Adaptive Diversification

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University of British Columbia

KITP
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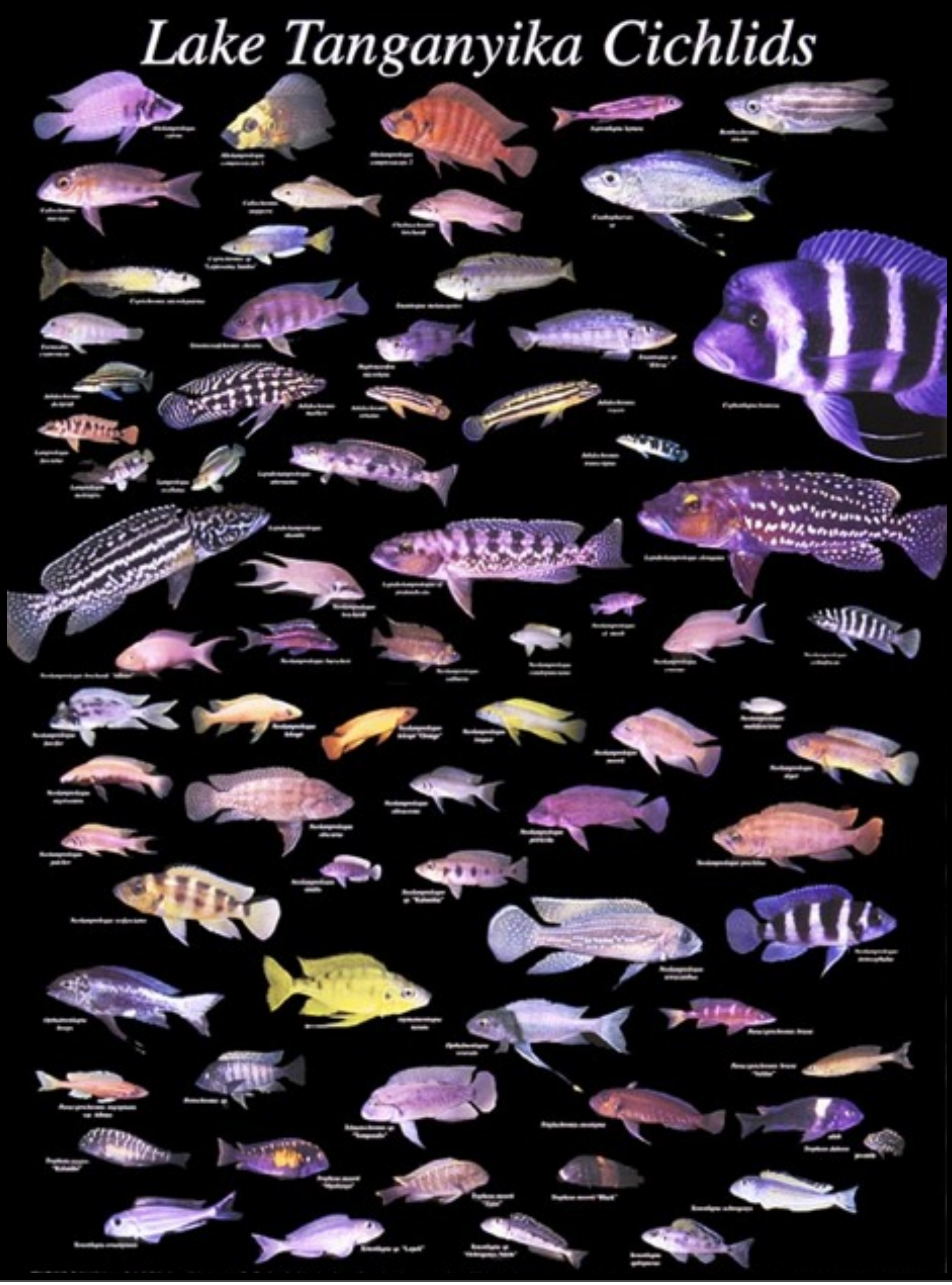
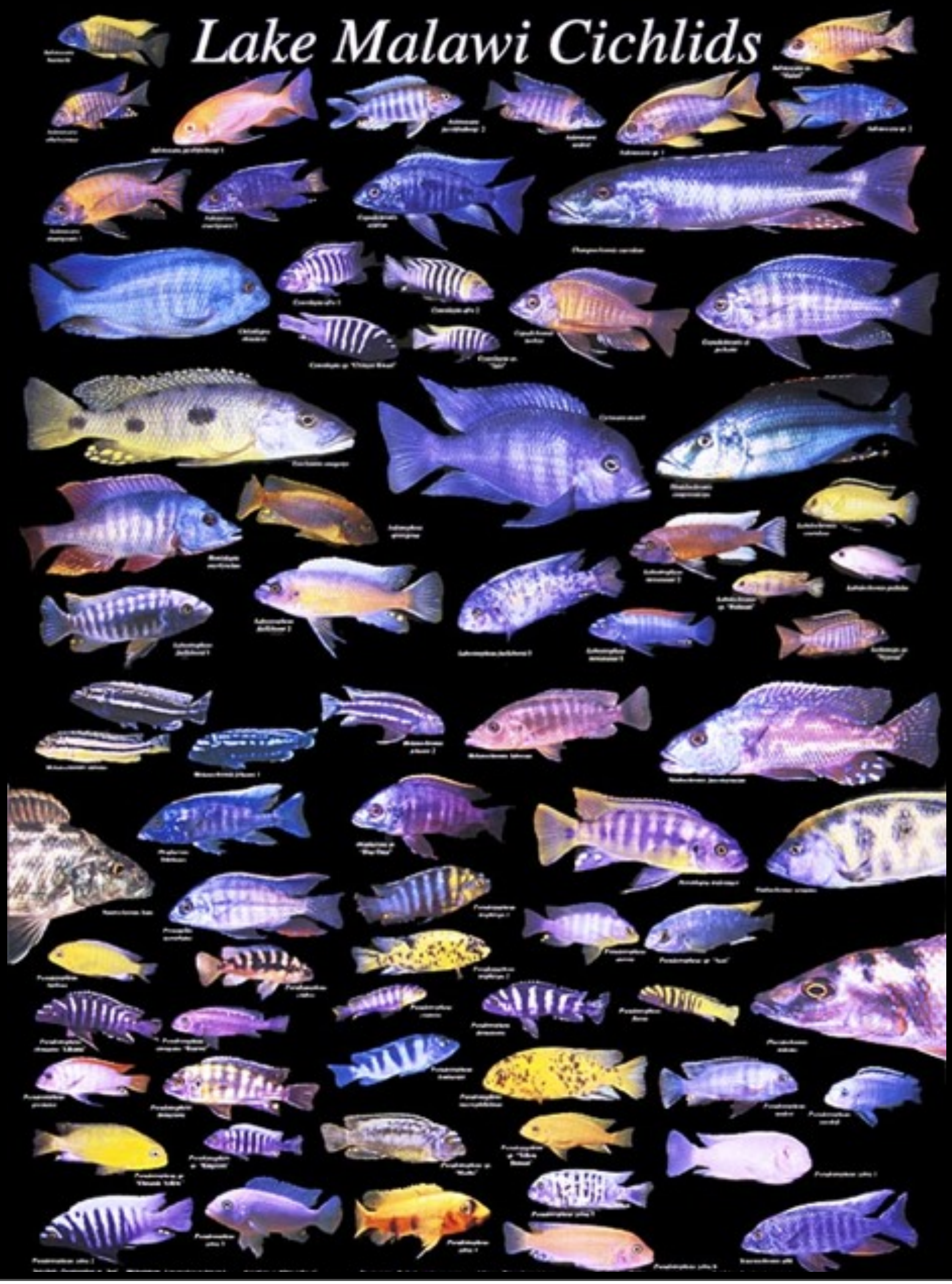
Adaptive radiation of Cichlid fishes in African rift lakes





Phenotypic diversityin morphology, behaviour, colour...

