_A p_t / \bar{w}$$

Migration $$p_{t+1} = \left(1 - m\right) p_t + m P_t$$

Drift $$P\left[p_{t+1} = \frac{k}{N}\right] = \binom{N}{k} p_t^k q_t^{N-k}$$

Basics of evolution

Mutation / Selection / Migration / Drift

What else?

Basics of evolution

Mutation / Selection / Migration / Drift

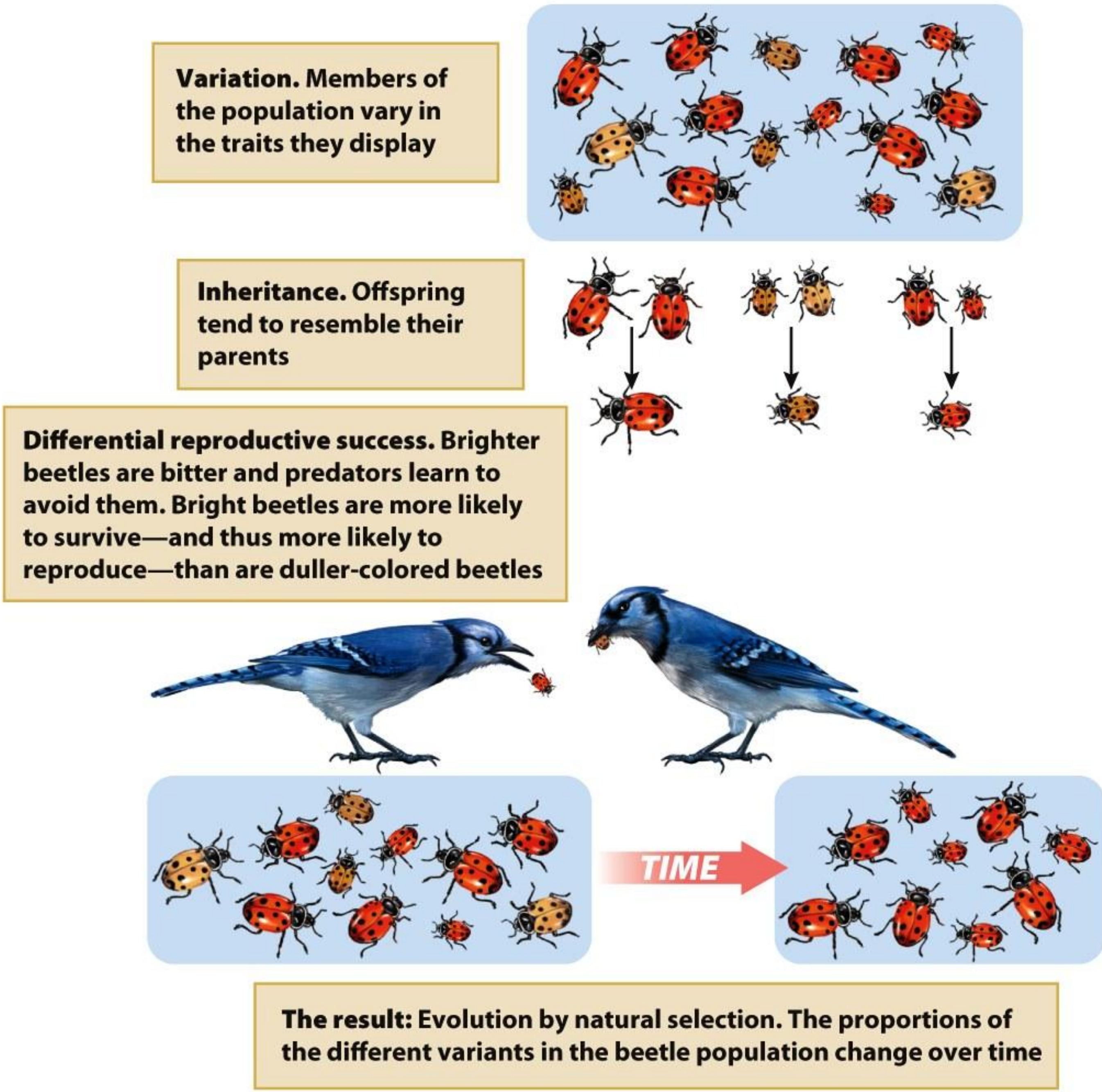
What else?

- Homogamy vs. panmixia (mating system)
- Dominance
- Recombination
- Epistasis (on selection)
- Plasticity (environmental dependence)
- Epigenetic effects

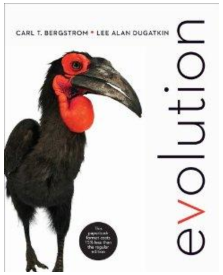
Basics of evolution

Conditions for the evolution of traits

- Differential success
- Standing variance of trait values
- Heritability of trait values



Evolution, 1/e Figure 3.2



Bergstrom & Dugatkin, "*Evolution*"

