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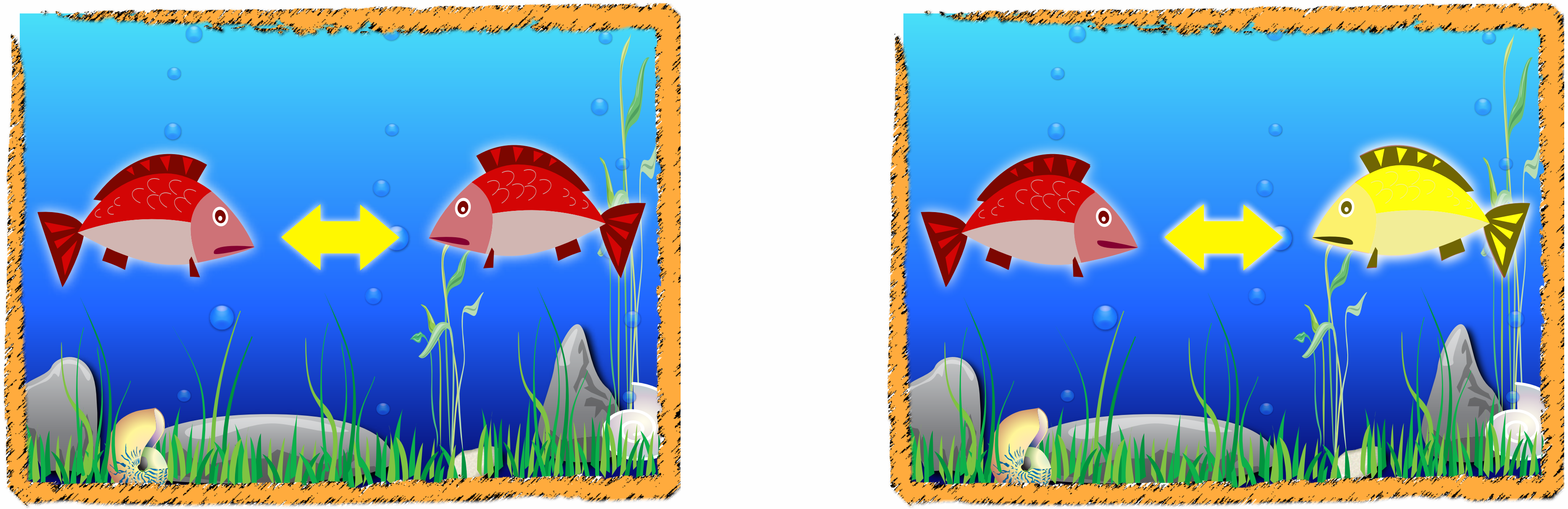
Intraspecific competition

- combining population genetics, game theory and adaptive dynamics

Montreal, Nov. 7, 2013

Preliminary

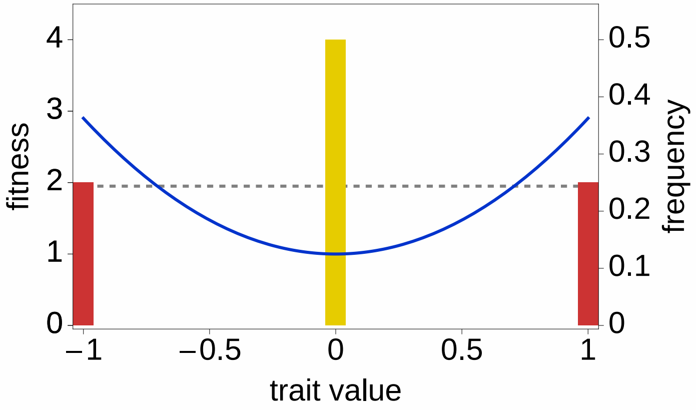
- Frequency-dependent selection = population composition affects fitness of genotypes



- Frequency-dependence arises naturally in many ecological situations

Sympatric speciation (Dieckmann and Doebeli, 1999 Nature, & many more):

- Disruptive selection ⇒ heterozygote disadvantage



Motivation

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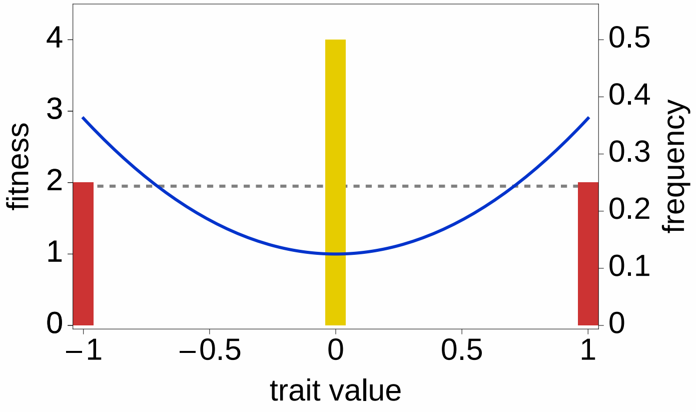
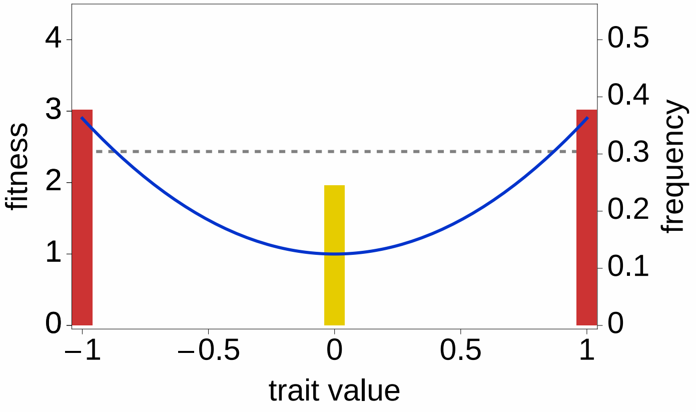
- Disruptive selection ⇒ heterozygote disadvantage
- Evol. of assortative mating ⇒ unfit heterozygotes reduced





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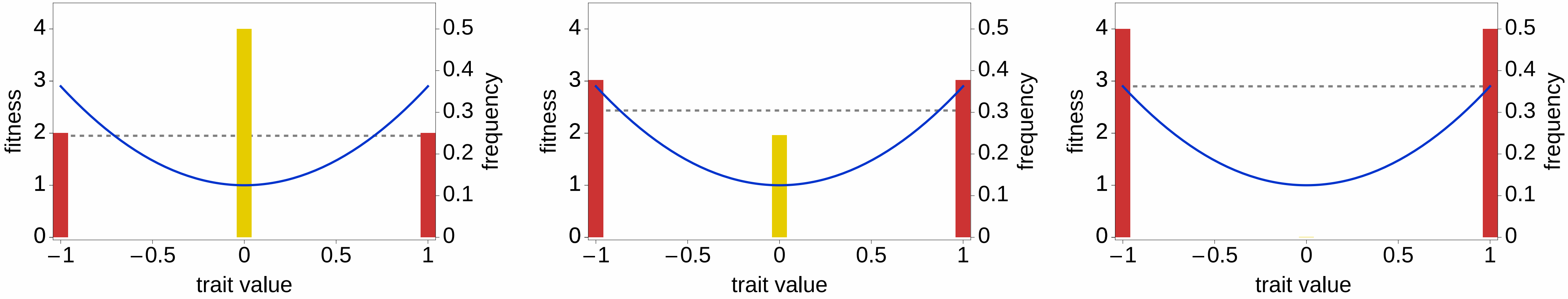

