Selection and Adaptation

Outline

- Evidence for evolution
- Selection and adaptation
- Variation:
  - Mutation
  - Recombination
  - Genetic Drift

A mathematical approach

What is evolution?

- Evolution is change in gene frequencies

The Ingredients in Darwin’s theory

- Populations of replicating individuals

- Heritable variation

- Differential reproduction

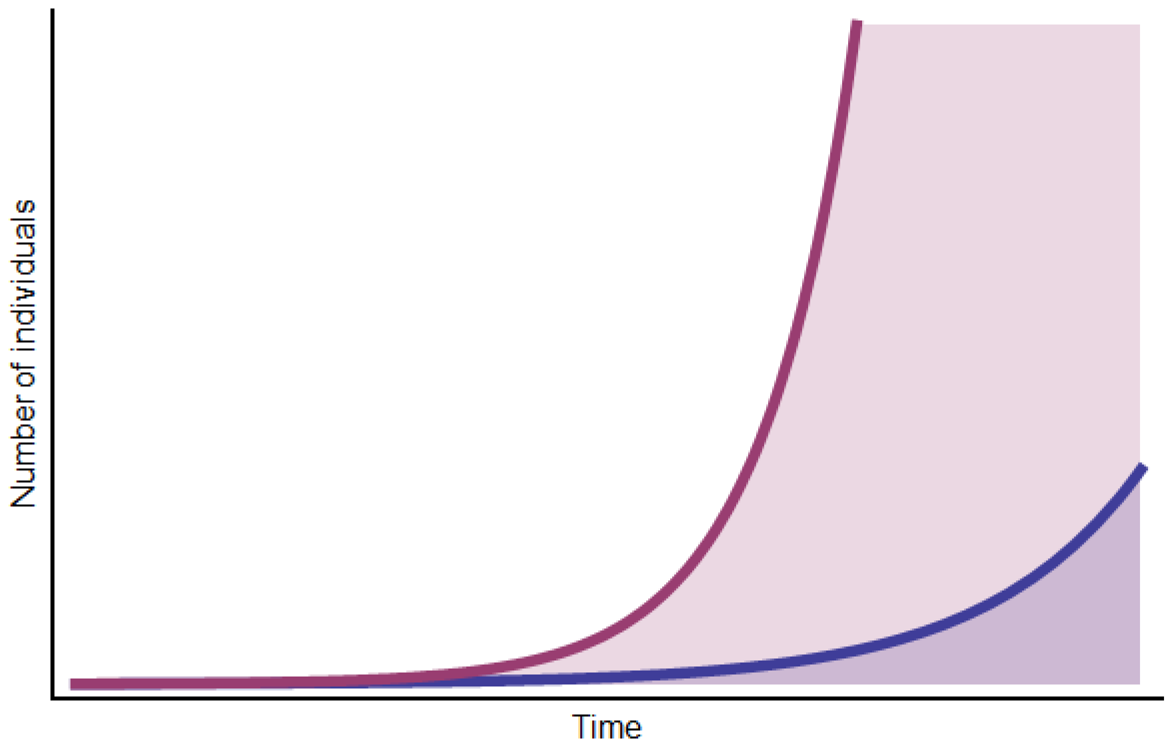
Nothing special about biological systems

- The basic ingredients can and are applied to many other systems:
  - Evolutionary computation
  - Artificial life
  - Evolutionary art
  - Memetics
  - Evolutionary epistemology
  - …

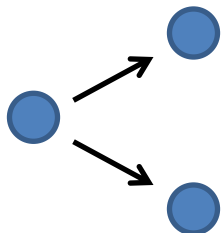
Replicators

- Entities that have the ability to reproduce or that are copied.
  - Organisms
  - RNA ribozymes
  - Computer programs
  - …

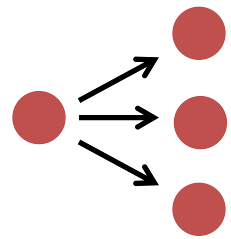
Differential reproduction



The replicator equation



$n_a(t+1) = 2n_a(t)$

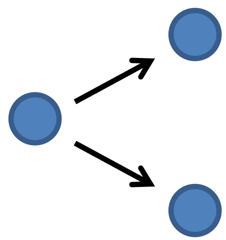


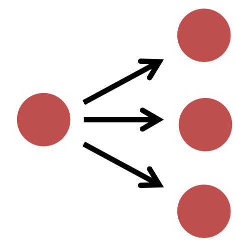
$n_A(t+1) = 3n_A(t)$

$$\begin{aligned} n_A(t+1) &= W_A n_A(t) \\ n_a(t+1) &= W_a n_a(t) \end{aligned}$$

$$\begin{aligned} p_A &= \frac{n_A}{n_A + n_a} \\ p_a &= \frac{n_a}{n_A + n_a} \end{aligned}$$

The replicator equation



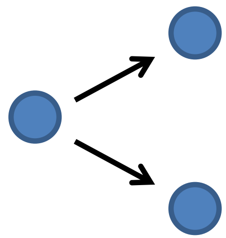


$$n_a(t+1) = W_a n_a(t) \qquad n_A(t+1) = W_A n_A(t)$$

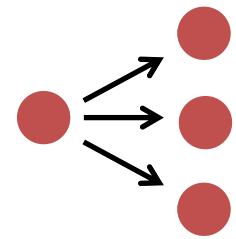
$$\begin{aligned} p(t+1) &= \frac{n_A(t+1)}{n_A(t+1)+n_a(t+1)} \\ &= \frac{W_A n_A(t)}{W_A n_A(t) + W_a n_a(t)} \end{aligned}$$

$$\begin{aligned} p(t+1) &= \frac{W_A p(t)}{W_A p(t) + W_a(1-p(t))} \\ &= \frac{W_A}{\overline{W}} p(t) \end{aligned}$$