DEFINING ADAPTATION

Defining adaptation

VOLUME 68, NO. 1 MARCH 1993

THE QUARTERLY REVIEW *of* BIOLOGY

ADAPTATION AND THE GOALS OF EVOLUTIONARY RESEARCH

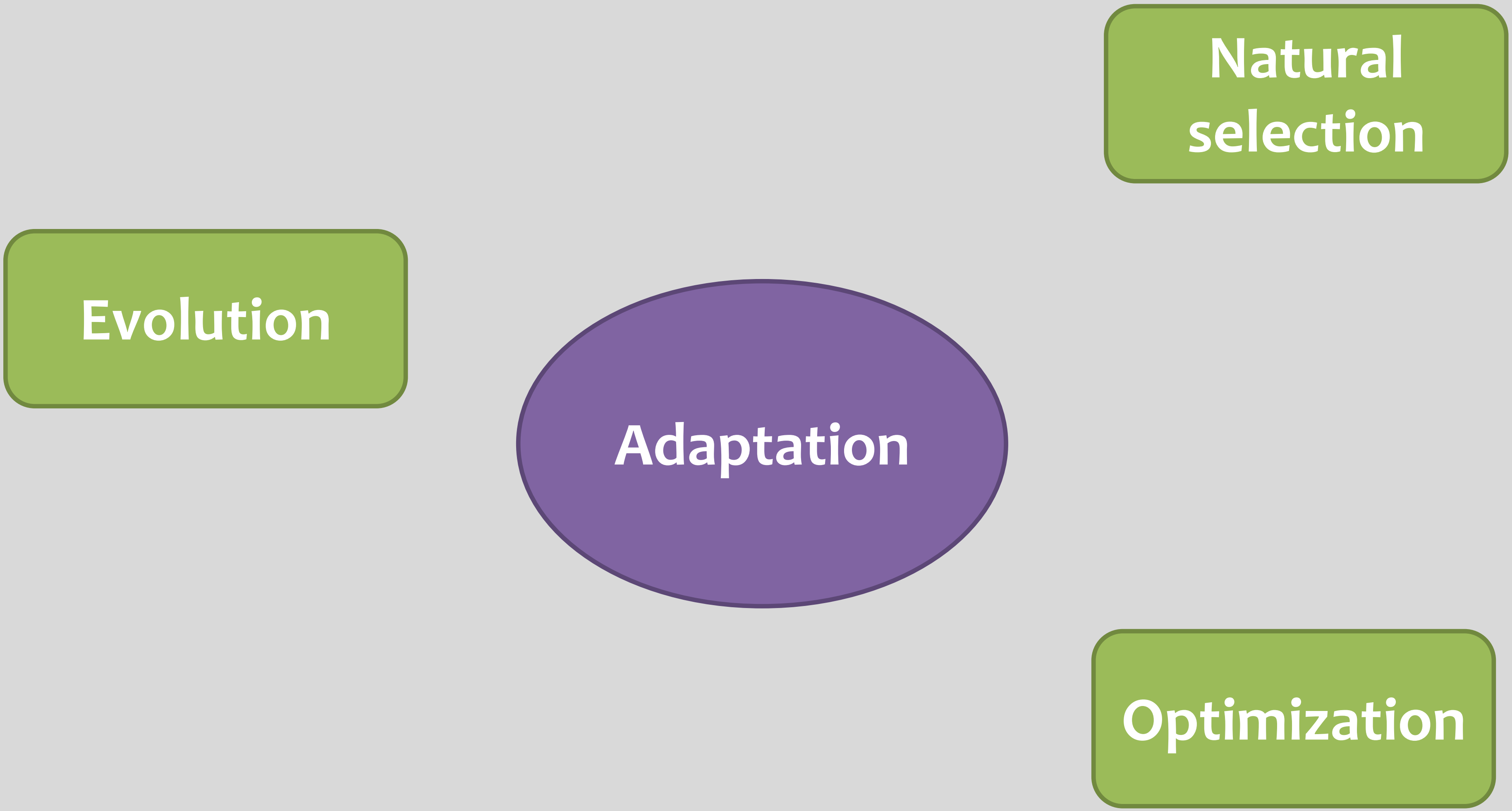
HUDSON KERN REEVE

Museum of Comparative Zoology, Harvard University
Cambridge, Massachusetts 02138 USA

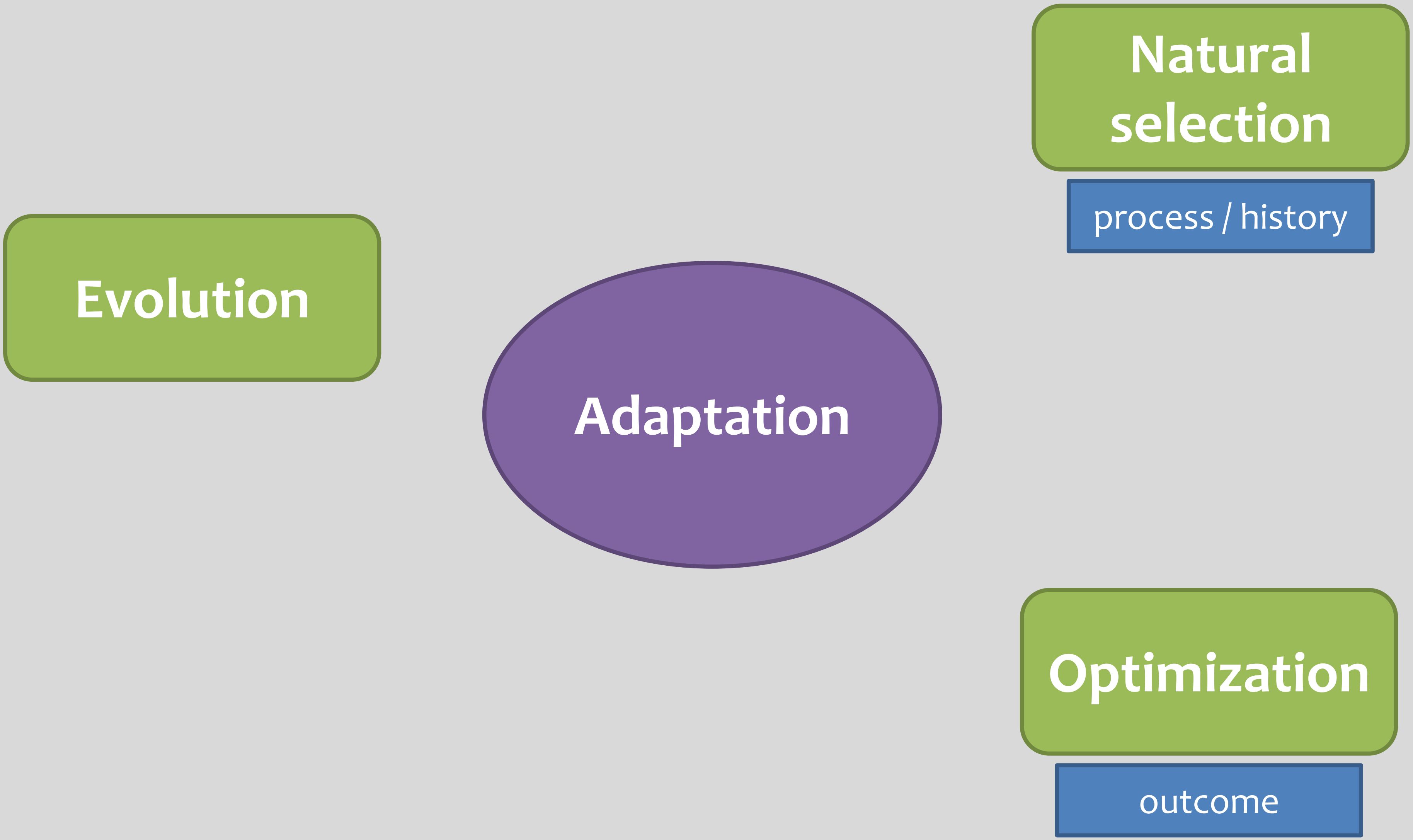
PAUL W. SHERMAN*

Section of Neurobiology and Behavior, Cornell University
Ithaca, New York 14853 USA