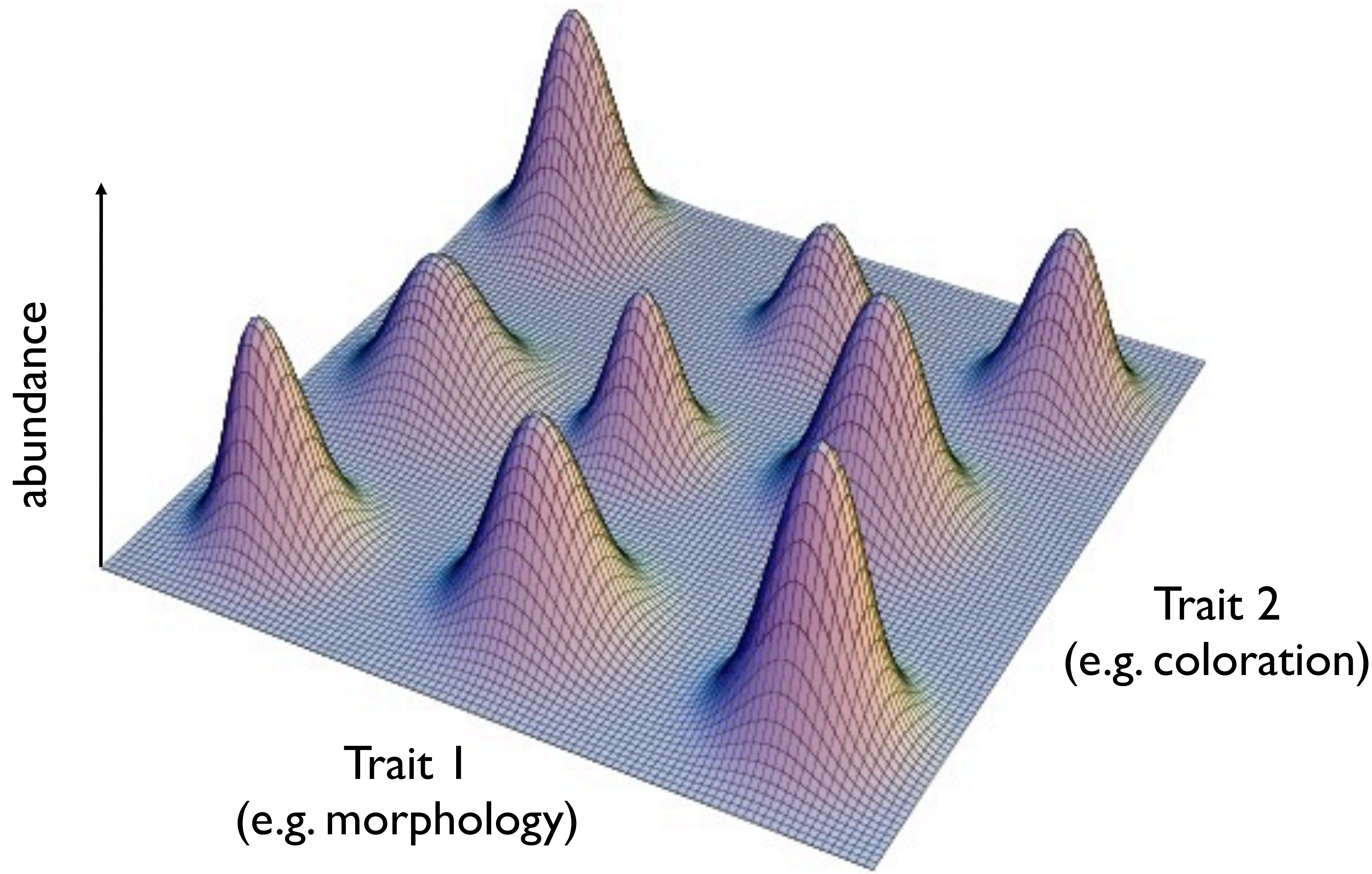








Diversifity: multiple peaks in phenotype space



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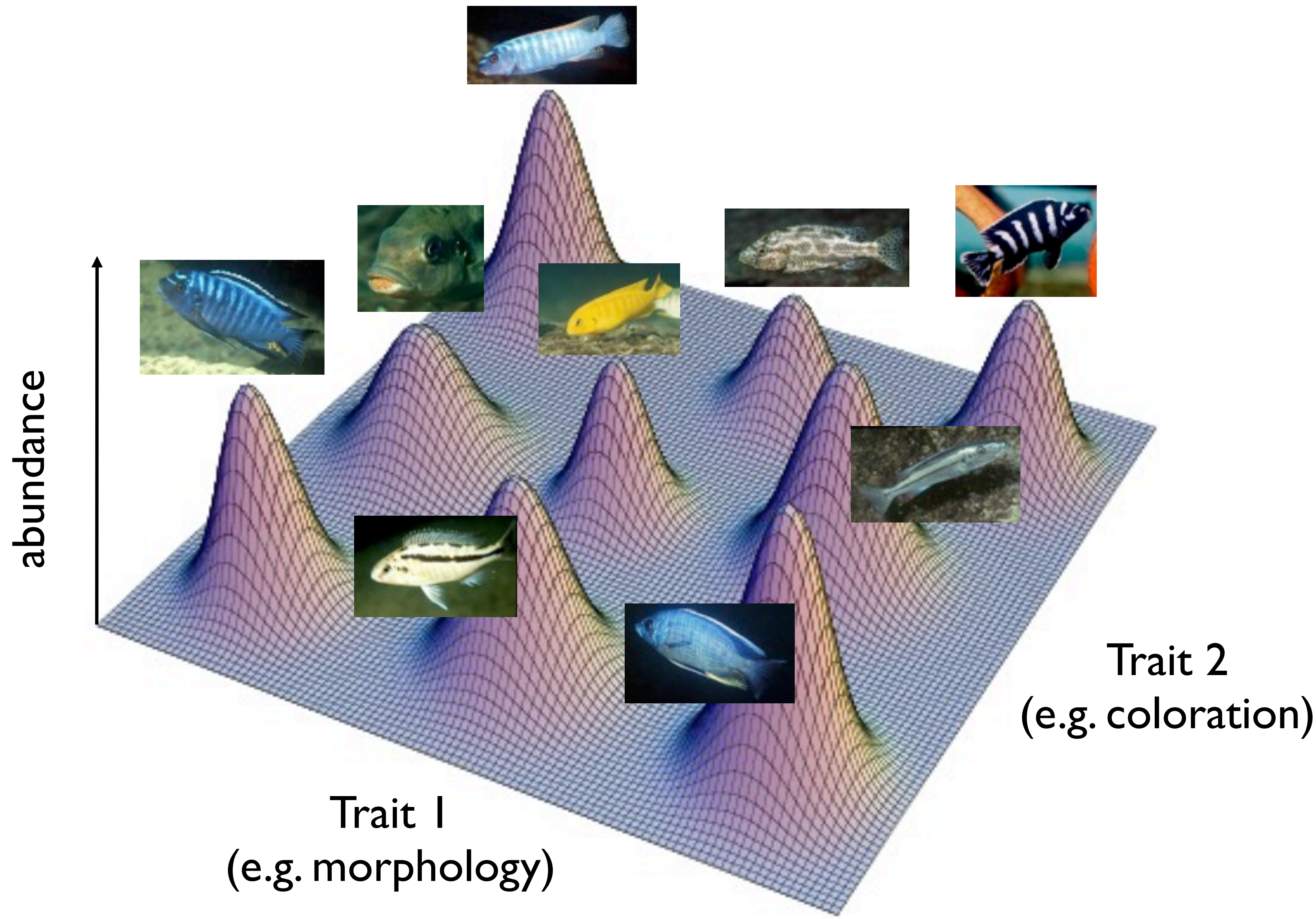
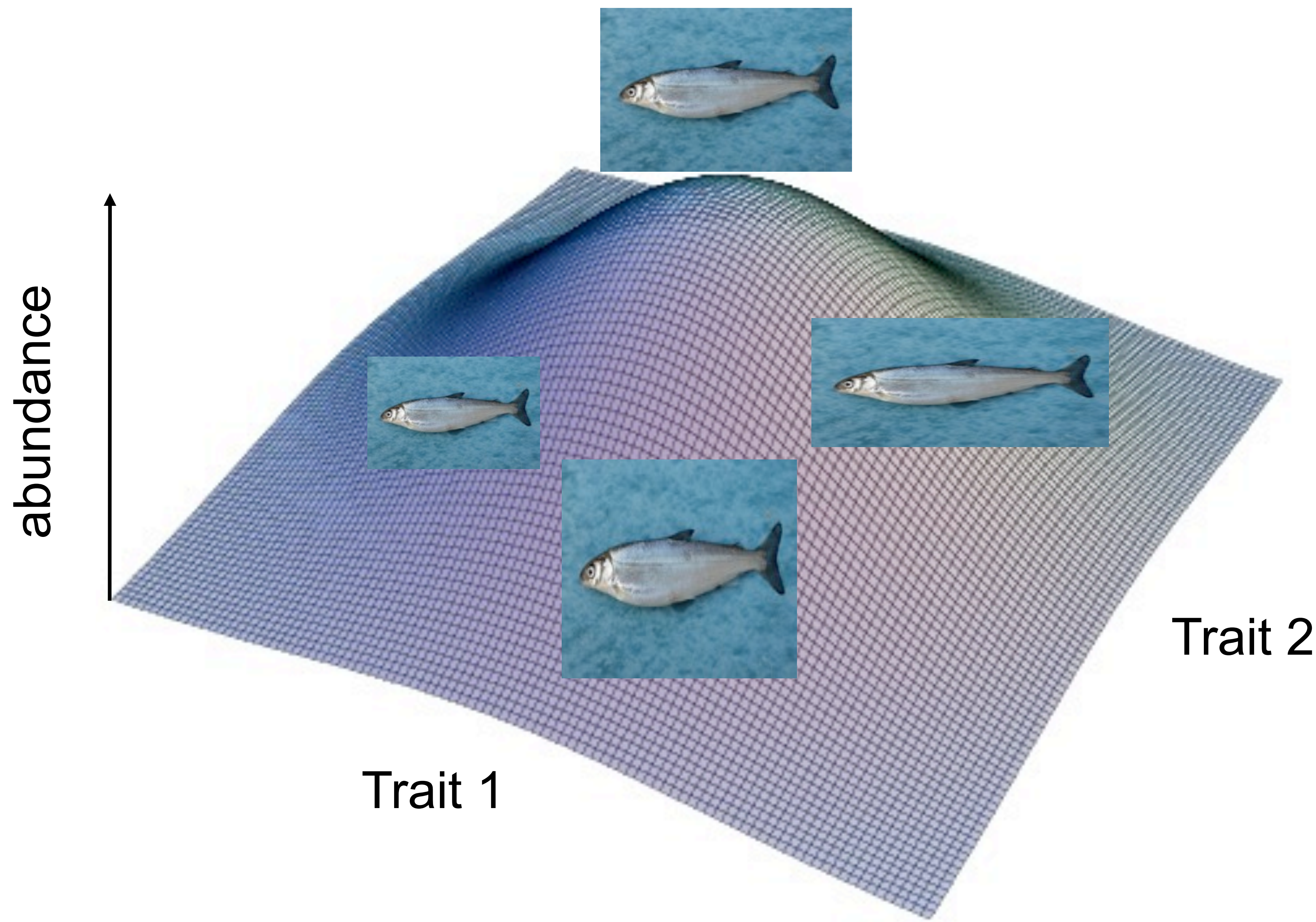
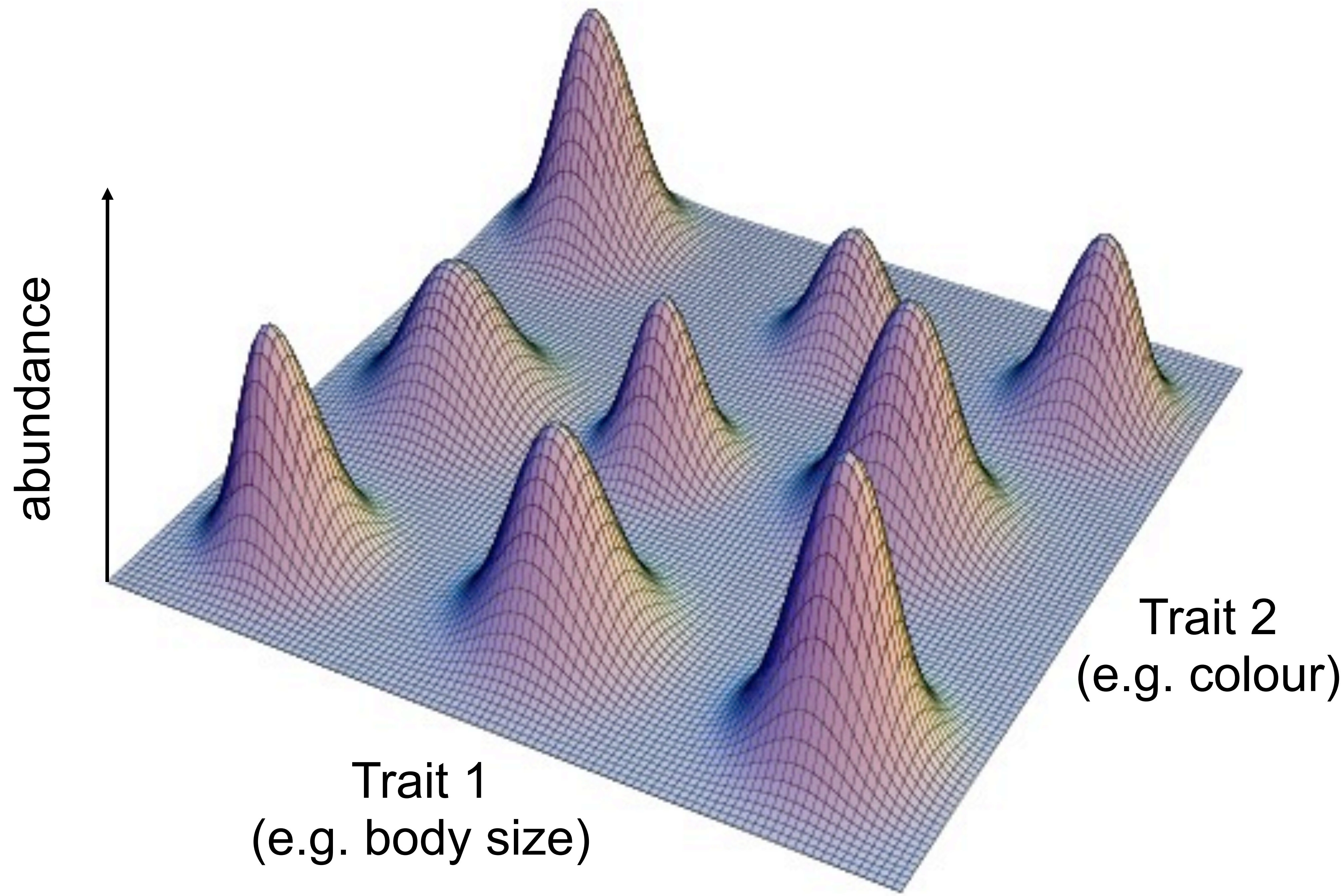