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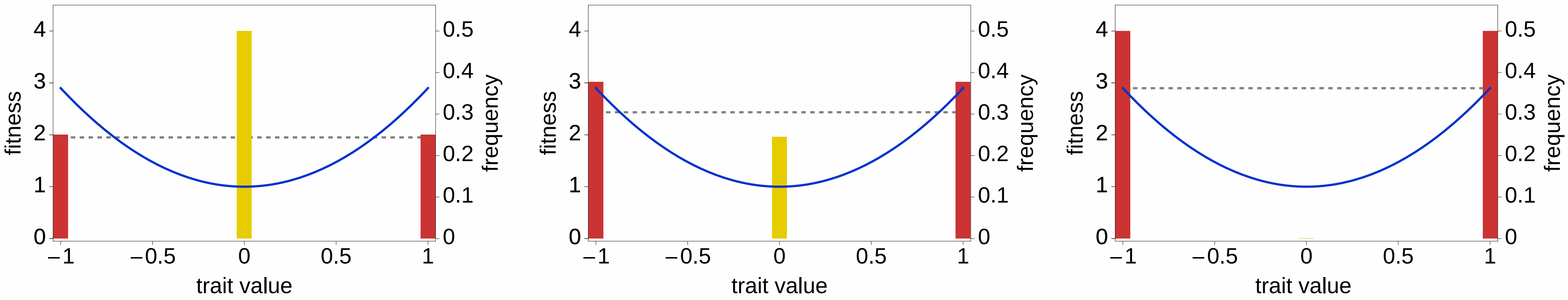
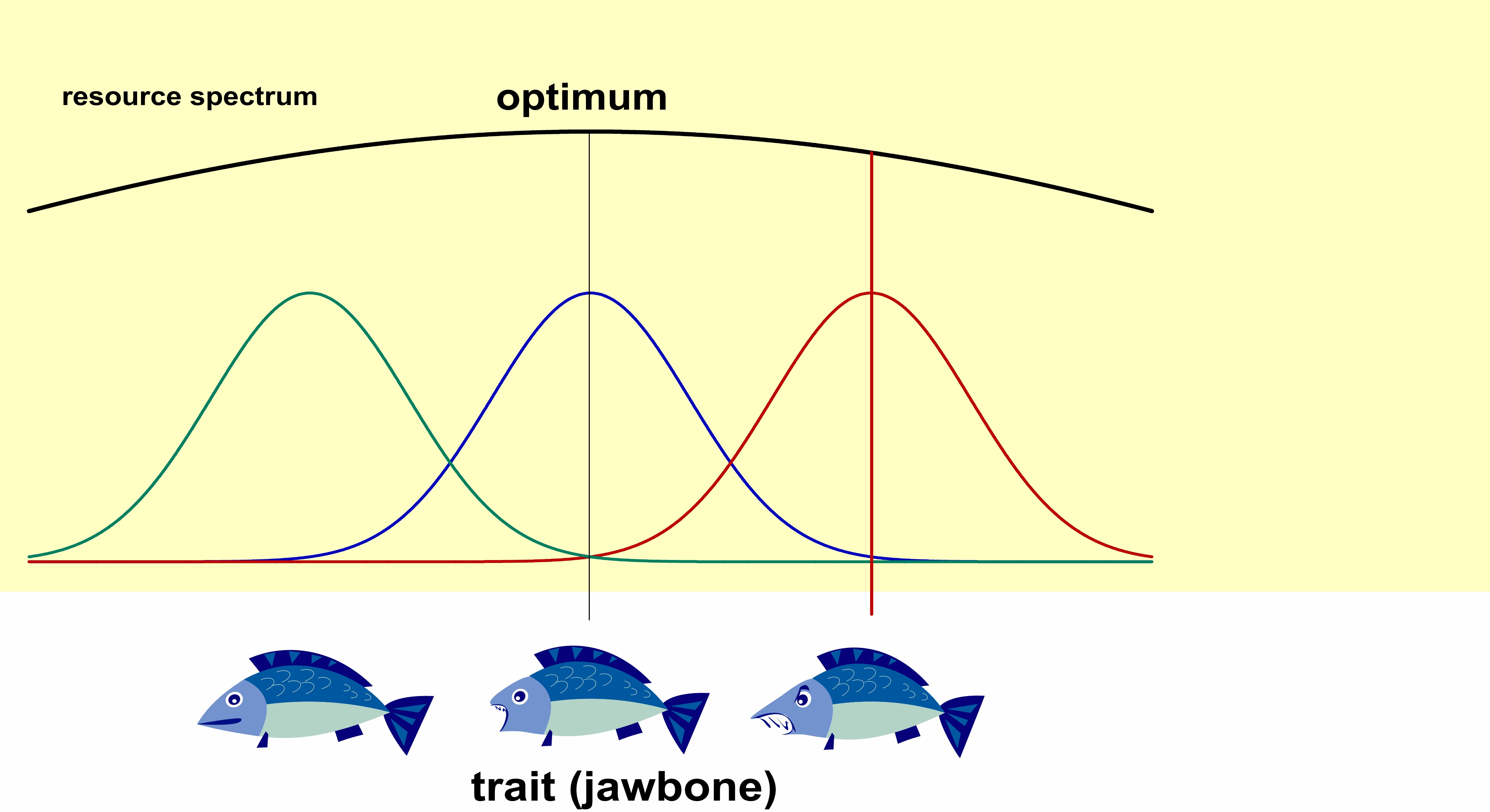


Disruptive selection from negative frequency-dependent selection

Motivated by intraspecific competition ⇒ today's topic

Resource competition



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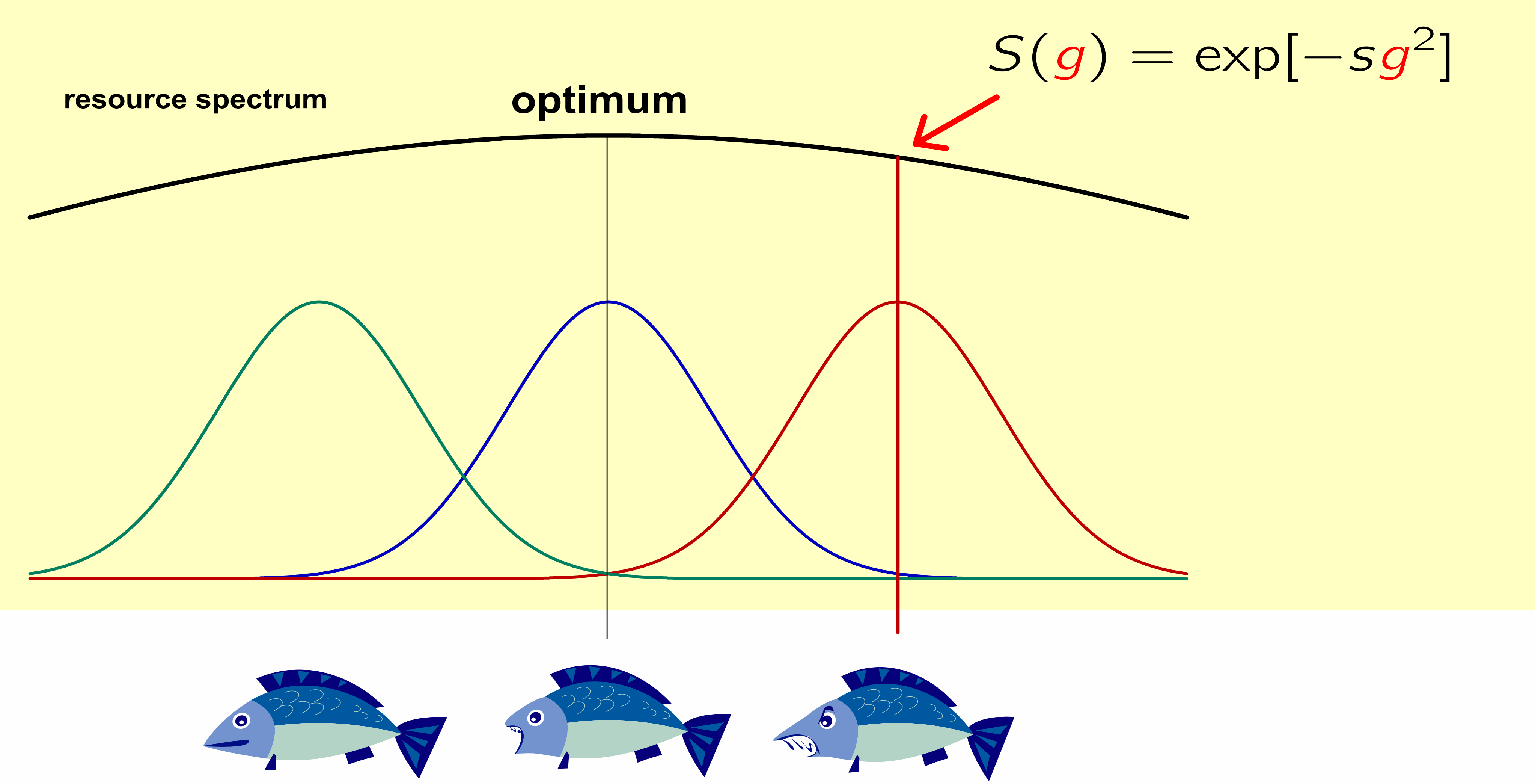