Defining adaptation



Defining adaptation



Defining adaptation

History-based definitions

- Features built by natural selection for their current role (Gould & Vrba)
- A derived character that evolved in response to a specific selective agent (Harvey & Pagel)
- Biological machinery or process shaped by natural selection to help solve one or more problems faced by the organism (Williams & Nesse)
- A is an adaptation for task T in population P iff A **became prevalent** in P because **there was selection** for A, where the selective advantage of A was due to the fact that A helped performed task T (Sober)

Defining adaptation

History-based definitions

– Features built by natural selection for their current role (Gould & Vrba)

Character arising through past natural selection

Problem: what character doesn't?

became prevalent in P because **there was selection** for A, where the selective advantage of A was due to the fact that A helped performed task T (Sober)

Defining adaptation

Nonhistorical definitions

– A feature of the organism which interacts operationally with some factor of its environment so that the individual survives and reproduces (Bock)

– Greater ecological-physiological efficiency than is achieved **by other members of the populations** (Mayr)

– An aspect of the developmental pattern which facilitates the survival and/or reproduction of its carrier in a certain succession of environments (Dobzhansky)

– A strategy that has the highest per capita growth given the conditions (Mitchell & Valone)

Defining adaptation

Nonhistorical definitions

– A feature of the organism which interacts operationally with some factor of its environment so

Character conferring the best fitness among available ones

Minor problem: can this happen?

(Dobzhansky)

– A strategy that has the highest per capita growth given the conditions (Mitchell & Valone)

Defining adaptation

A synthesis of definitions (Reeve & Sherman)

A phenotypic variant that results in the **highest fitness** among a **specified set** of variants in a **given environment**

Defining adaptation

A synthesis of definitions (**Reeve & Sherman**)

A phenotypic variant that results in the **highest fitness** among a **specified set** of variants in a **given environment**

- ✓ "optimization" in some sense
- ✓ among available variants (contingent on history)
- ✓ conditional on environmental state

Defining adaptation

A synthesis of definitions (Reeve & Sherman)

A phenotypic variant that results in the **highest fitness** among a **specified set** of variants in a **given environment**

Pending question:

what is fitness?

THE CONCEPT(S) OF FITNESS

The concept(s) of fitness

The simplest: growth = fitness

$$\frac{dN}{dt} = \underbrace{r(N)}_{\text{Growth rate}} N$$

$$N_{t+1} = \underbrace{\lambda(N_t)}_{\text{Reproductive ratio}} N_t$$

The concept(s) of fitness

The simplest: growth = fitness

$$\frac{dN}{dt} = \underbrace{r(N)}_{\text{Growth rate}} N \qquad N_{t+1} = \underbrace{\lambda(N_t)}_{\text{Reproductive ratio}} N_t$$

Problem: what if all genotypes grow or decline together?