No pattern in phenotype space: no diversity

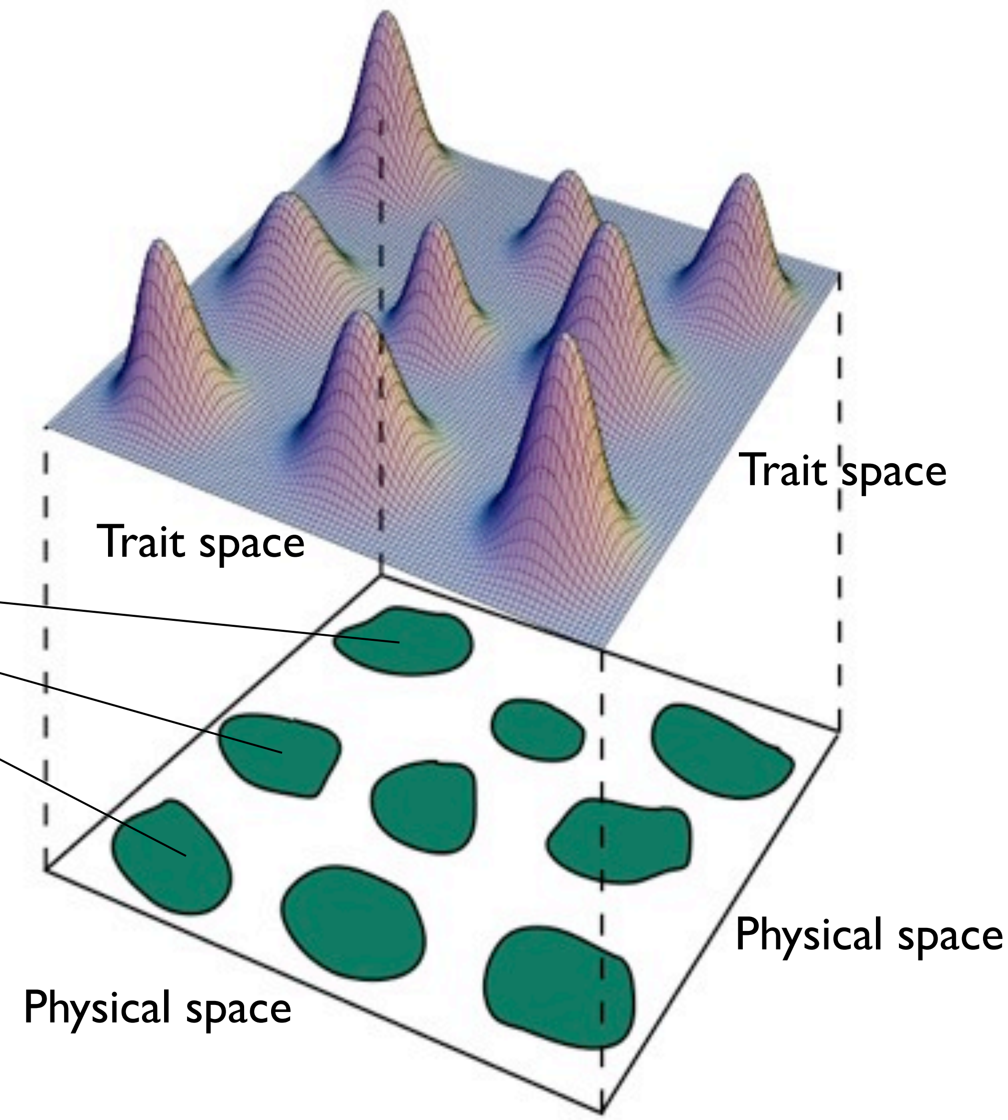


Diversification = Pattern formation in phenotype space



Diversification in geographic isolation

Different phenotypes favoured in isolated habitats



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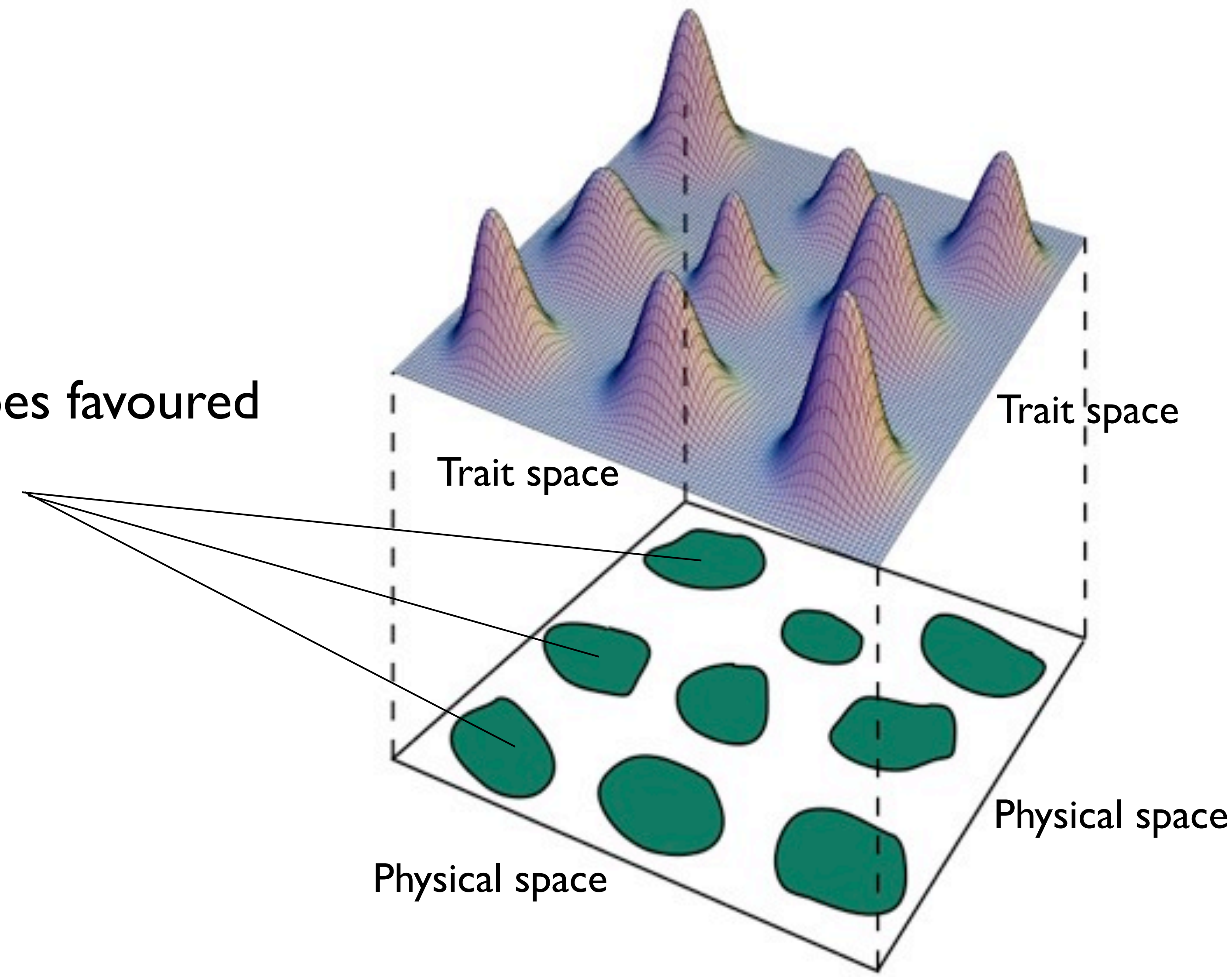
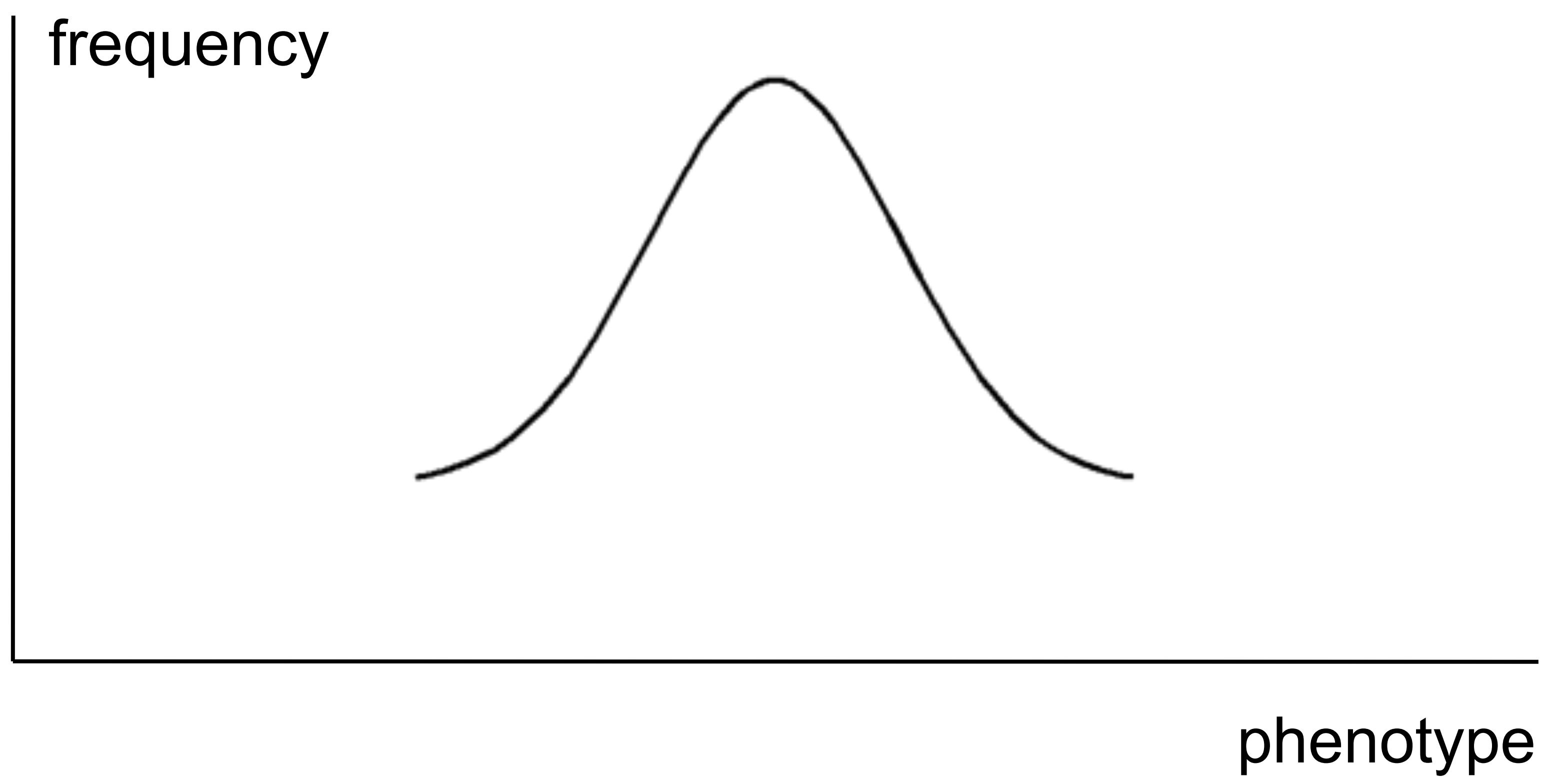