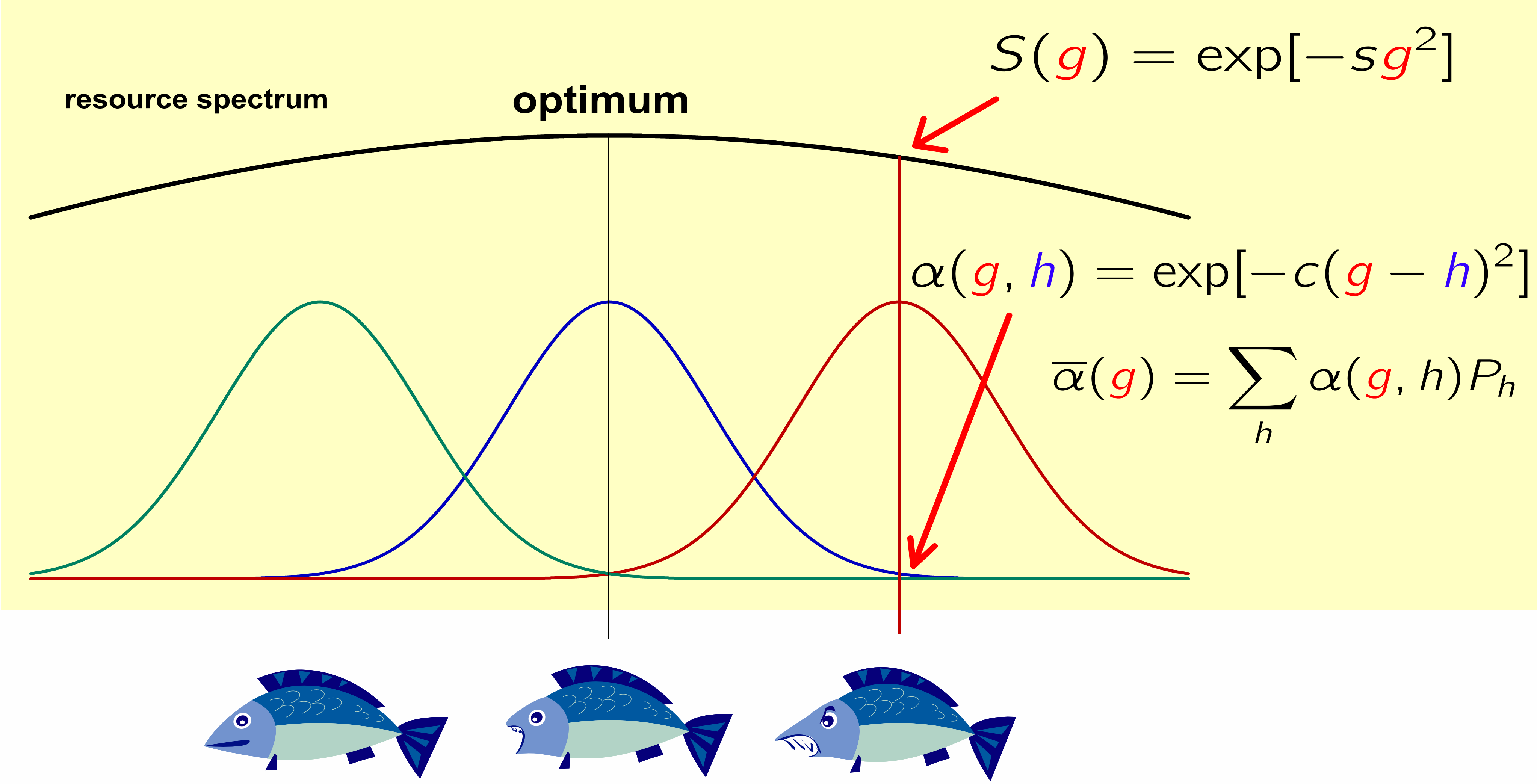
$$S(g) = \exp[-sg^2]$$

resource spectrum

optimum

trait (jawbone)

Resource competition



resource spectrum

optimum

$$S(g) = \exp[-sg^2]$$

$$\alpha(g,h) = \exp[-c(g-h)^2]$$

$$\overline{\alpha}(g) = \sum_h \alpha(g,h)P_h$$

trait (jawbone)

Interactions are symmetric: $\alpha(g,h) = \alpha(h,g)$

Roughgarden model

Roughgarden (1972, Am. Nat.); Slatkin (1979, Genetics)

$$W(g) = 1 + r - \frac{rN}{S(g)} \sum_h \alpha(g, h) P(h)$$

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- Non-generic behavior: continuous coexistence in asexual case
- If resident pop. at optimum ⇒ extreme phenotypes have highest fitness
- Extreme phenotypes have higher density-dependent effect

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$$W(g) = S(g)\Big(\rho - \frac{N}{\kappa}\sum_{h} \alpha(g,h)P(h)\Big)$$

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- Avoids non-generic behavior
- If resident pop. at optimum ⇒ extreme phenotypes do not have highest fitness
- Stabilizing sel. & competition occur at different stages of selection cycle

Christiansen-Loeschcke model

Christiansen and Loeschcke (1980, TPB)

$$W(g) = 1 + K\left(S(g) - N\sum_{h}\alpha(g,h)P(h)\right)$$

- Not so frequently used
- Derived from Lotka-Volterra competition equations
- Overcomes most weak-points of other models
- Gradient system in continuous time (with and without density-dependence) (Matessi & Schneider, 2009)

Wildcard Model

Even better (Matessi & Schneider, 2009 TPB):

$$W(g) = S(g) + f(N)\sum_{h} \alpha(g,h)P(h) + \gamma(\mathbf{P}, N)$$

- $\alpha(g,h) = \alpha(h,g) \ldots$ constant (g, h can be multi-dimensional)
- $f(N), f'(N) > 0$

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- Other models are special cases as well
- Roughgarden and Bulmer models special cases for weak selection