⇨ distinguish absolute from relative growth rate

⇨ may depend on context / density / frequency

The concept(s) of fitness

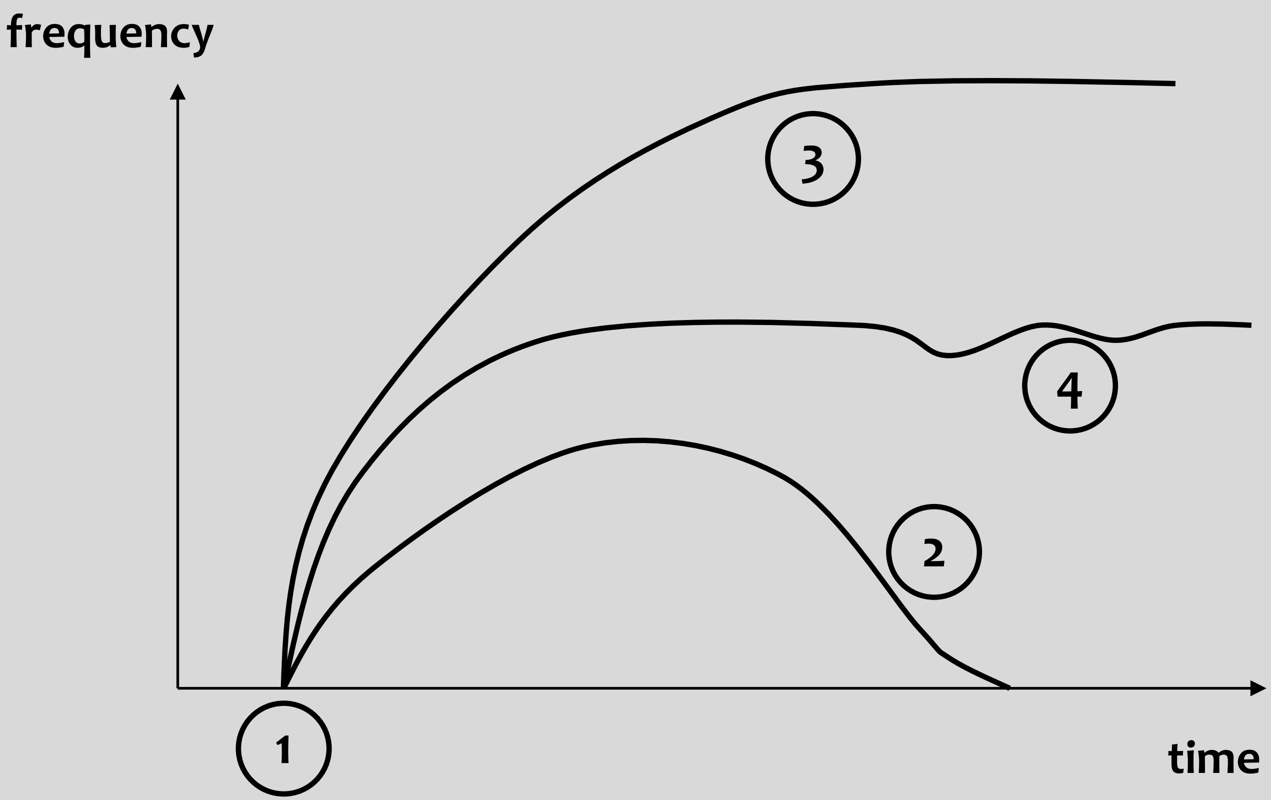
The simple: selection = fitness

$$\frac{dN}{dt} = r(N)N \qquad N_{t+1} = \lambda(N_t)N_t$$

$$\frac{df_i}{dt} = \underbrace{\left[r_i(\vec{N}) - \bar{r} \right]}_{\text{Relative growth rate}} f_i \qquad f_{it+1} = \frac{\lambda_i\left(\vec{N}_t\right)}{\bar{\lambda}\left(\vec{N}_t\right)} f_{it}$$

The concept(s) of fitness

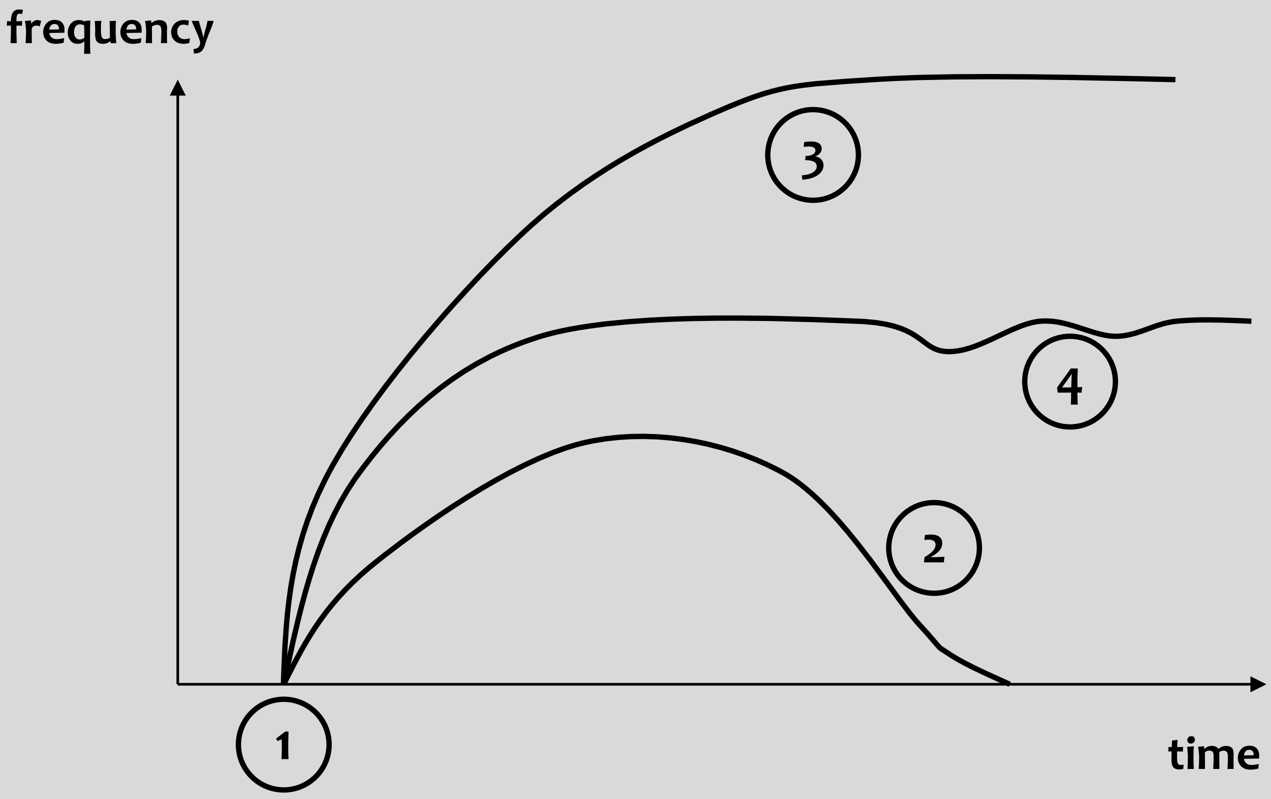
What for?