The replicator equation



$$n_a(t+1) \quad = \quad W_a n_a(t)$$



$$n_A(t+1) \quad = \quad W_A n_A(t)$$

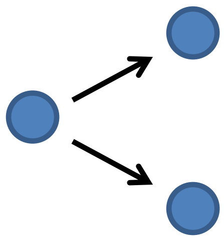
Mean Fitness

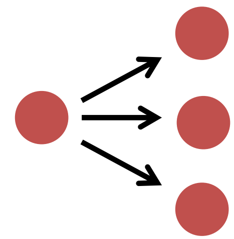
$$\overline{W} = W_A p(t) + W_a(1 - p(t))$$

Mean number of offspring

The absolute numbers do not matter: only relative differences are important

The replicator equation

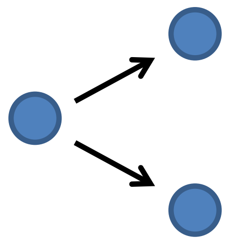


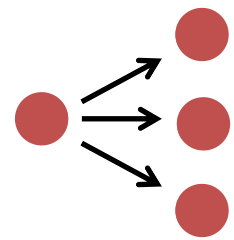


$$n_a(t+1) \quad = \quad W_a n_a(t) \qquad\qquad n_A(t+1) \quad = \quad W_A n_A(t)$$

$$\begin{aligned} \Delta p &= p(t+1) - p(t) \\ &= \frac{W_A}{\overline{W}} p(t) - p(t) \\ & \frac{W_A - W_a}{\overline{W}} p(1-p) \end{aligned}$$

The replicator equation

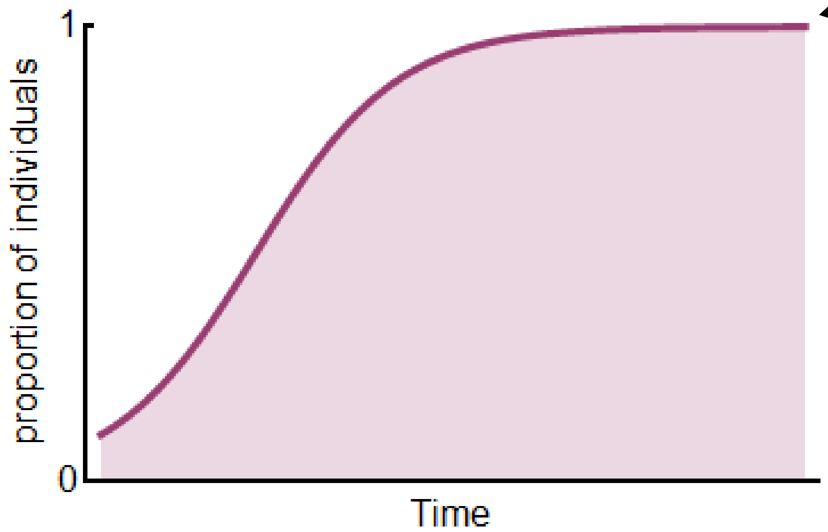




$$n_a(t+1) \quad = \quad W_a n_a(t) \qquad\qquad n_A(t+1) \quad = \quad W_A n_A(t)$$

$$\Delta p_{t+1} \quad = \quad \frac{\Delta W}{\overline{W}} p_t(1-p_t)$$

Fixation of allele A



What is fitness?

- Doesn't mean just differential reproduction under exponential growth
  - Differential reproduction can be due to many differences:
    - Differential death
    - Different life cycles
  - Populations do not need to be in exponential growth:
    - Constant population size
    - Changing population sizes

Many genes:
additive traits

$$z = \alpha_1 X_1 + \alpha_2 X_2 + ...+ = \sum \alpha_i X_i$$

$X_1 X_2$	trait value	frequency
00	0	$(1-p_1)(1-p_2)$
10	α_1	$p_1(1-p_2)$
01	α_2	$(1-p_1)p_2$
11	$\alpha_1 + \alpha_2$	$p_1 p_2$

Many genes: additive traits

$$z = \alpha_1 X_1 + \alpha_2 X_2 + ... + = \sum \alpha_i X_i$$

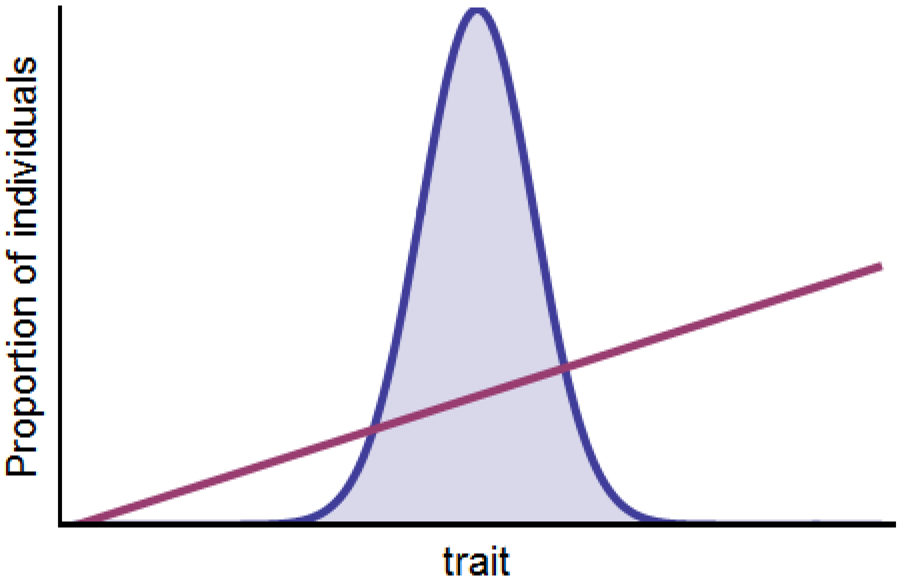
The mean of the trait is:

$$\overline{z} = \alpha_1 p_1 + \alpha_2 p_2 + ... = \sum \alpha_i p_i$$

The variance of the trait is:

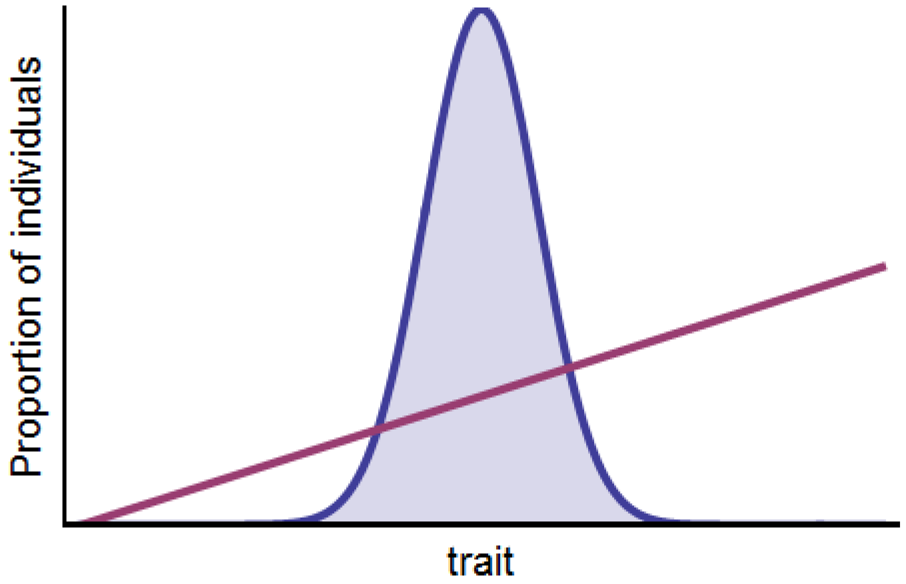
$$Var(z) = \sum \alpha_i^2 p_i (1 - p_i)$$

Effect of selection:



$$\Delta p_i = \beta \alpha_i p_i (1 - p_i)$$

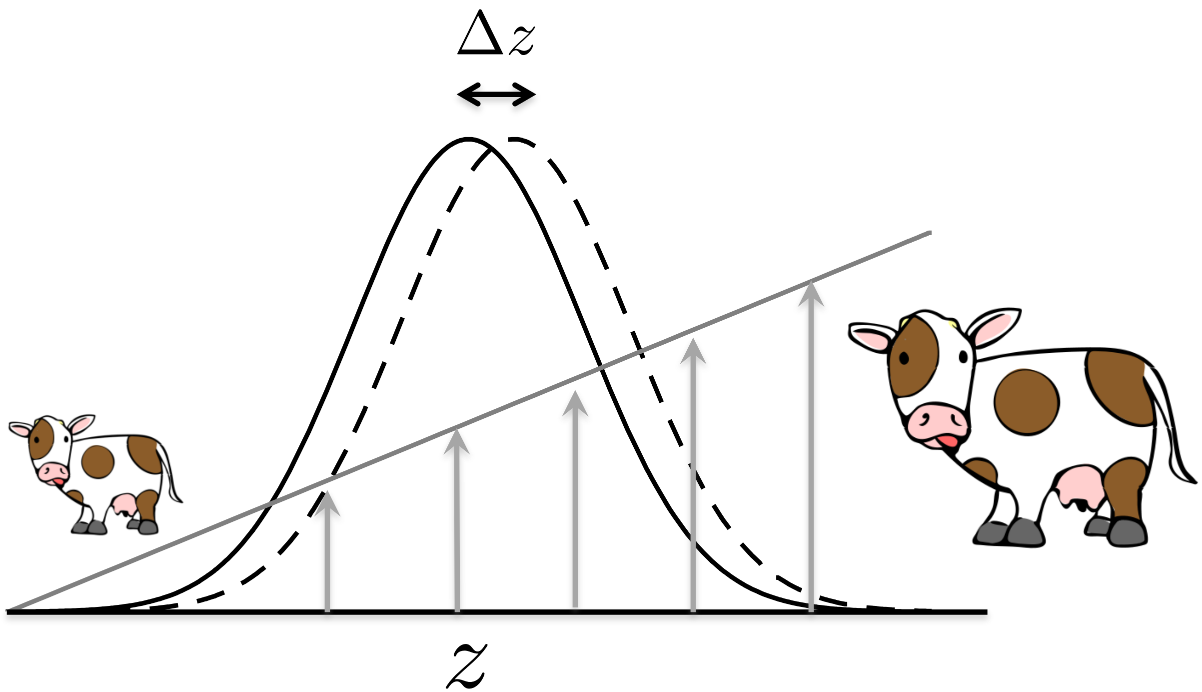
Effect of selection:



$$\Delta \overline{z} = \sum \alpha_i \Delta p_i$$

$$\Delta \overline{z} = \beta \sum \alpha_i^2 p_i (1 - p_i)$$

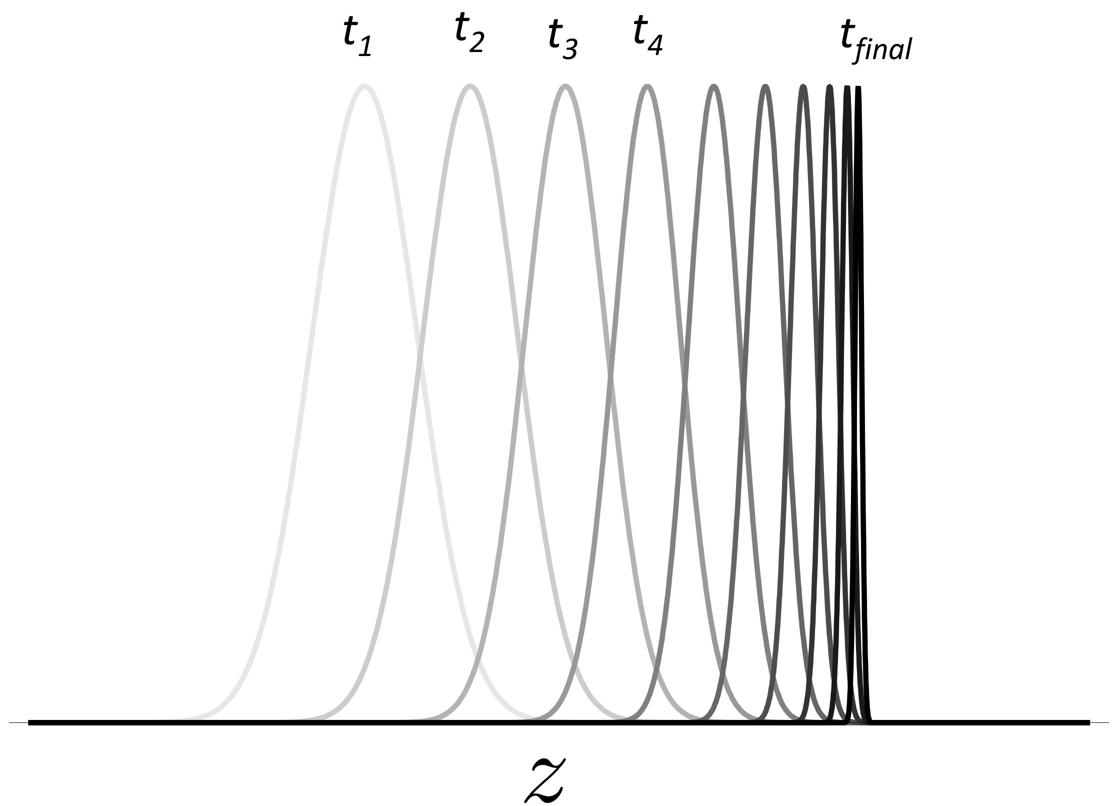
Selection on Variation
Fisher's fundamental theorem



$$\Delta z = \beta \, \mathrm{Var}(z)$$

The response of a population to selection is proportional to the (additive) variance in fitness

The fuel of selection is variation



Can we calculate the total response of a population?

$$u(p_0) = \frac{1-e^{2Nsp_0}}{1-e^{2Ns}} \approx p_0 + p_0(1-p_0)Ns$$

$$\begin{aligned} R_\infty &= \sum_i \alpha_i (u(p_0) - p_0) \\ &\approx \sum_i \alpha_i p_0 (1-p_0) Ns \\ &= \beta N \sum_i \alpha_i^2 p_0 (1-p_0) \\ &= \beta N V_A^0 \end{aligned}$$

Can we calculate the total response of a population?

$$\begin{aligned} \langle \Delta p_i \rangle &= 0 \\ \langle \Delta p_i^2 \rangle &= \frac{p_i(1-p_i)}{N} \end{aligned}$$

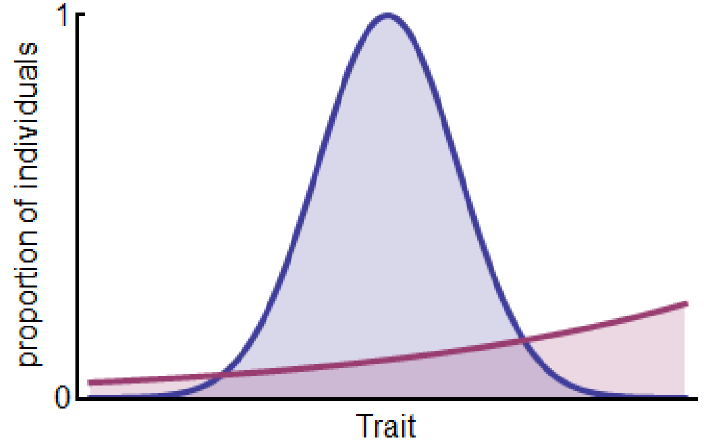
$$\langle (pq)_i^{t+1} \rangle = (p + \Delta p)(1 - p - \Delta p) = (1 - F)\,(pq)_i^t$$

$$\langle V_A^{t+1} \rangle = \left(1 - \frac{1}{N}\right) V_A^t$$

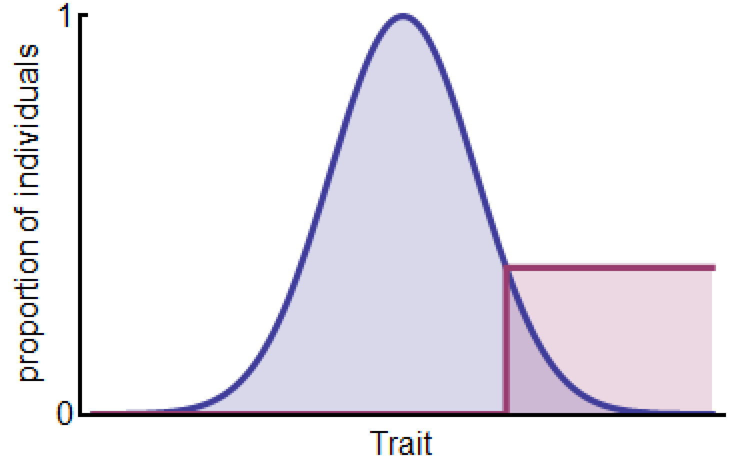
$$\begin{aligned} R_\infty &= \beta \sum_{t=0}^{\infty} V_A^t = \beta \sum_{t=0}^{\infty} V_A^0 \left(1 - \frac{1}{N}\right)^t \\ &= \beta N V_A^0 \end{aligned}$$