Dynamics

Alleles $A_1, \dots A_n$ determine trait

g_{ij} trait of genotype A_iA_j

$$W_i = \sum_{j=1}^{n} W(g_{ij})p_j \text{ ... marginal fitnesses of } A_i$$

$$\overline{W} = \sum_{i=1}^{n} W_i p_i \text{ ... mean fitnesses}$$

Change in allele-frequencies:

$$p_i' = p_i \frac{W_i}{\overline{W}} \quad \text{and} \quad N' = \overline{W} N \quad \dots \text{ discrete time}$$

$$\dot{p}_i = p_i(W_i - \overline{W}) \quad \text{and} \quad \dot{N} = (\overline{W} - 1)N \quad \dots \text{ continuous time}$$

Dynamics

- Continuous time:
  - $\Lambda = f(N)\left(2\sum_{i,j=1}^{n} S(g_{ij})p_i p_j - f(N)\sum_{i,j,k,l=1} \alpha(g_{ij}, g_{kl})p_i p_j p_k p_l\right)$

    maximized along every trajectory

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  - All trajectories converge to the set of equilibria
  - one-locus with dominance in trait
  - multilocus with quasi-linkage equilibrium
  - with and without density-dependence

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Lessard Model

- Lessard (1986, TPB)
- Two phenotypes (strategies, behavioral patterns) C_1 and C_2
- Payoff matrix $(f_{ij})_{i,j\in\{1,2\}}$ (not necessarily symmetric)
- A_iA_j expresses C_1 with probability h_{ij} (C_2 with probability $1 - h_{ij}$)
- $W_{ij}^{(L)} = \left[\overline{h} f_{11} + \left(1 - \overline{h}\right) f_{12}\right] h_{ij} + \left[\overline{h} f_{21} + \left(1 - \overline{h}\right) f_{22}\right] (1 - h_{ij})$

  fitness of A_iA_j; $\overline{h} = \sum_{k,l=1}^{n} h_{kl} p_k p_l$ ... frequency of strat. C_1 in pop.

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  $\Rightarrow$ special case of WCM

m-phenotype Model

- m phenotypes $C_1, \ldots, C_m$
- Symmetric payoff matrix $F = (f_{ij})_{i,j \in \{1,\ldots,m\}}$
- $A_i A_j$ expresses C_u with probability $h_{ij}^{(u)}$
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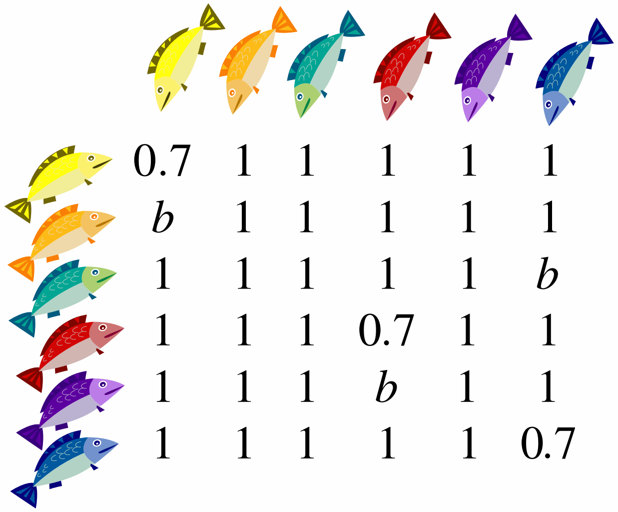
Symmetric competition is important



0.7	1	1	1	1	1
b	1	1	1	1	1
1	1	1	1	1	*b*
1	1	1	0.7	1	1
1	1	1	*b*	1	1
1	1	1	1	1	0.7

Long-term evolution

Short-term evolution - change in genotype distribution

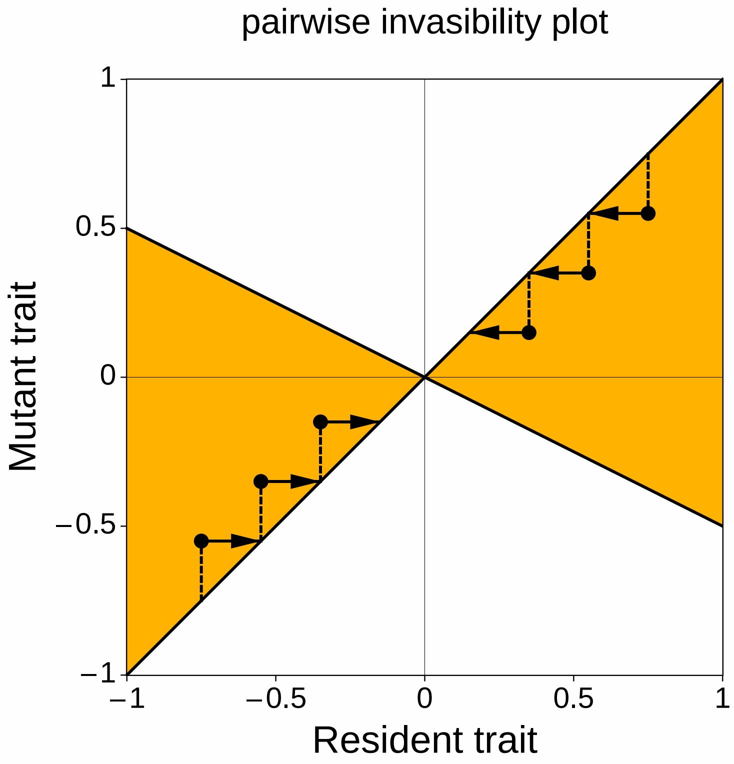
Long-term evolution

Short-term evolution - change in genotype distribution

Long-term evolution - successive invasion & possible fixation of mutants

Population genetics vs. adaptiv dynamics

- Adaptive dynamics
  - long-term evolution
  - neglect complex genetics, focus on ecological realism
  - optimization process



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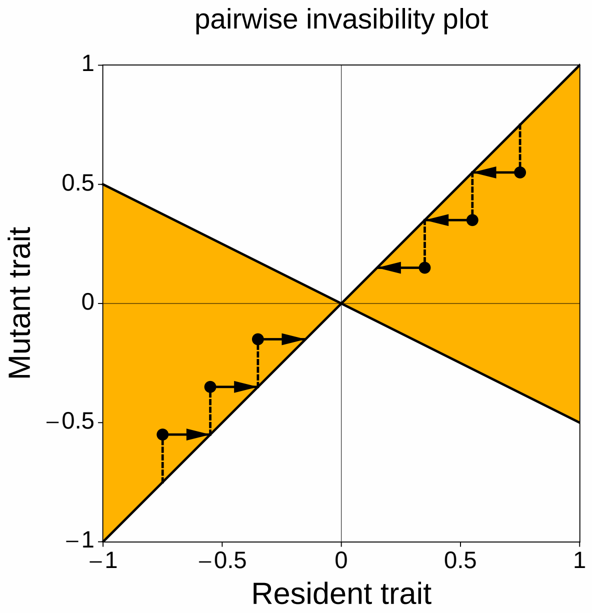
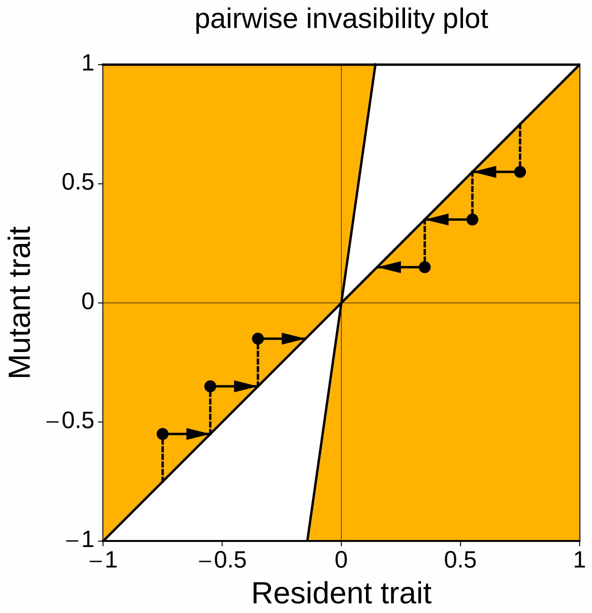