1. invasibility
2. persistence
3. fixation
4. coexistence

The concept(s) of fitness

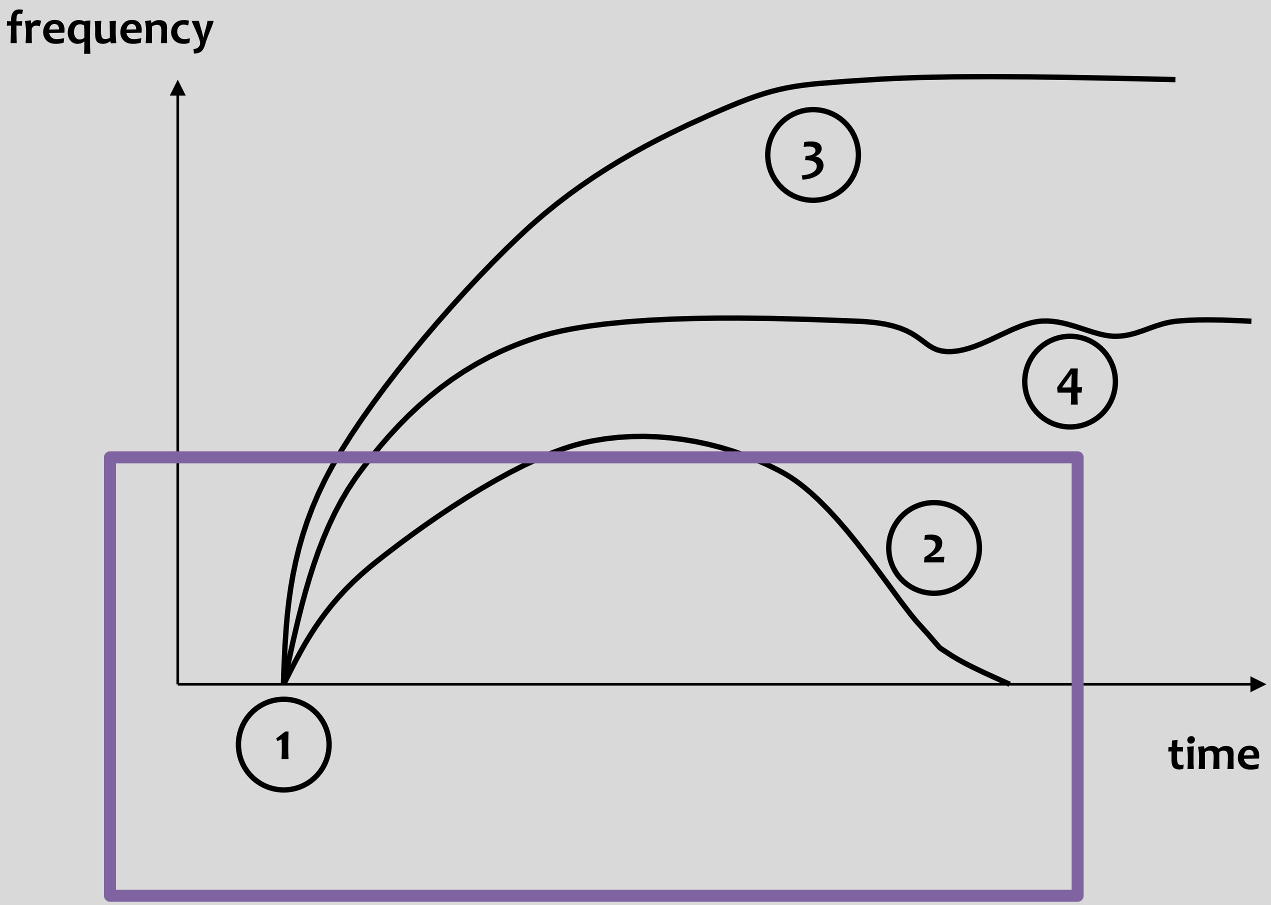
What for?



1. invasibility
2. persistence
3. ~~fixation~~
4. ~~coexistence~~

The concept(s) of fitness

What for?



1. invasibility
2. persistence
3. ~~fixation~~
4. ~~coexistence~~

Same problem: what happens with rare genotypes?

The concept(s) of fitness

The simple: **selection = fitness** when rare

$$\underbrace{\left(r_i(\vec{N}) - \overline{r}\right)_{f_i \to 0^+}}_{\text{Invasion fitness}}$$

The concept(s) of fitness

The complex: unstable absence = fitness

The concept(s) of fitness

The complex: **unstable absence = fitness**

$$\left(r_i(\vec{N}) - \bar{r} \right)_{f_i \to 0^+}$$

The concept(s) of fitness

The complex: unstable absence = fitness

$$\left(r_i(\vec{N}) - \bar{r}\right)_{f_i \to 0^+}$$

$$\frac{df_i}{dt} = \left[r_i(\vec{N}) - \bar{r}\right] f_i$$

The concept(s) of fitness

The complex: unstable absence = fitness

$$\left(r_i(\vec{N}) - \bar{r}\right)_{f_i \to 0^+}$$

$$\left.\frac{d\vec{f}}{dt}\right|_{f_i \approx 0} \approx \underbrace{\mathbf{J}.\vec{f}}$$

Jacobian matrix

$$g_i = \left(r_i - \bar{r}\right) f_i \qquad \mathbf{J} = \left(\partial g_i / \partial f_j\right)_{ij}$$

The concept(s) of fitness

The complex: unstable absence = fitness

$$\left.\frac{d\vec{f}}{dt}\right|_{f_i \approx 0} \approx \underbrace{\mathbf{J}}_{\text{Jacobian matrix}}.\vec{f}$$

More generally:

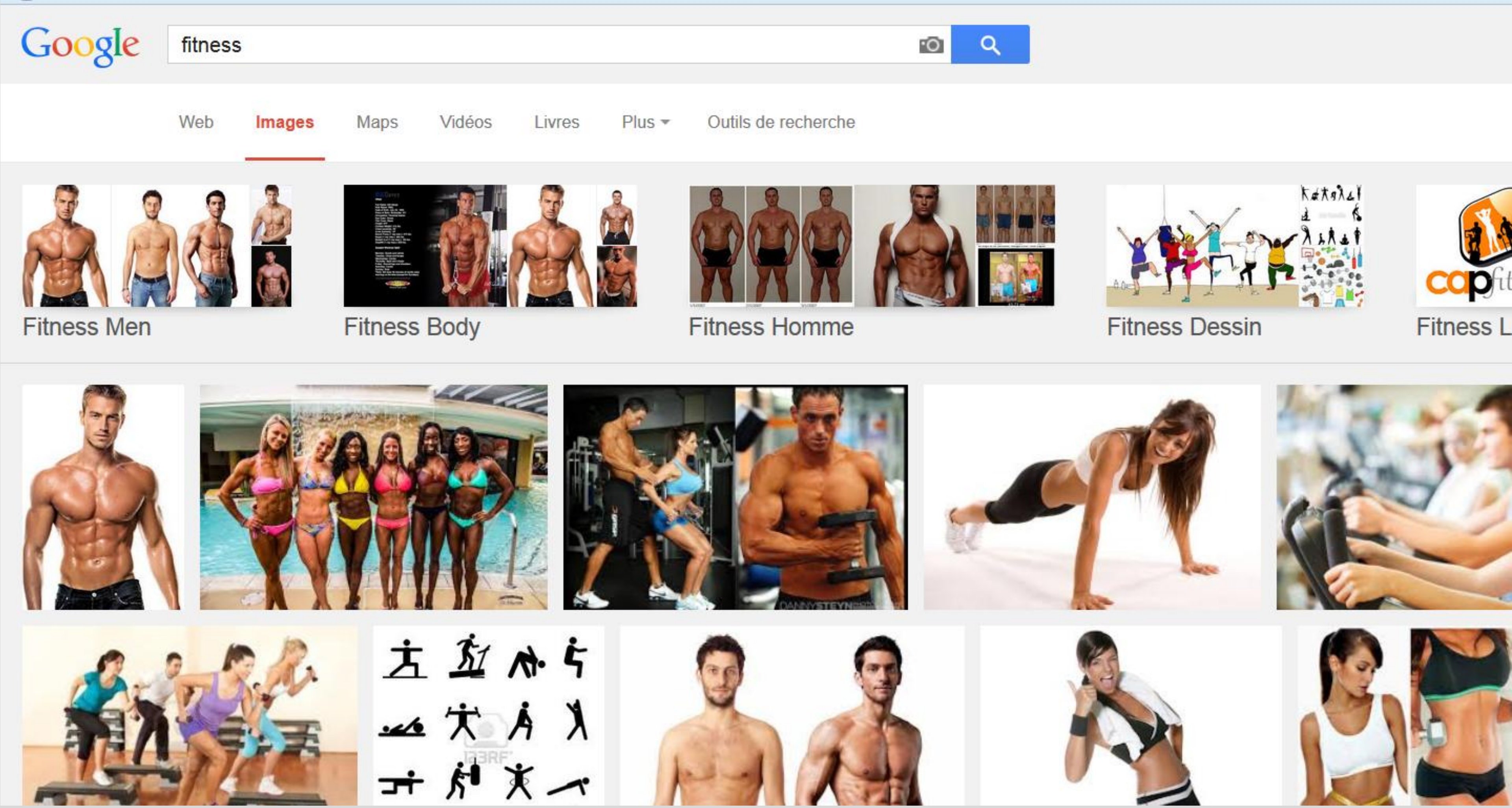
define invasion fitness as the leading eigenvalue of the Jacobian in the absence of the focal type