Different Forms of Selection

- Directional Selection

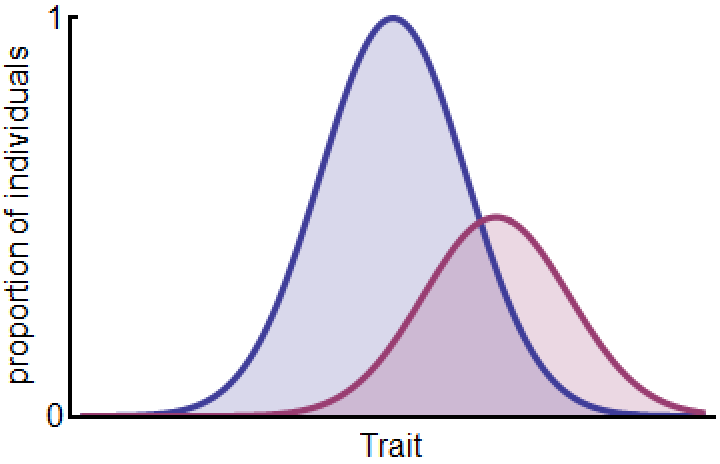


- Truncation Selection

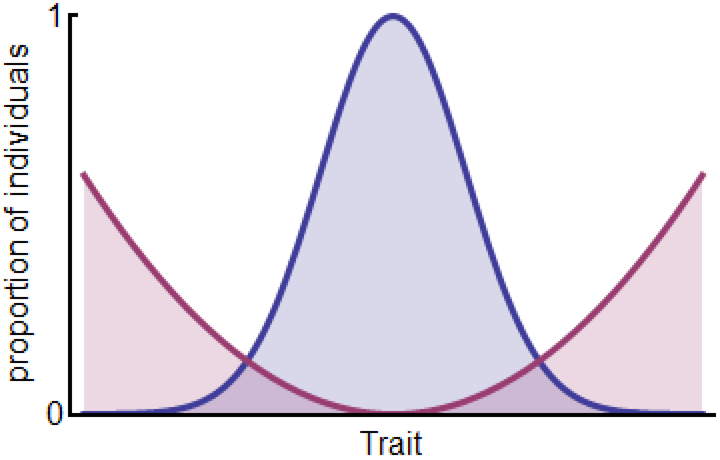


Different Forms of Selection

- Stabilizing Selection



- Disruptive selection



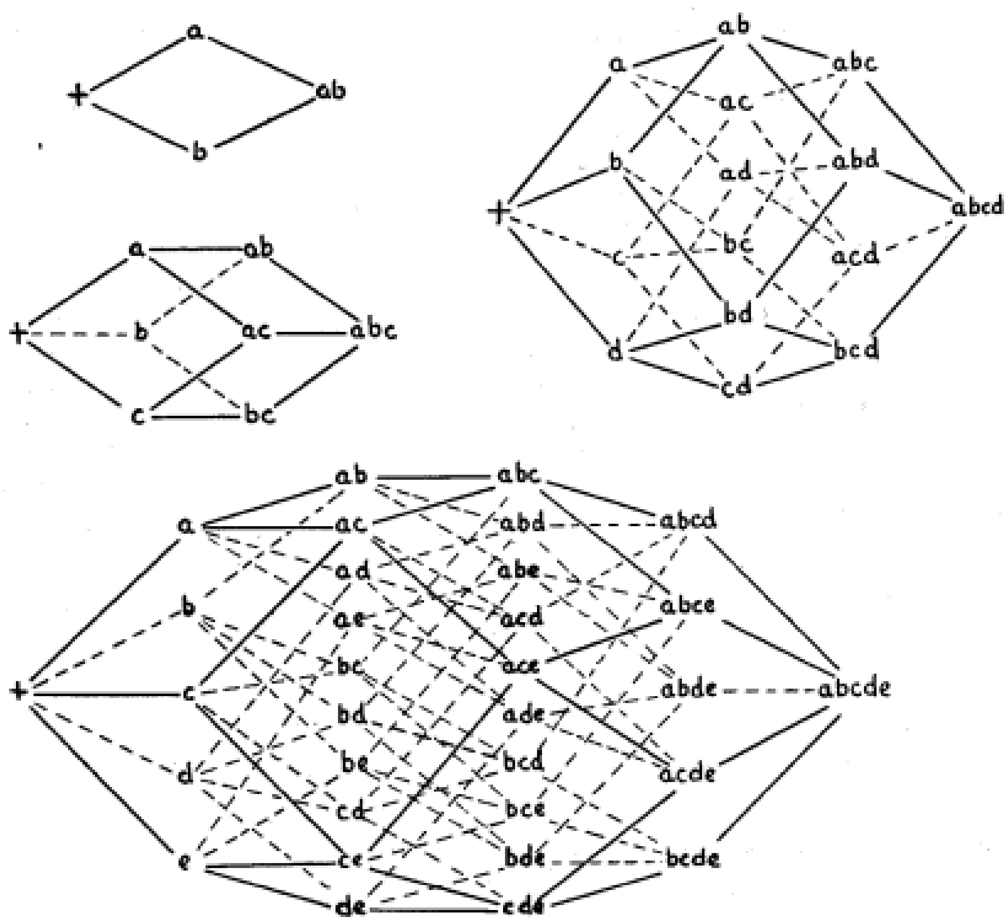
Different forms of selection

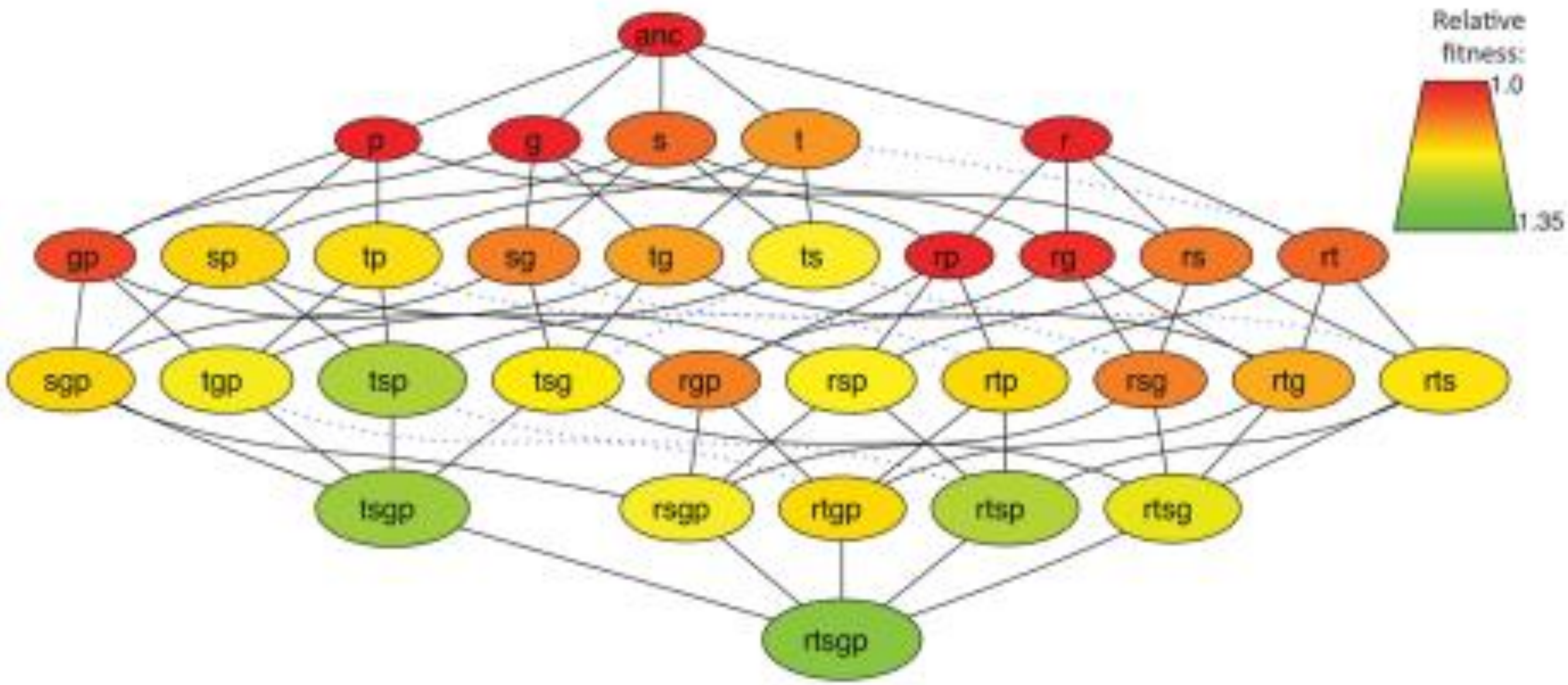
- Fluctuating selection
  - Selection changes over time, independently of the frequencies of genotypes
    - e.g. the environment is changing due to external factors
- Frequency dependent selection
  - Selection changes as frequencies of genotypes change.
    - e.g.: rare genotypes have an advantage over common ones.
    - Ecological interactions

Fitness Landscapes

- Several kinds of fitness landscapes
  - Genotype – fitness landscapes
  - Allele frequencies – fitness landscapes
    - Mean fitness landscapes
  - Phenotype-fitness landscapes