pairwise invasibility plot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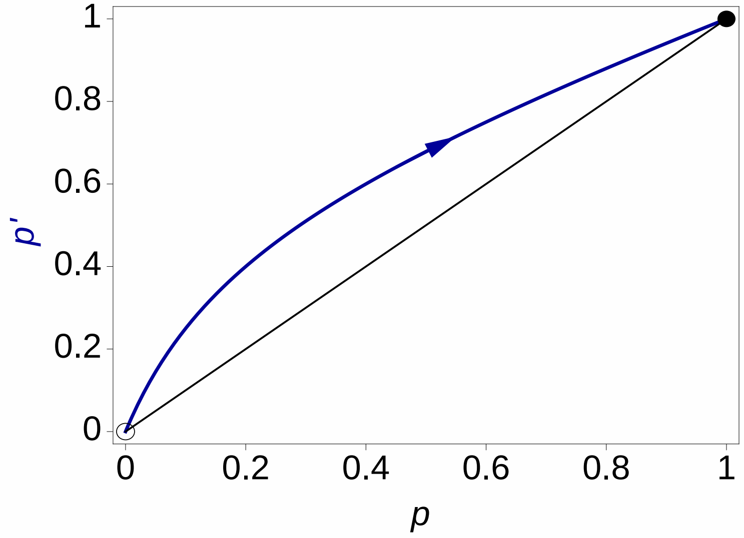

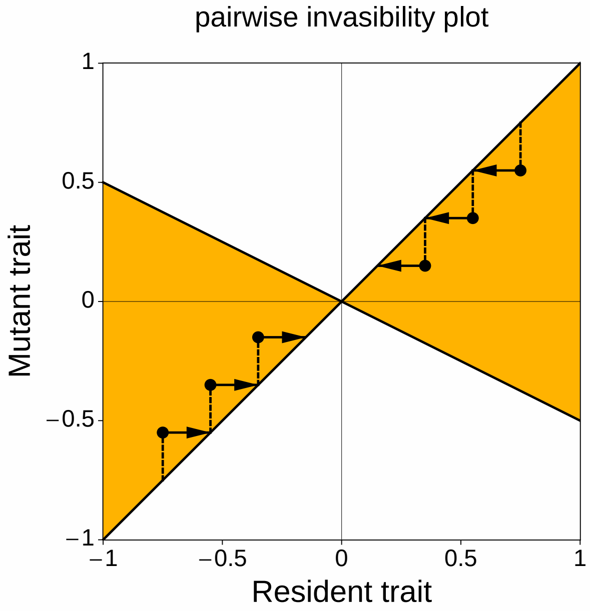
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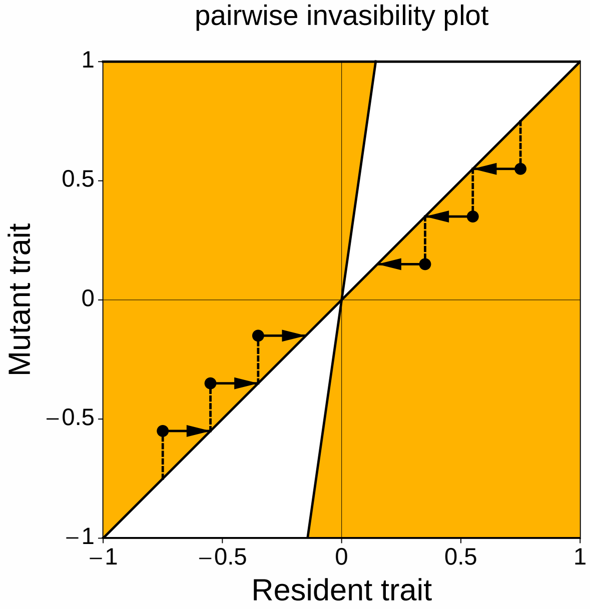
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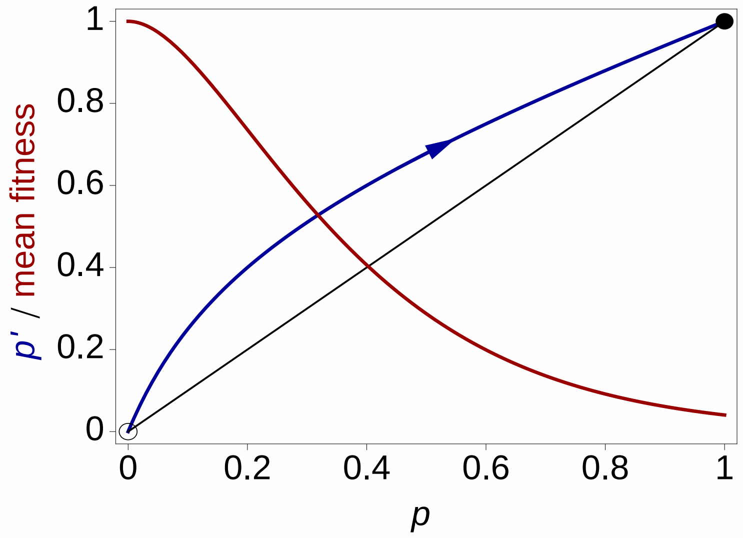

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  - complex genetics rather than ecological realism (to keep models feasible)
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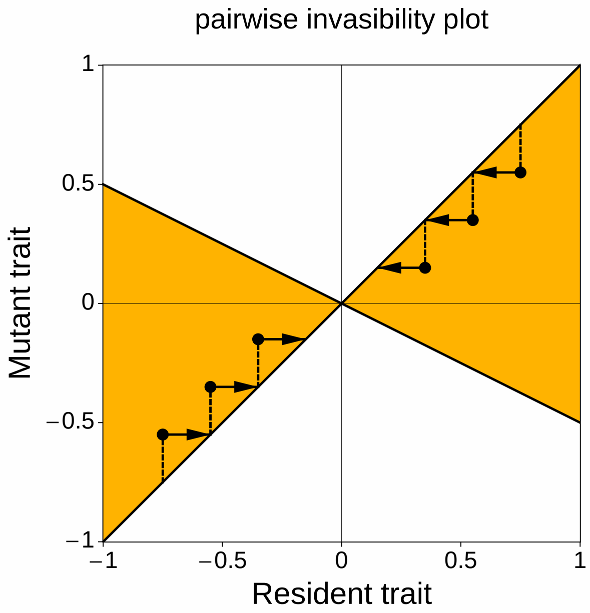