The concept(s) of fitness

Even more generally:

define invasion fitness as any criterion that qualifies whether the leading eigenvalue of the Jacobian in the absence of the focal type has negative real part

More than one fitness criterion might exist!



FITNESS IN DIFFERENT GUISES

Fitness in different guises

Population genetics fitness

With selection only

$$p_{it+1} = \frac{w_i\left(\vec{P}_t\right)}{\bar{w}\left(\vec{P}_t\right)} p_{it}$$

$$\lambda_i = \frac{w_i\left(\vec{P}^*\right)}{\bar{w}\left(\vec{P}^*\right)}$$

Fitness in different guises

Population genetics fitness

Divergent selection in habitats x and y

Life cycle: Reproduction, regulation, total migration

$$\lambda_i = q_x \frac{w_{ix}}{\bar{w}_x} + q_y \frac{w_{iy}}{\bar{w}_y}$$

Model = soft selection (Levene 1953)

Fitness in different guises

Population genetics fitness

Divergent selection in habitats x and y

Life cycle: Reproduction, total migration, regulation

$$\lambda_i = \frac{q_x w_{ix} + q_y w_{iy}}{q_x \bar{w}_x + q_y \bar{w}_y}$$

Model = hard selection (Dempster 1955; Ravigné et al. 2004)

Fitness in different guises

Population genetics fitness

Divergent selection + environmental variability

Use matrices for reproduction, migration, … events

$$\lambda = \max\left[\mu \in \mathrm{Sp}\left\{\mathbf{R.E.S.D}\right\}\right]$$ **Levene's model**

$$\lambda = \max\left[\mu \in \mathrm{Sp}\left\{\mathbf{R.E.D.S}\right\}\right]$$ **Ravigné's model**

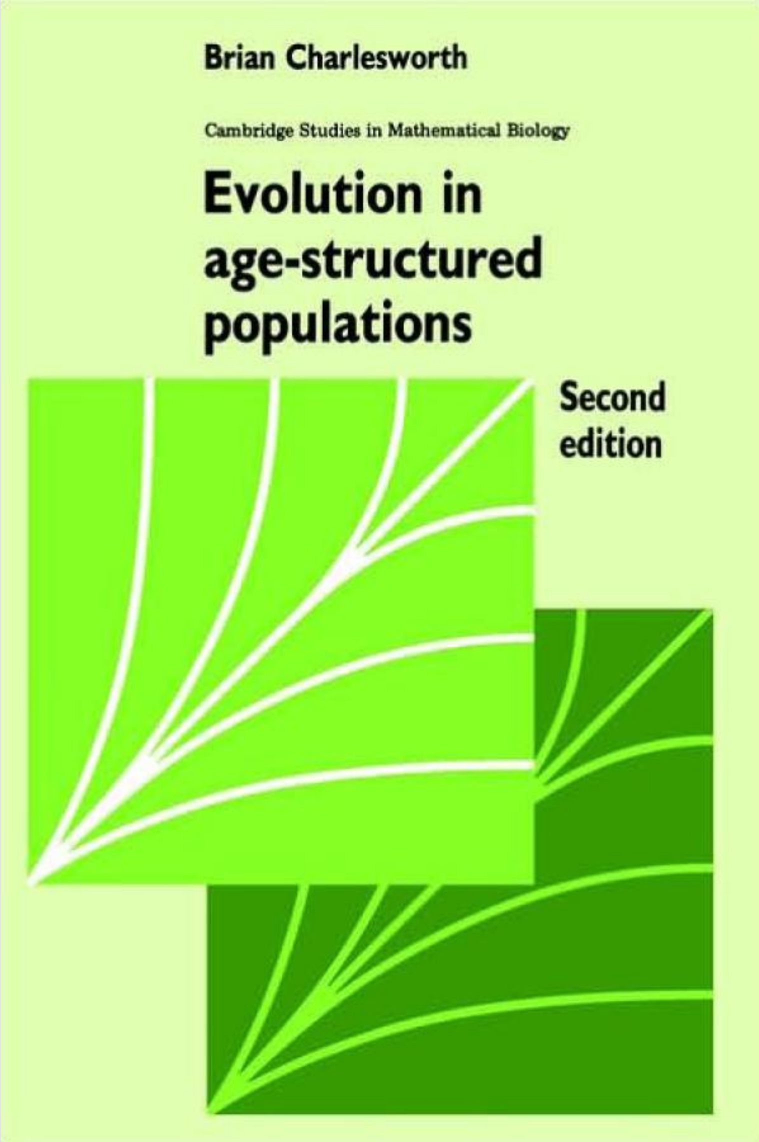
$$\lambda = \max\left[\mu \in \mathrm{Sp}\left\{\mathbf{E.D.S}\right\}\right]$$ **Dempster's model**