"[ ]The theory of selection among variations can explain the slow transformation of a single species in time, but it cannot, in itself, explain the splitting of species into diverse lines." (Levins and Lewontin, 1985)

Adaptive speciation due to
ecological interactions in single (well-mixed) habitat:



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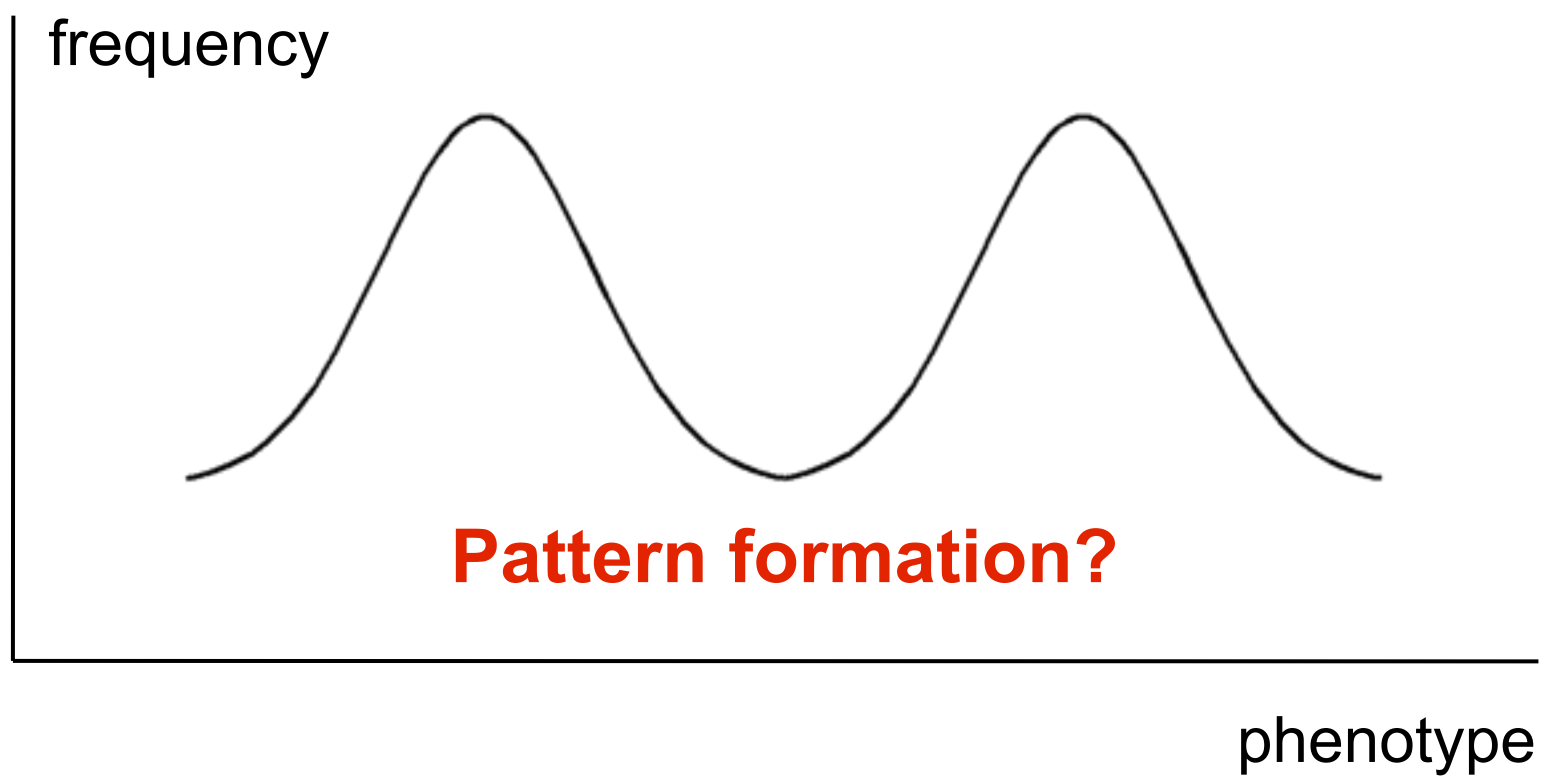
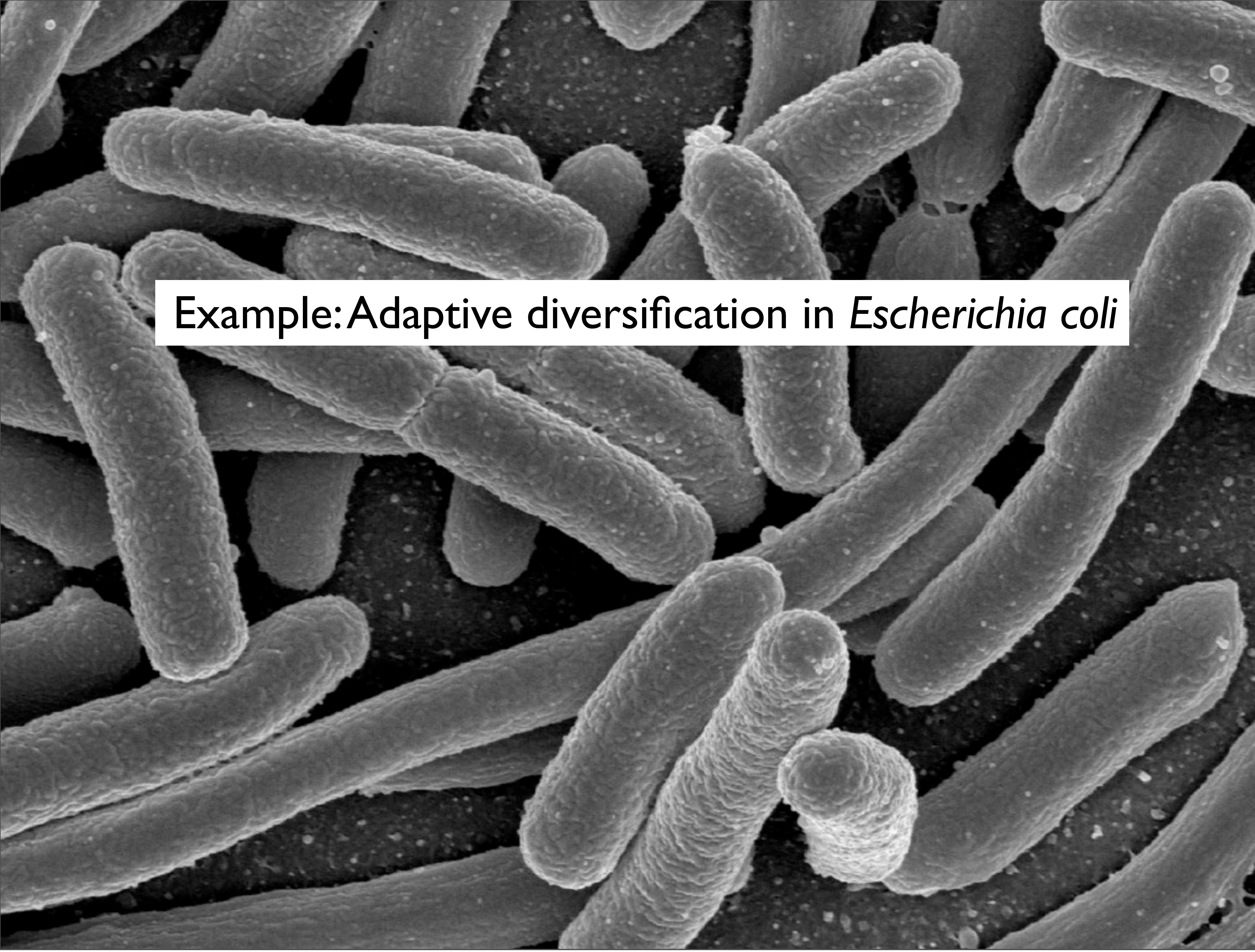