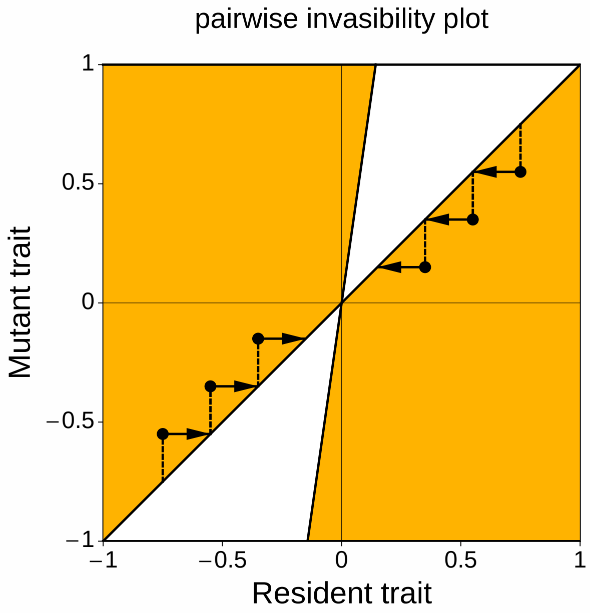

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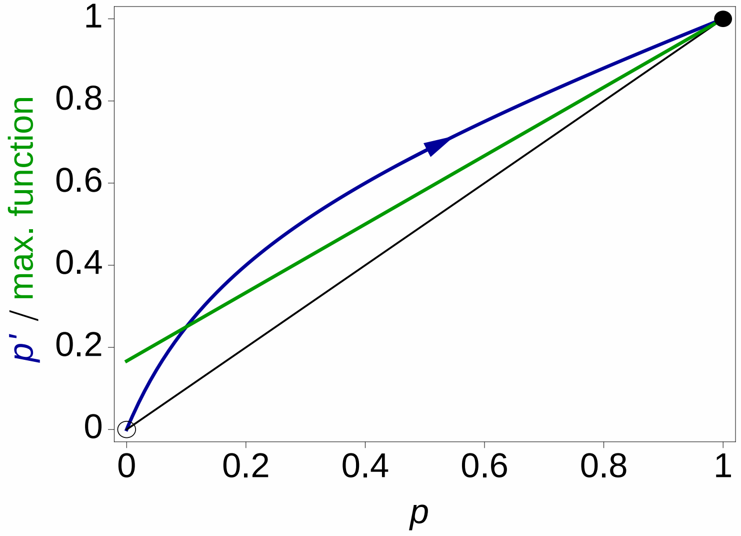

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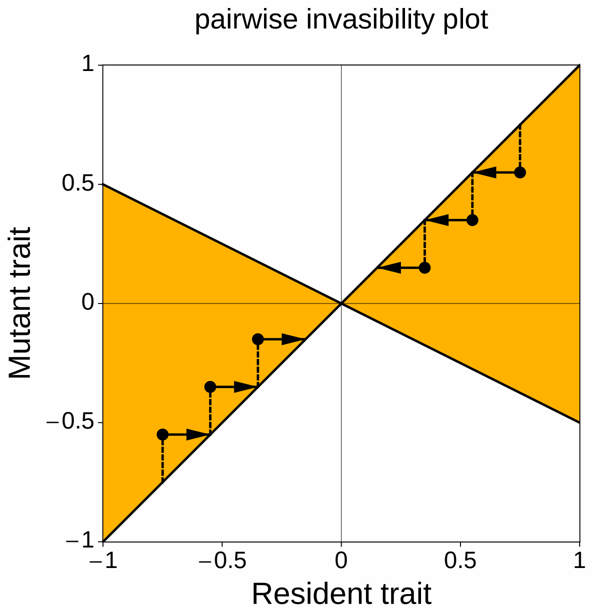

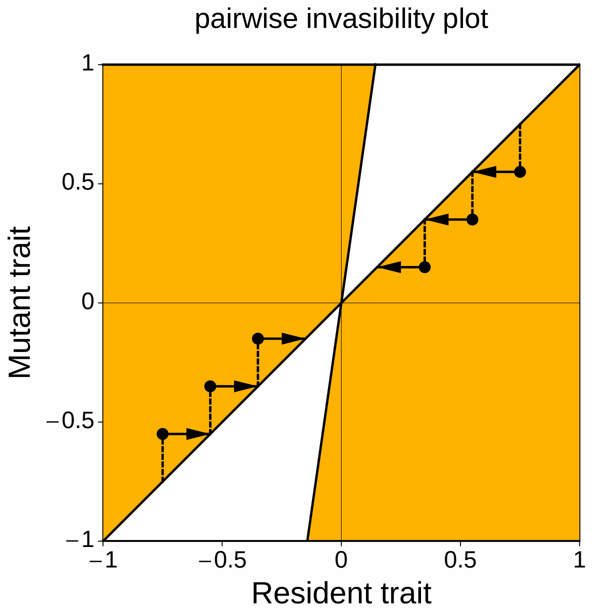

Weak selection

Weak-selection approximation to intraspecific-competition models:

$$S(g) \approx 1 - sg^2\,, \quad \alpha(g,h) \approx 1 - c(g-h)^2$$

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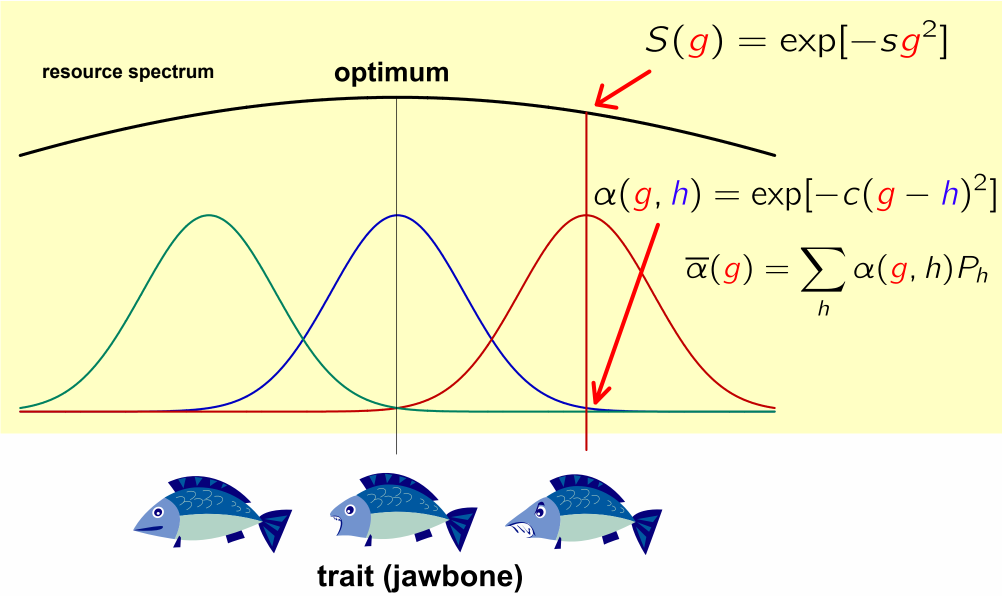

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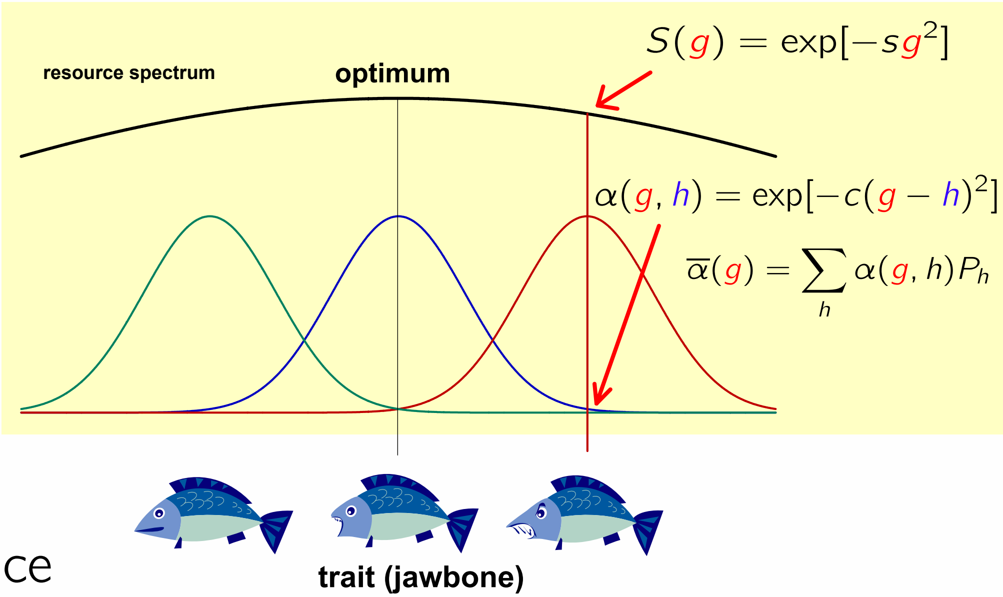
- $\overline{G} = \sum_g g P_g$... mean genotypic value
- φ function of $\boldsymbol{P}$, e.g. $\varphi = 2cV_G$
- $V_G = \sum_g \left(g - \overline{G}\right)^2 P_g \ldots$ genotypic variance