…

Massol 2013

Fitness in different guises

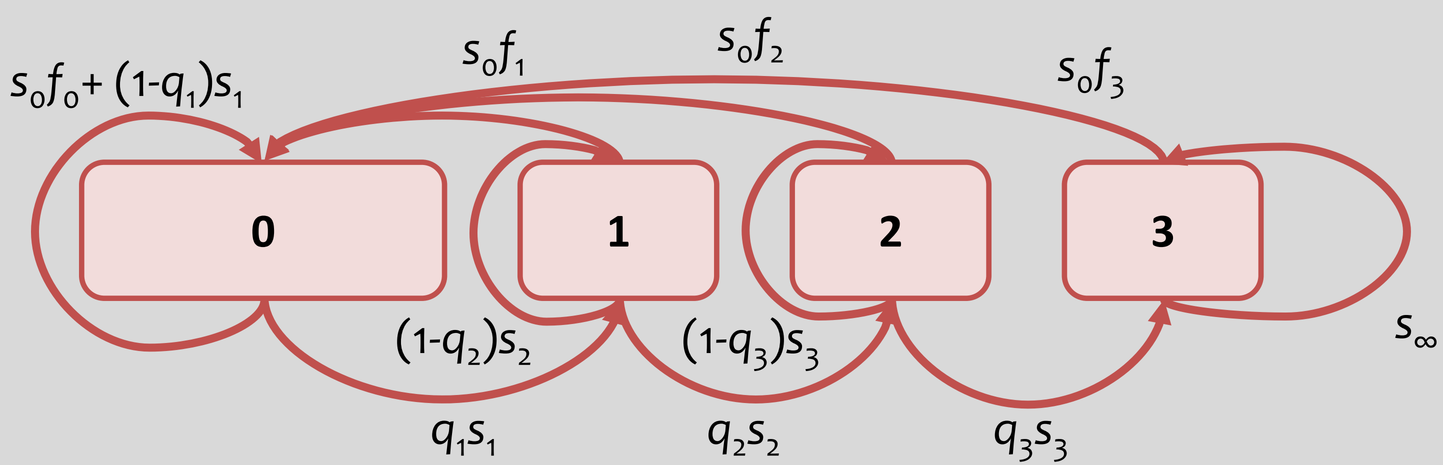
Stage-structured populations



Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \begin{pmatrix} s_0 f_0 + (1-q_1)s_1 & s_0 f_1 & s_0 f_2 & s_0 f_3 \\ q_1 s_1 & (1-q_2)s_2 & 0 & 0 \\ 0 & q_2 s_2 & (1-q_3)s_3 & 0 \\ 0 & 0 & q_3 s_3 & s_\infty \end{pmatrix} \mathbf{N}_t$$



Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \big(\underbrace{\mathbf{F}}_{}+\underbrace{\mathbf{G}}_{}\big)\mathbf{N}_t$$

Fecundity + Survival/change in stage

$$\mathbf{N}_{t+1} = \begin{pmatrix} s_0 f_0 + (1-q_1)s_1 & s_0 f_1 & s_0 f_2 & s_0 f_3 \\ q_1 s_1 & (1-q_2)s_2 & 0 & 0 \\ 0 & q_2 s_2 & (1-q_3)s_3 & 0 \\ 0 & 0 & q_3 s_3 & s_\infty \end{pmatrix} \mathbf{N}_t$$

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \underbrace{(\mathbf{F}}_{} + \underbrace{\mathbf{G})}_{}\mathbf{N}_t$$

Fecundity + Survival/change in stage

$$\mathbf{F} = s_0 \begin{pmatrix} f_0 & f_1 & f_2 & f_3 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} = \mathbf{e}_0 \mathbf{f}^T$$

$$\mathbf{e}_0 = (1, 0, 0, 0)$$

$$\mathbf{f} = s_0 (f_0, f_1, f_2, f_3)$$

$$\mathbf{G} = \begin{pmatrix} (1-q_1)s_1 & 0 & 0 & 0 \\ q_1 s_1 & (1-q_2)s_2 & 0 & 0 \\ 0 & q_2 s_2 & (1-q_3)s_3 & 0 \\ 0 & 0 & q_3 s_3 & s_\infty \end{pmatrix}$$

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \underbrace{(\mathbf{F}}_{} + \underbrace{\mathbf{G})}_{}\mathbf{N}_t$$

Fecundity + Survival/change in stage

Formula for fitness

(≠ maximal eigenvalue)

$$\mathbf{F} = \mathbf{e}_0 \mathbf{f}^T$$

$$\mathbf{e}_0 = (1,0,0,0)$$

$$\mathbf{f} = s_0 (f_0, f_1, f_2, f_3)$$

$$W = \mathbf{f}^T . (\mathbf{I} - \mathbf{G})^{-1} . \mathbf{e}_0$$

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \left(\mathbf{F} + \mathbf{G}\right)\mathbf{N}_t$$

Fecundity + Survival/change in stage

Formula for fitness

(≠ maximal eigenvalue)

Time passed in each stage

$$\mathbf{F} = \mathbf{e}_0 \mathbf{f}^T$$

$$W = \mathbf{f}^T . \left(\mathbf{I} - \mathbf{G}\right)^{-1} . \mathbf{e}_0$$

$$\mathbf{e}_0 = \left(1,0,0,0\right)$$

$$\mathbf{f} = s_0 \left(f_0, f_1, f_2, f_3\right)$$

Stage-wise fecundity

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = (\mathbf{F} + \mathbf{G})\mathbf{N}_t$$

demonstration, french way

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \left(\mathbf{F} + \mathbf{G}\right)\mathbf{N}_t$$

$$\mathbf{F} + \mathbf{G} - \lambda\mathbf{I} = \left(\mathbf{I} - \mathbf{G}\right)\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - 1)\mathbf{I}\right) - \mathbf{I}\right]$$

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \left(\mathbf{F} + \mathbf{G}\right)\mathbf{N}_t$$

$$\mathbf{F} + \mathbf{G} - \lambda\mathbf{I} = \left(\mathbf{I} - \mathbf{G}\right)\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - 1)\mathbf{I}\right) - \mathbf{I}\right]$$

$$\lambda \in \mathrm{Sp}\left[\mathbf{F} + \mathbf{G}\right] \Leftrightarrow 1 \in \mathrm{Sp}\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - 1)\mathbf{I}\right)\right]$$