Adaptive Diversification

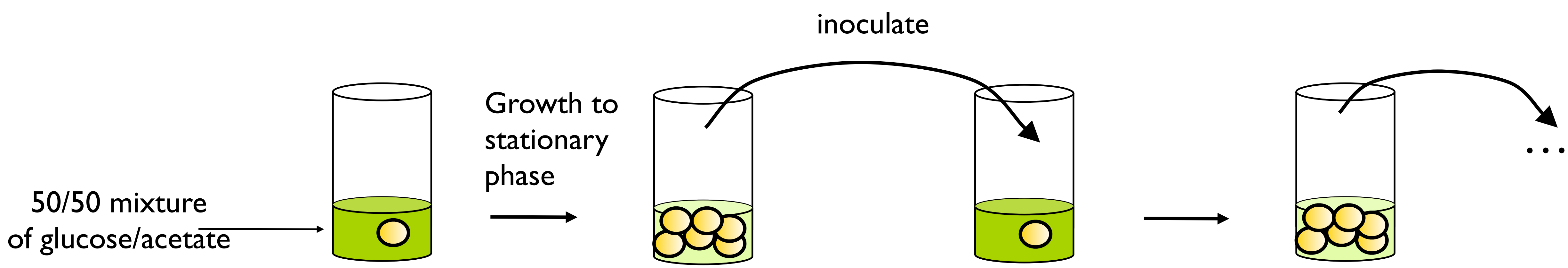
1. An empirical example
2. Two different theoretical approaches
3. Adaptive diversification in high-dimensional phenotype spaces

Example: Adaptive diversification in *Escherichia coli*

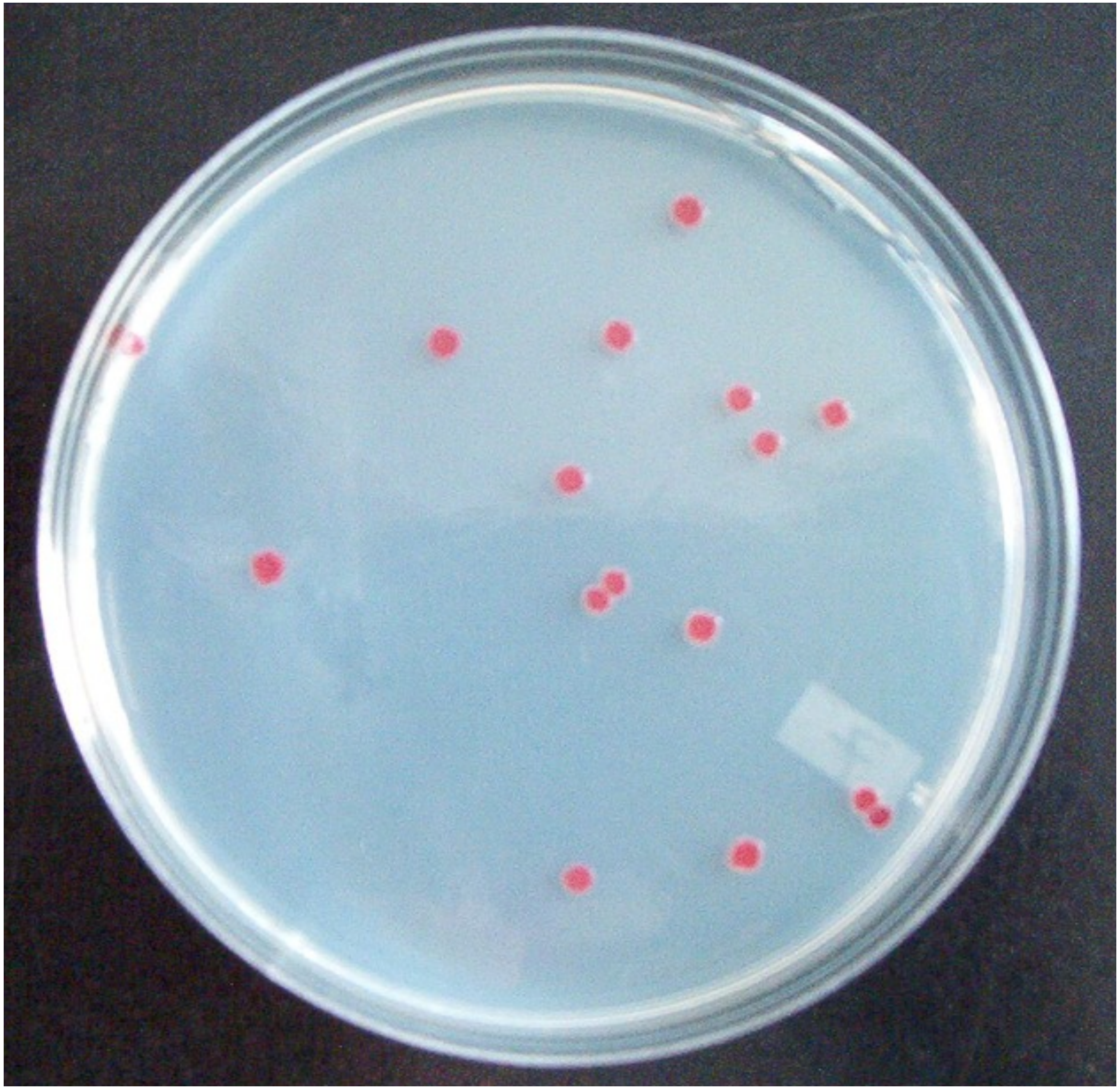


Long-term evolution experiments with *E. Coli*

- Environment: two limiting carbon sources (50% glucose, 50% acetate), well-mixed populations
- Replicate experimental lines propagated in serial batch cultures for ~1,000 generations:



Diversification in colony morphology in 10 out of 10 replicate populations:



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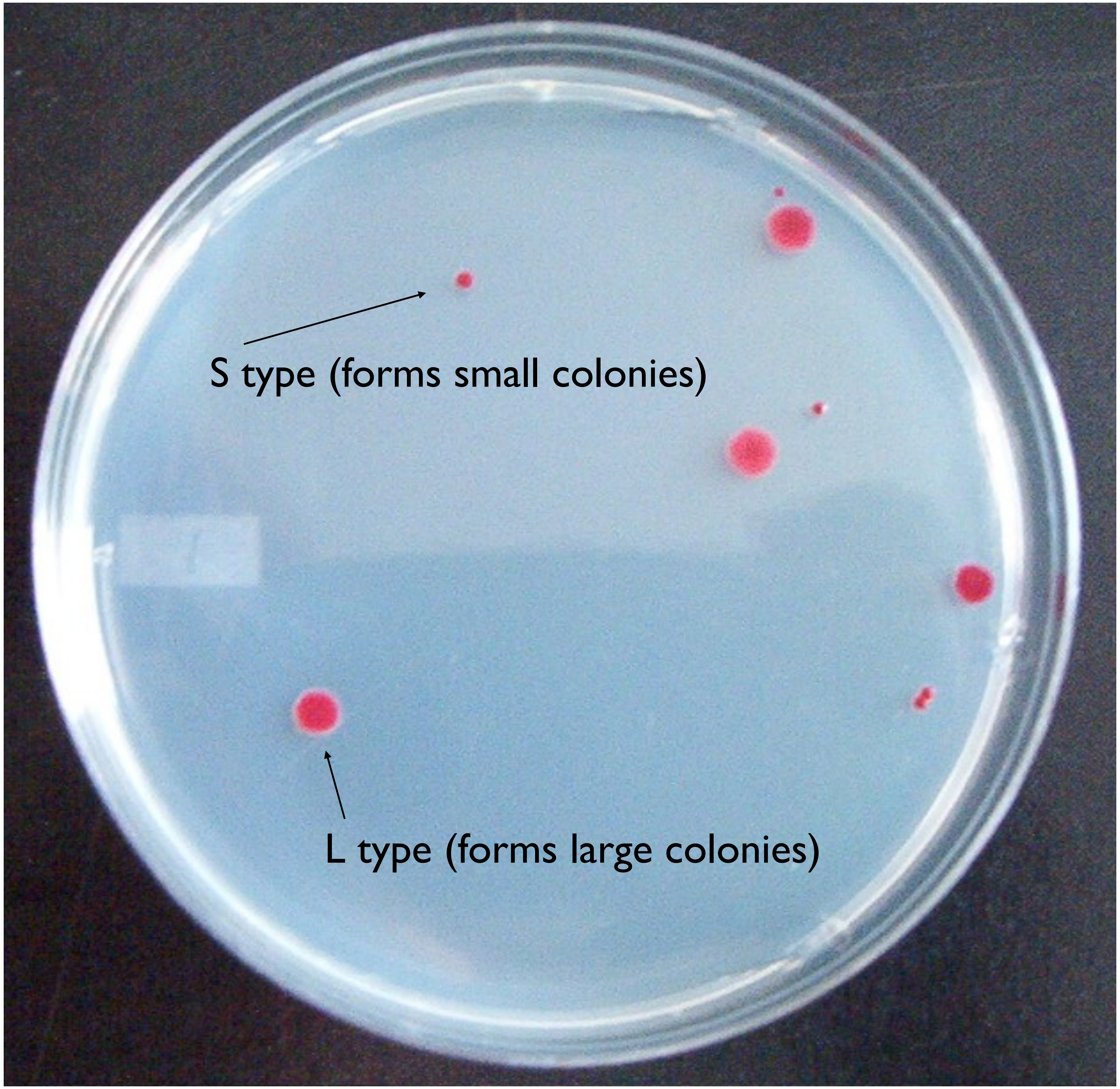
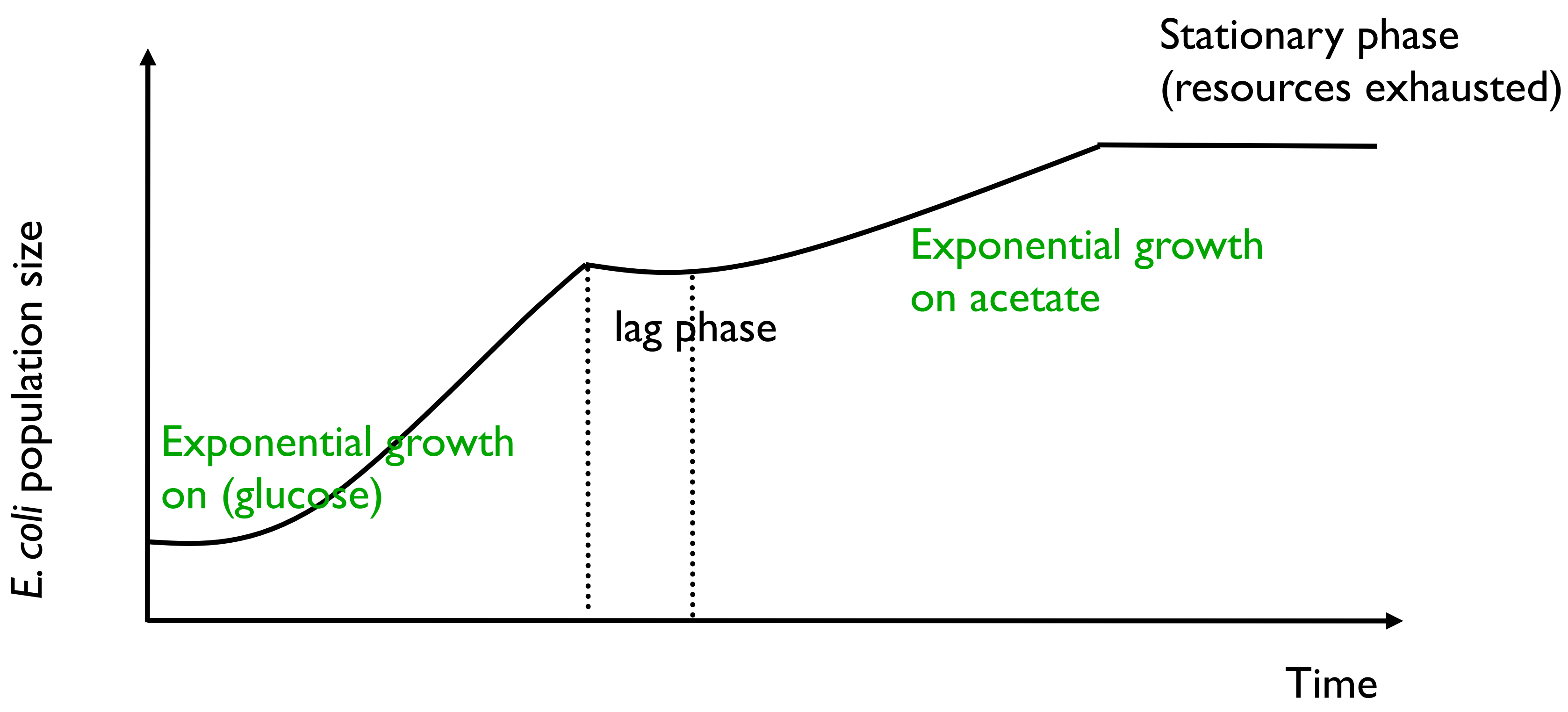


Diauxy: sequential use of two different resources in batch culture (phenotypic plasticity in seasonal environment)