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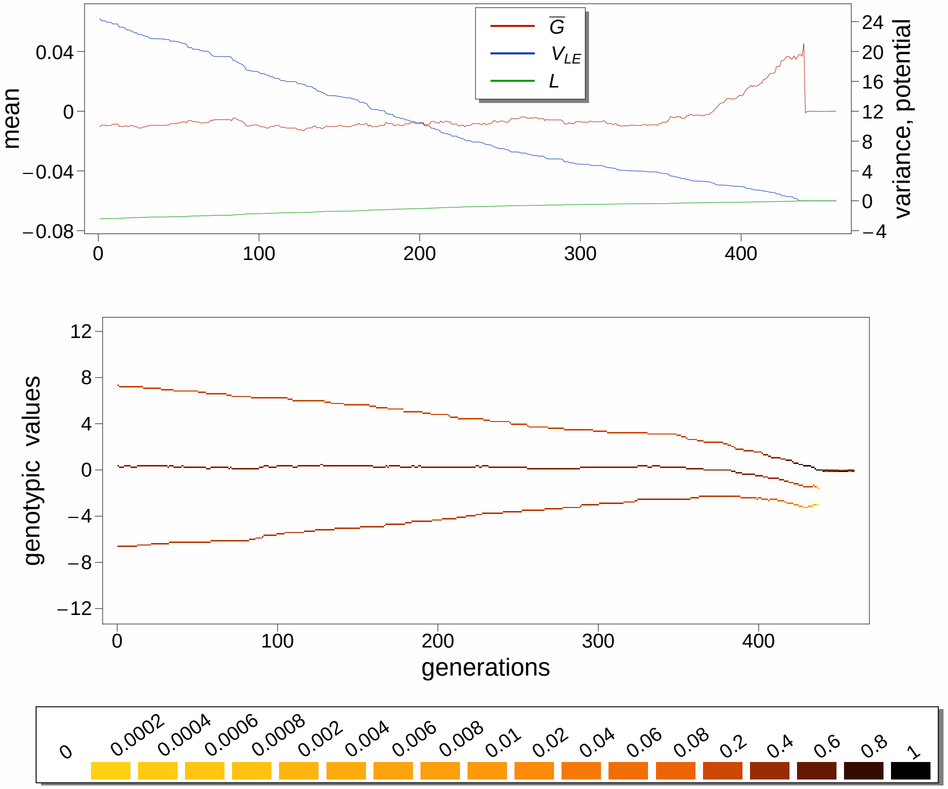
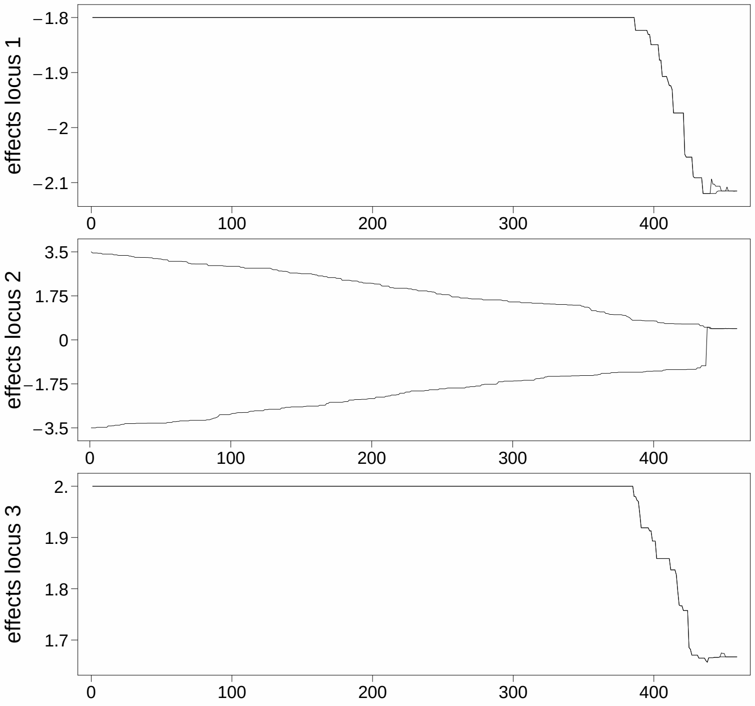
Weak selection

Assume:

- Trait determined additively by finitely many multiallelic loci (no dominance or epistasis in the trait)
- Selection is sufficiently weak $\Rightarrow$ quasi-linkage equilibrium
- Allelic effects per locus constraint
- Equilibrium reached before next mutation occurs

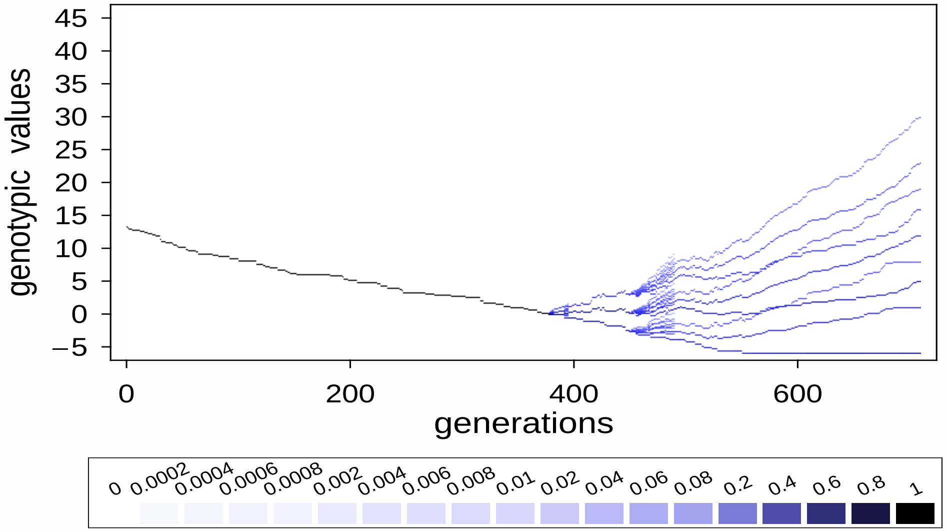
$c < s$ (stabilizing selection)