Genotype fitness landscapes





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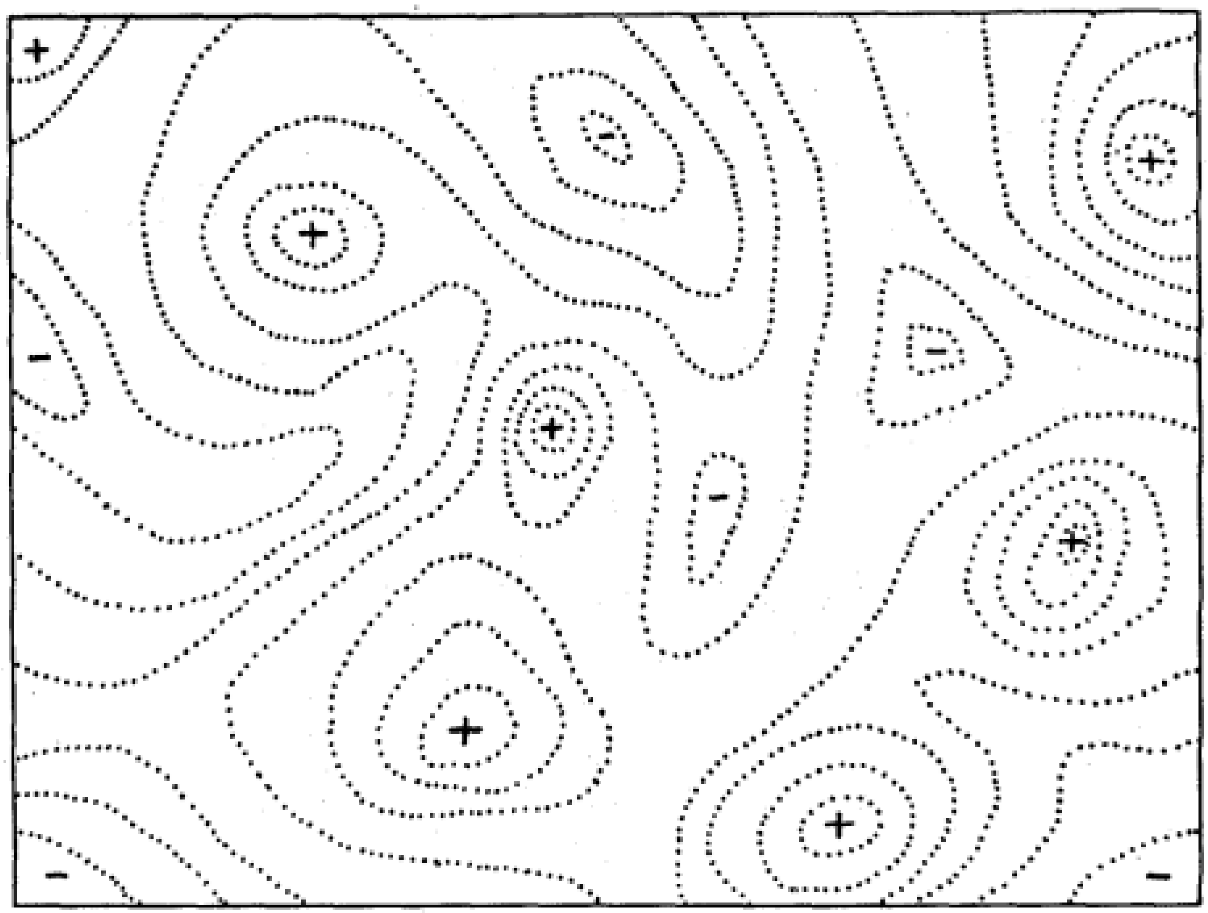
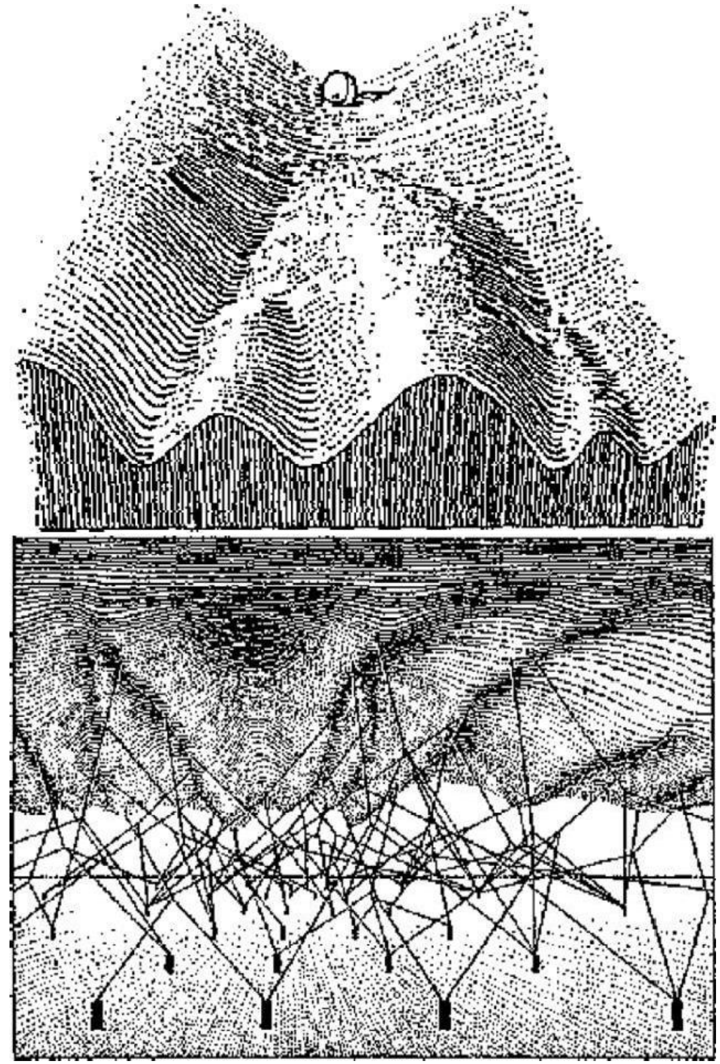
Relative fitness:
1.0
1.35