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \left(\mathbf{F} + \mathbf{G}\right)\mathbf{N}_t$$

$$\mathbf{F} + \mathbf{G} - \lambda\mathbf{I} = \left(\mathbf{I} - \mathbf{G}\right)\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - \mathbf{1})\mathbf{I}\right) - \mathbf{I}\right]$$

$$\lambda \in \mathrm{Sp}\left[\mathbf{F} + \mathbf{G}\right] \Leftrightarrow 1 \in \mathrm{Sp}\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - \mathbf{1})\mathbf{I}\right)\right]$$

$$\max\left\{\mathrm{Sp}\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\left(\mathbf{F} - (\lambda - \mathbf{1})\mathbf{I}\right)\right]\right\}$$ is a strictly decreasing function of λ

Fitness in different guises

Stage-structured populations

$$\mathbf{N}_{t+1} = \left(\mathbf{F}+\mathbf{G}\right)\mathbf{N}_t$$

$$\mathbf{F}+\mathbf{G}-\lambda\mathbf{I} = \left(\mathbf{I}-\mathbf{G}\right)\left[\left(\mathbf{I}-\mathbf{G}\right)^{-1}\left(\mathbf{F}-(\lambda-\mathbf{1})\mathbf{I}\right)-\mathbf{I}\right]$$

$$\lambda \in \mathrm{Sp}\left[\mathbf{F}+\mathbf{G}\right] \Leftrightarrow 1 \in \mathrm{Sp}\left[\left(\mathbf{I}-\mathbf{G}\right)^{-1}\left(\mathbf{F}-(\lambda-\mathbf{1})\mathbf{I}\right)\right]$$

$$\max\left\{\mathrm{Sp}\left[\left(\mathbf{I}-\mathbf{G}\right)^{-1}\left(\mathbf{F}-(\lambda-\mathbf{1})\mathbf{I}\right)\right]\right\}$$ is a strictly decreasing function of λ

$$\lambda > 1 \in \mathrm{Sp}\left[\mathbf{F}+\mathbf{G}\right] \Leftrightarrow \max\left\{\mathrm{Sp}\left[\left(\mathbf{I}-\mathbf{G}\right)^{-1}\mathbf{F}\right]\right\} > 1$$

Fitness in different guises

Stage-structured populations

$$\lambda > 1 \in \mathrm{Sp}\left[\mathbf{F}+\mathbf{G}\right] \Leftrightarrow \max\left\{\mathrm{Sp}\left[\left(\mathbf{I}-\mathbf{G}\right)^{-1}\mathbf{F}\right]\right\} > 1$$

$$\mathbf{F} = \mathbf{e}_0 \mathbf{f}^T$$

$$\mathbf{e}_0 = \left(1,0,0,0\right)$$

$$\mathbf{f} = s_0\left(f_0, f_1, f_2, f_3\right)$$

Fitness in different guises

Stage-structured populations

$$\lambda > 1 \in \mathrm{Sp}\left[\mathbf{F} + \mathbf{G}\right] \Leftrightarrow \max\left\{\mathrm{Sp}\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\mathbf{F}\right]\right\} > 1$$

$$\mathbf{F} = \mathbf{e}_0 \mathbf{f}^T$$

$$\mathbf{e}_0 = \left(1, 0, 0, 0\right)$$

$$\mathbf{f} = s_0\left(f_0, f_1, f_2, f_3\right)$$

$$\mathrm{Sp}\left[\left(\mathbf{I} - \mathbf{G}\right)^{-1}\mathbf{F}\right] = \left\{0, \underbrace{\mathbf{f}^T\left(\mathbf{I} - \mathbf{G}\right)^{-1}\mathbf{e}_0}_{\text{Fitness!}}\right\}$$

Fitness!

w

Fitness in different guises

Stage-structured populations

$$\mathbf{F} = \mathbf{e}_0 \mathbf{f}^T$$

$$\mathbf{e}_0 = (1,0,0,0)$$

$$\mathbf{f} = s_0 \left(f_0, f_1, f_2, f_3 \right)$$

$$w = \mathbf{f}^T.\left(\mathbf{I} - \mathbf{G}\right)^{-1}.\mathbf{e}_0$$

A demographic re-interpretation

$$\mathbf{f}^T \left(\mathbf{I} - \mathbf{G}\right)^{-1} \mathbf{e}_0 = \overbrace{\sum_{k>0} \underbrace{\mathbf{f}^T \mathbf{G}^k \mathbf{e}_0}_{\text{Offspring produced at time } k}}^{\text{Lifetime offspring production}}$$

Thank you for your attention!

Further reading

Evolution, adaptation

Grafen A. (1999). Formal Darwinism, the individual-as-maximizing-agent analogy and bet-hedging. *Proc R Soc Lond B Biol Sci*, 266, 799-803.

Maynard Smith J. (1989). *Evolutionary Genetics.* Oxford University Press, Oxford.

Reeve H.K. & Sherman P.W. (1993). Adaptation and the goals of evolutionary research. *Q Rev Biol*, 1-32.

Further reading

Fitness

Caswell H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation, Second edition.* 2nd edn. Sinauer Associates, Inc. Publishers, Sunderland, Massachussets.

Charlesworth B. (1994). *Evolution in age-structured populations, Second edition.* 2nd edn. Cambridge University Press, Cambridge.

Diekmann O., Heesterbeek J.A.P. & Metz J.A.J. (1990). On the definition and the computation of the basic reproduction ratio R_0 in models for infectious diseases in heterogeneous populations. *J Math Biol,* 28, 365-382.

Roughgarden J. (1979). *Theory of Population Genetics and Evolutionary Ecology: an Introduction.* MacMillan publishing Co., Inc.

Further reading

Selection & population genetics

de Meeus T., Michalakis Y., Renaud F. & Olivieri I. (1993). Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol Ecol*, 7, 175-198.

Débarre F. & Gandon S. (2011). Evolution in heterogeneous environments: between soft and hard selection. *Am Nat*, 177, E84-E97.

Ravigné V., Olivieri I. & Dieckmann U. (2004). Implications of habitat choice for protected polymorphisms. *Evol Ecol Res*, 6, 125-145.

Wallace B. (1975). Hard and soft selection revisited. *Evolution*, 29, 465-473.