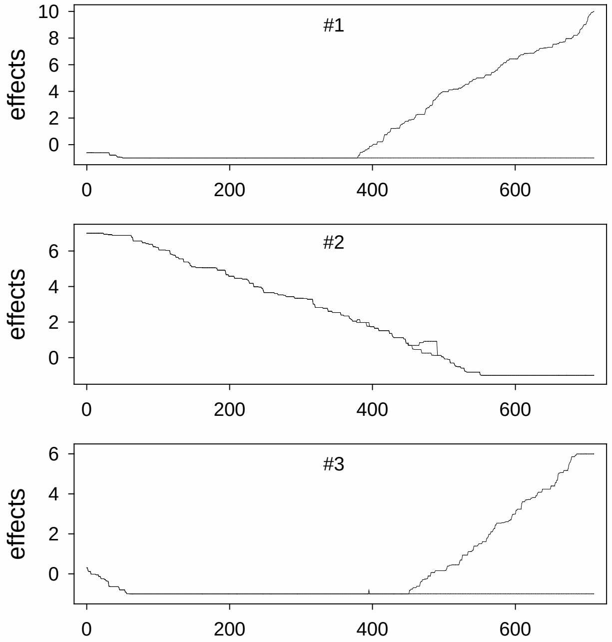




- V_G and $|\overline{G}|$ minimized under genetic constraints
- Unique phenotypic LTE is ultimately reached (convergent stable ESS)
- If $\overline{G} = 0$ possible $\Rightarrow V_G = \overline{G} = 0$ at LTE

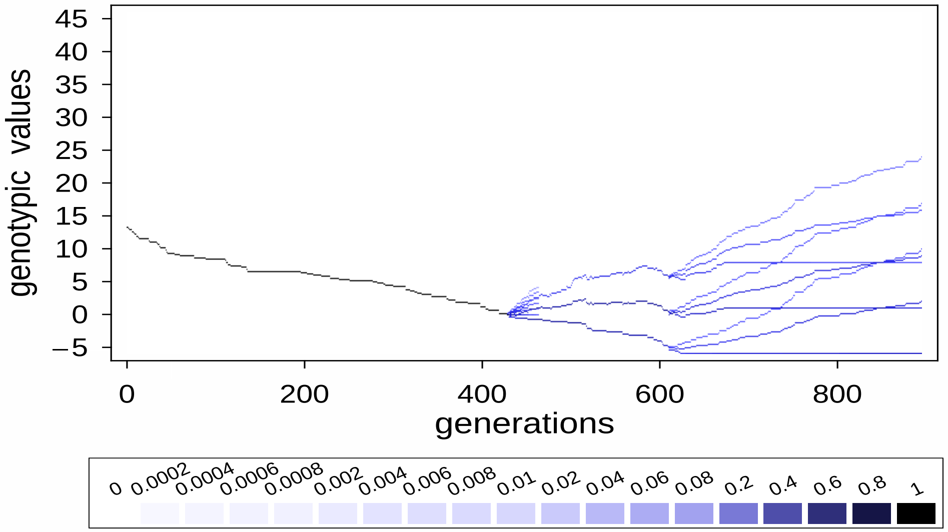
$c > s$ (disruptive selection)

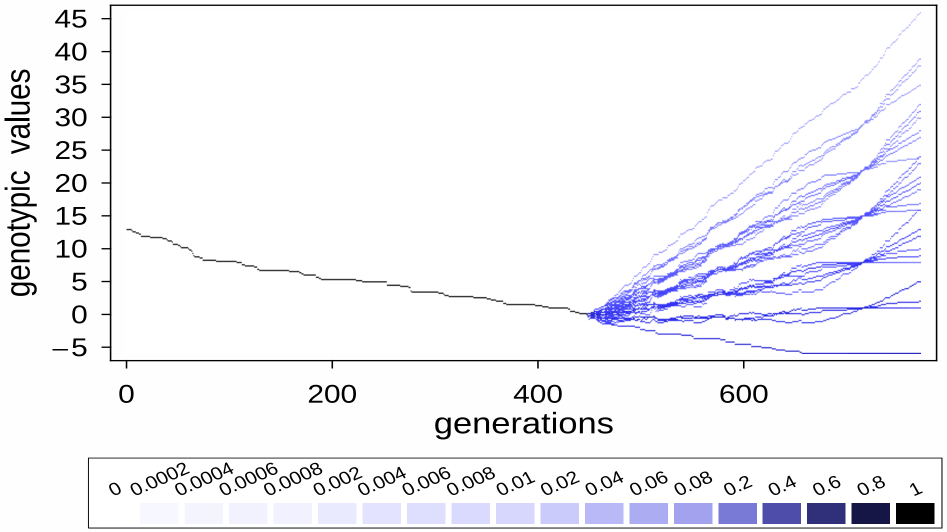


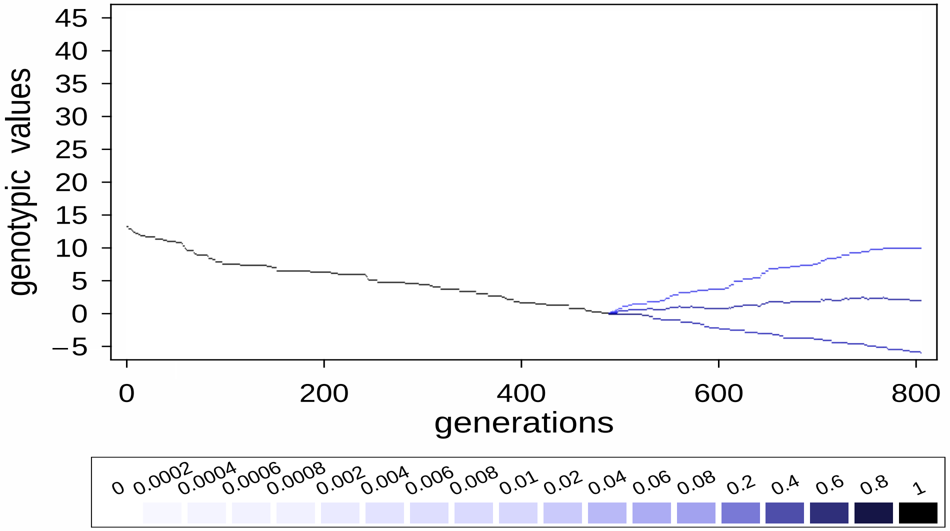


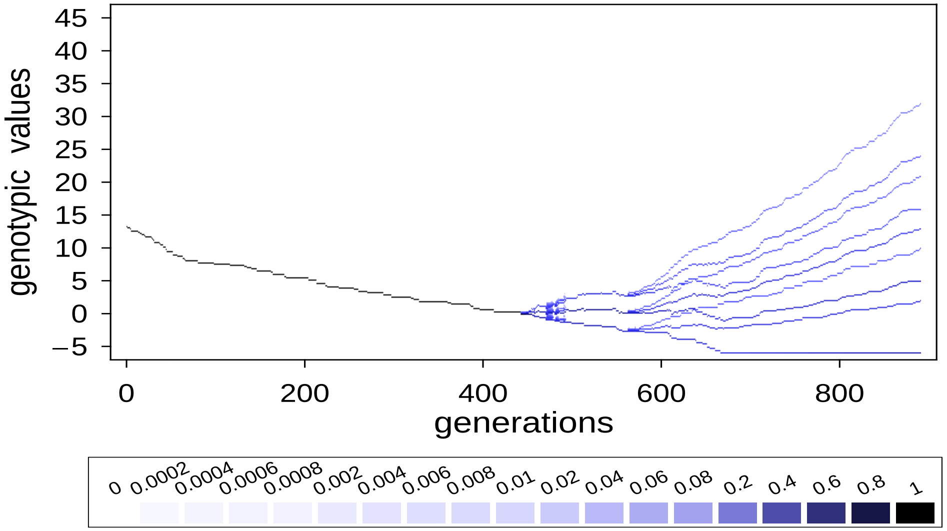
- Genotypic long-term equilibrium (LTE) reached (dynamical equilibrium immune against invasion of small mutations)
- V_G maximized & $|\overline{G}|$ minimized (under genetic constraints)
- The LTE is not necessarily unique

$c > s$ (disruptive selection)









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- Partly multi-locus genetics

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Conclusions

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Conclusions

The End

for today ... but