Mean fitness landscapes

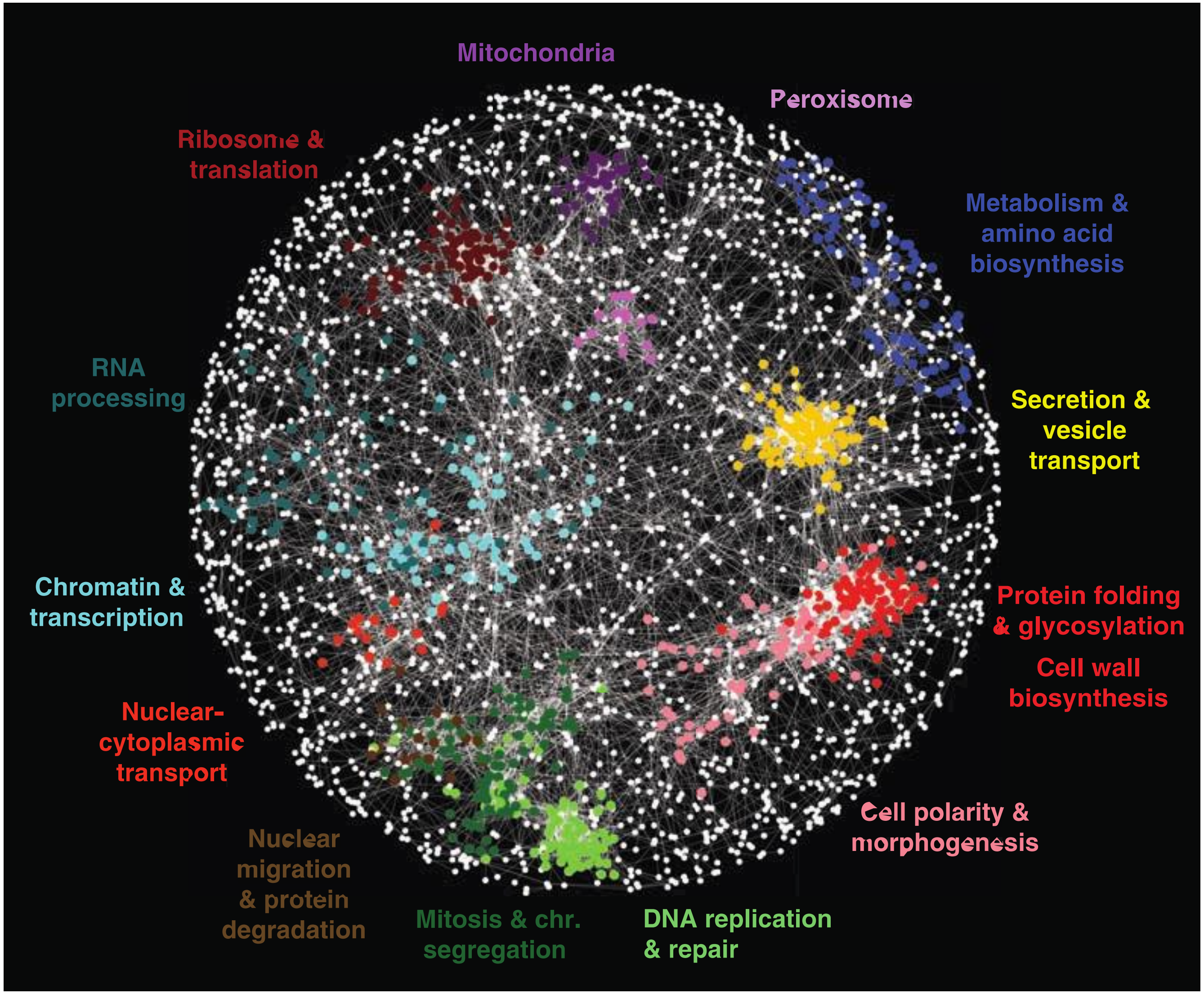


Gene interactions

- Gene interactions are ubiquitous in organisms
- The basis of complex traits
- Constrain what is possible and what is accessible



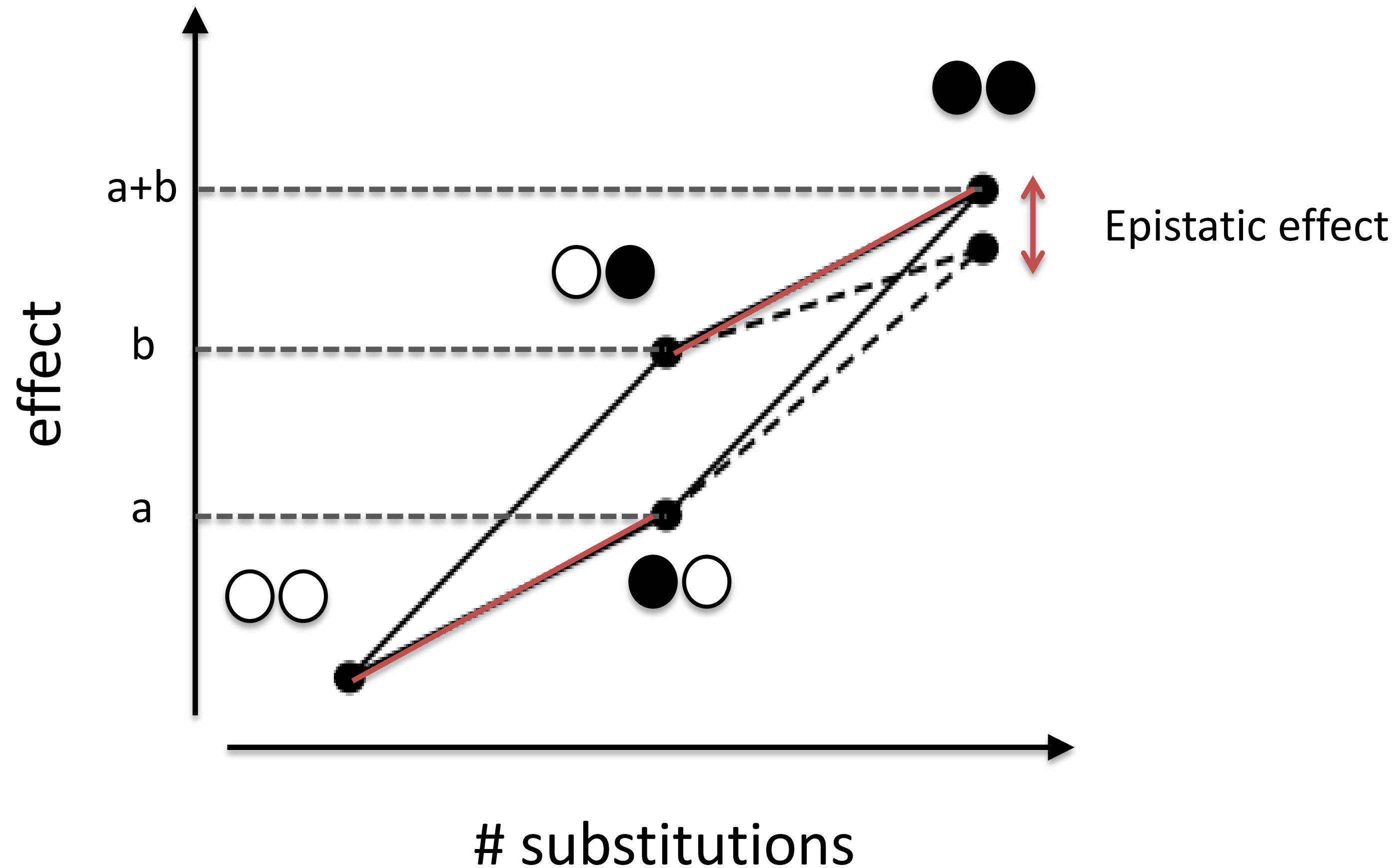
C.H. Waddington



Mitochondria
Peroxisome
Ribosome & translation
Metabolism & amino acid biosynthesis
RNA processing
Secretion & vesicle transport
Chromatin & transcription
Protein folding & glycosylation
Cell wall biosynthesis
Nuclear-cytoplasmic transport
Cell polarity & morphogenesis
Nuclear migration & protein degradation
Mitosis & chr. segregation
DNA replication & repair

Epistasis

The effect of a substitution depends on the background



Epistasis underlies major questions in Evolutionary Biology

- Limits to inferences about the outcomes of the evolutionary process
- Evolution of “variational” properties of organisms (robustness, evolvability, etc)
- Existence of multiple peaks in fitness landscapes (speciation, reproductive isolation)

Summary

- Differential reproduction comes in many forms
- Selection acts on variation and, typically, decreases it.
- Selection is the only force that leads to adaptation