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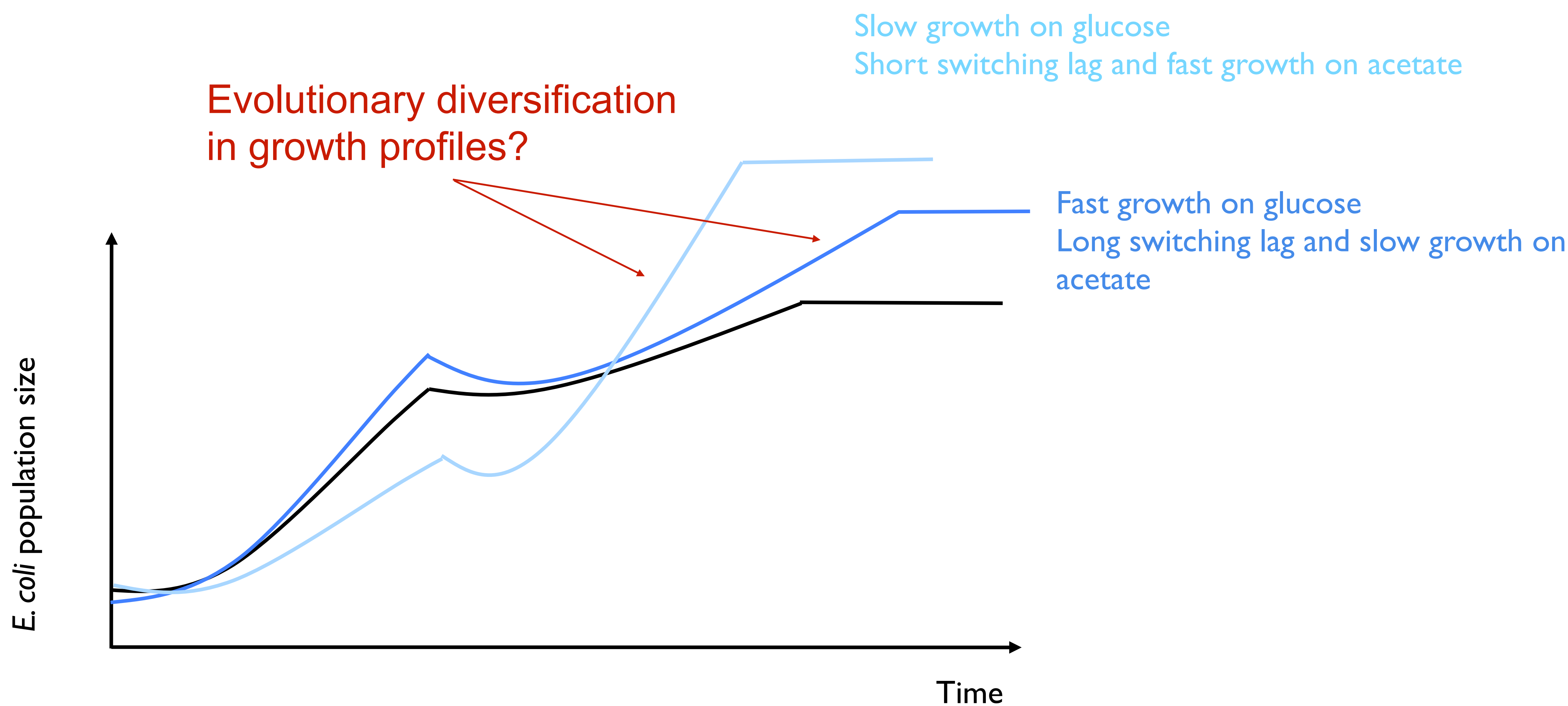
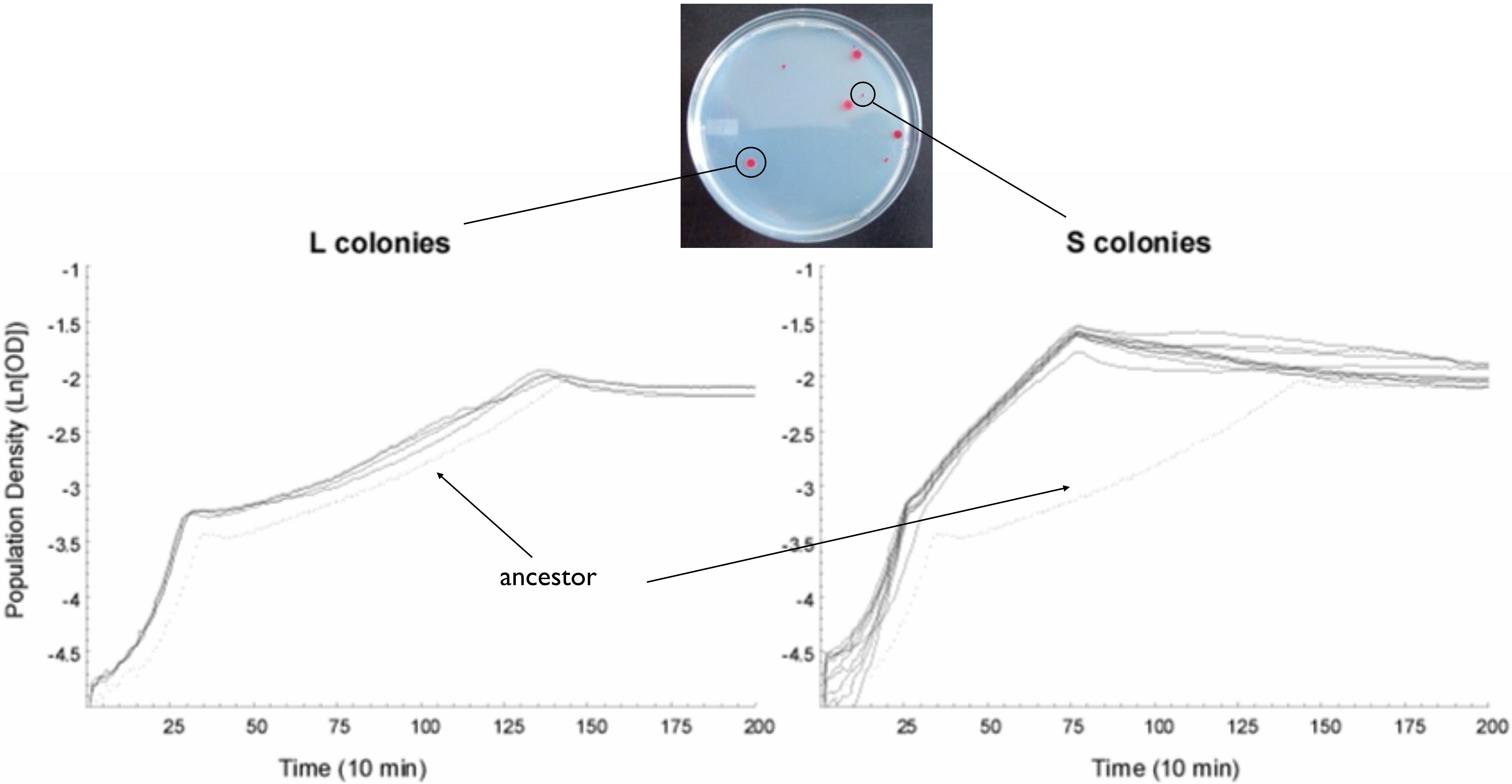
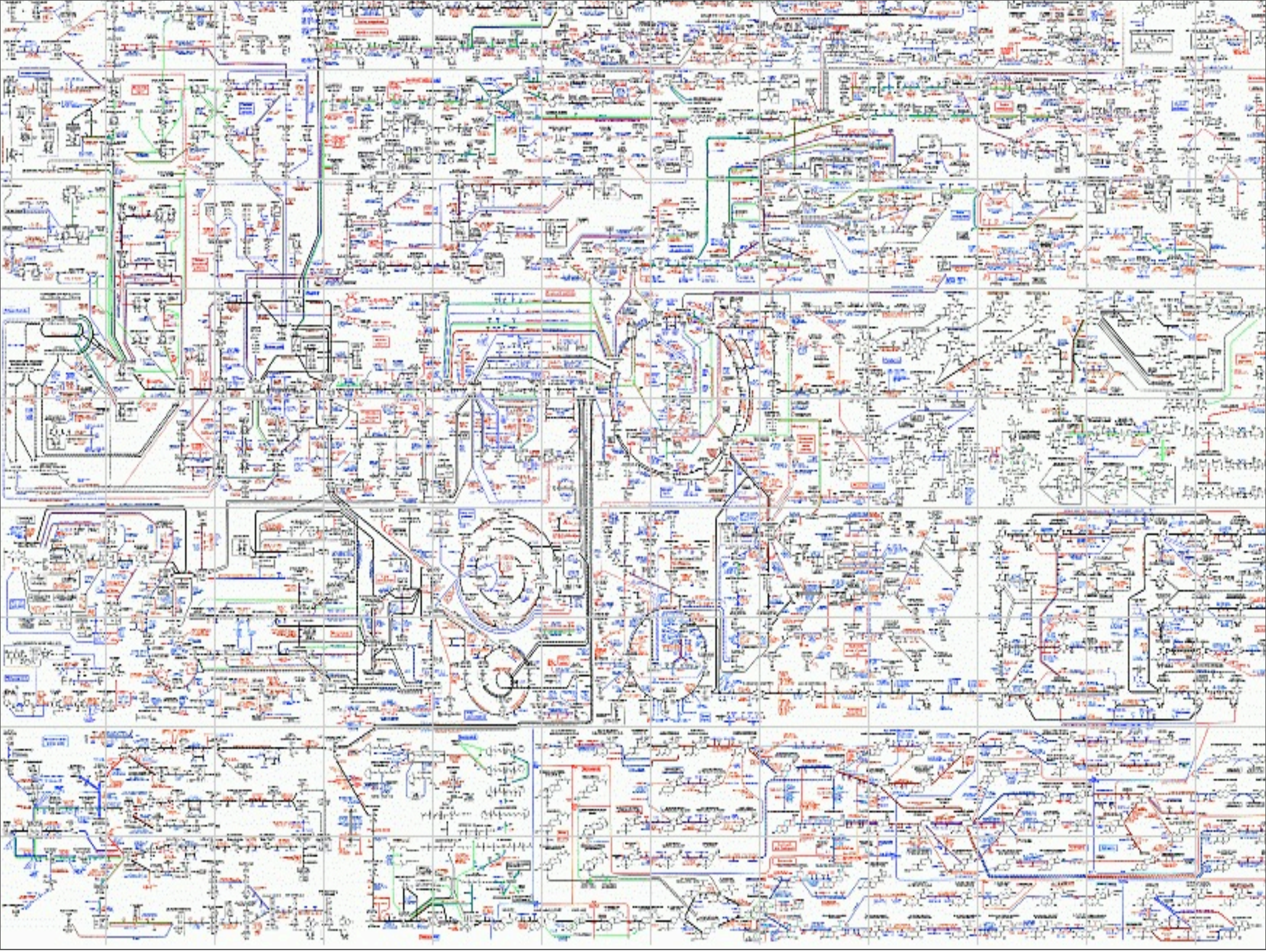
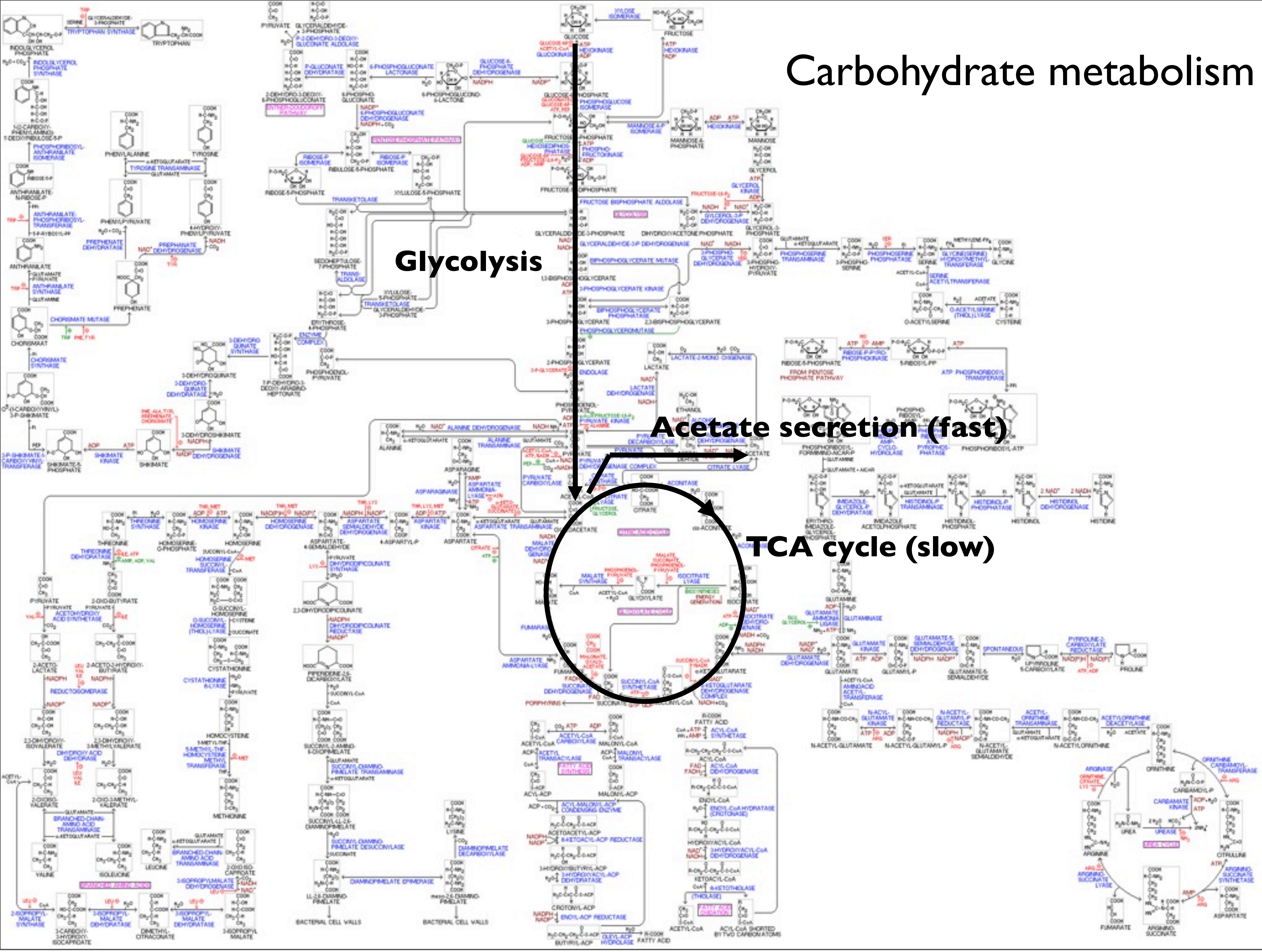


Large (L) and Small (S) colonies exhibit different diauxy behavior:



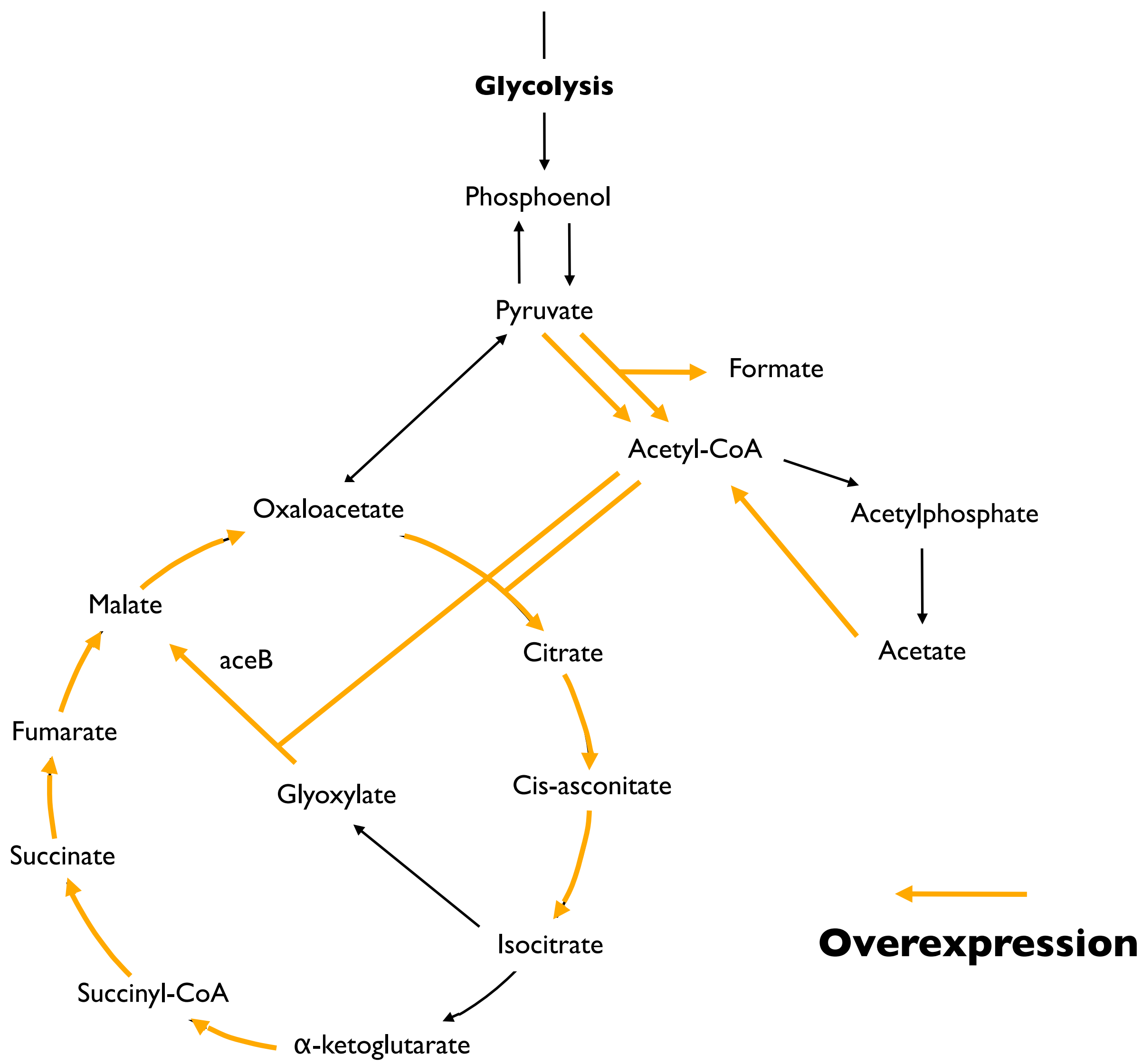


Carbohydrate metabolism

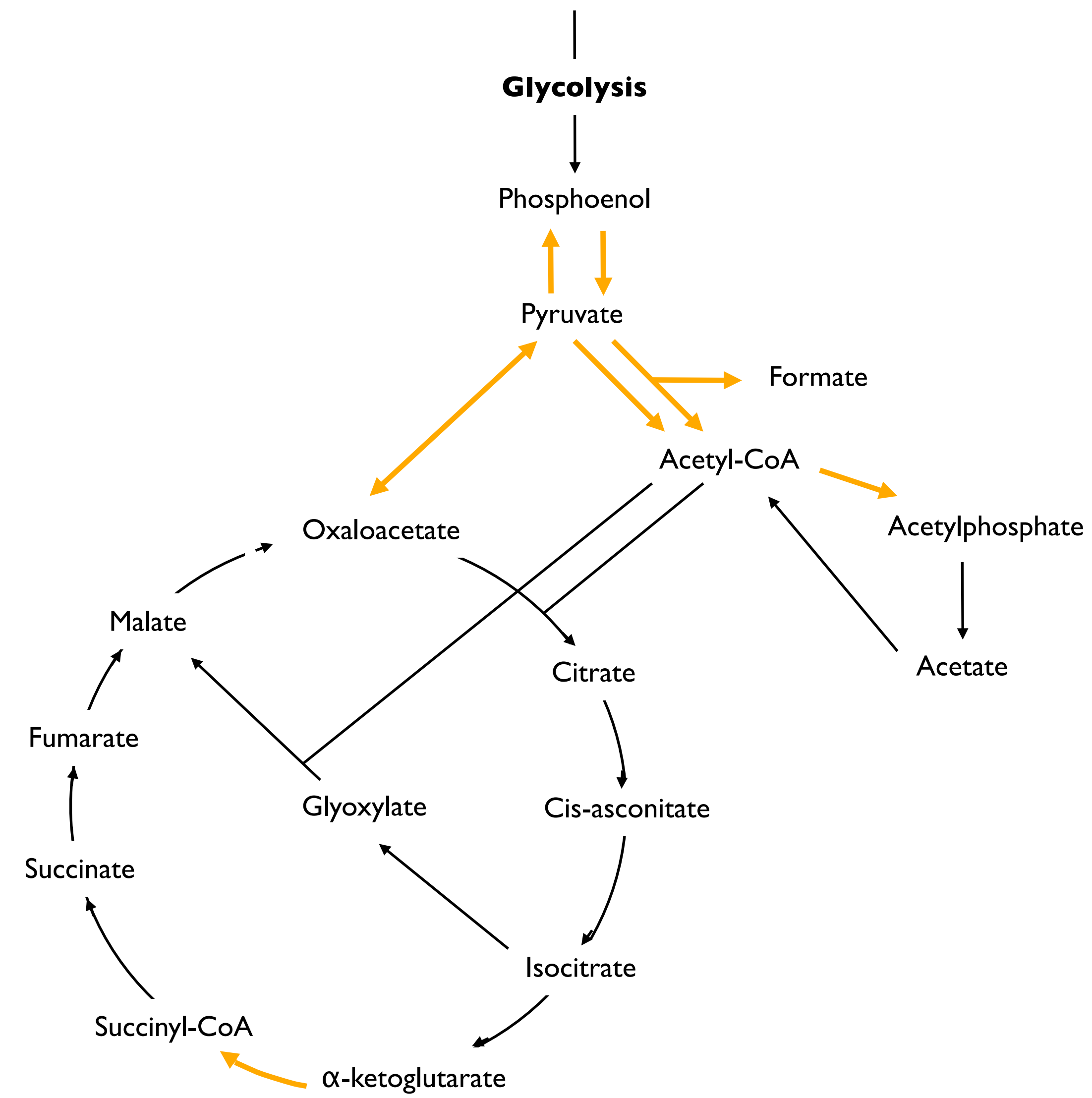


Difference in global gene expression: Increased TCA cycle activity in Smalls

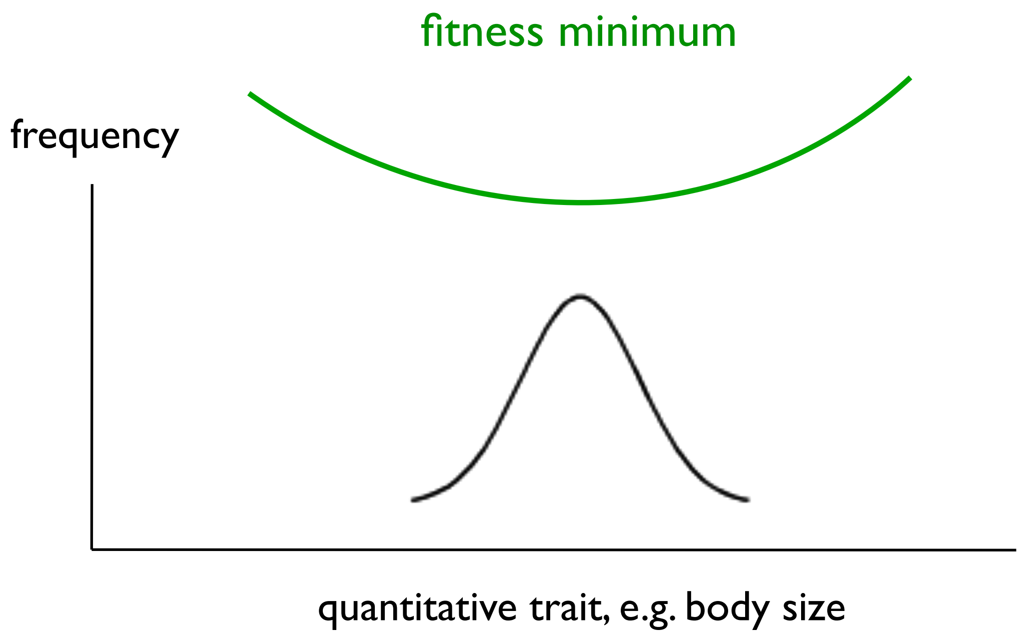
Small vs. ancestor:



Large vs. ancestor:



Adaptive Diversificiation



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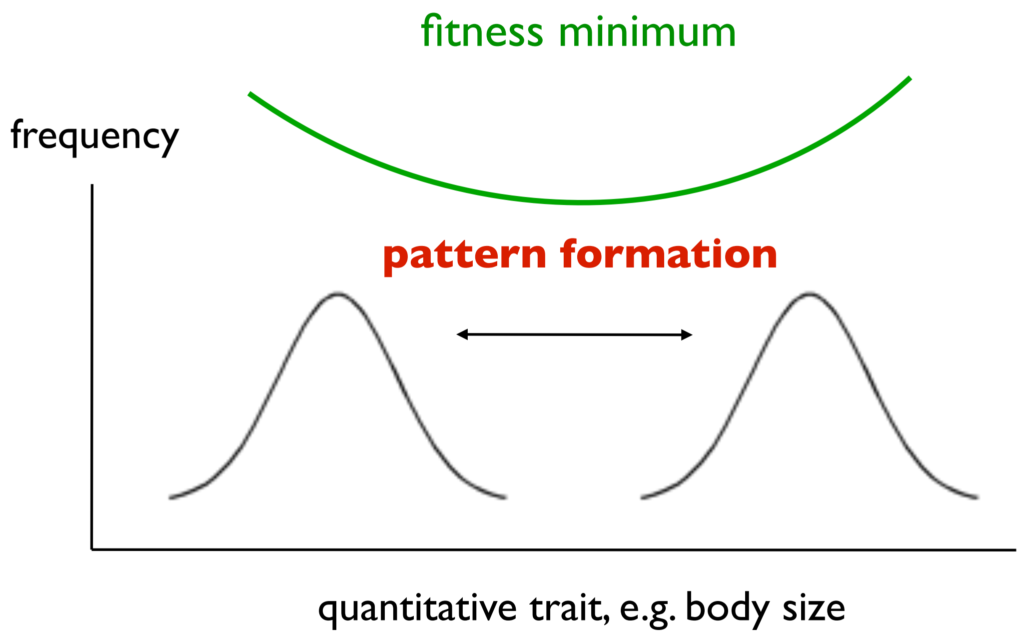

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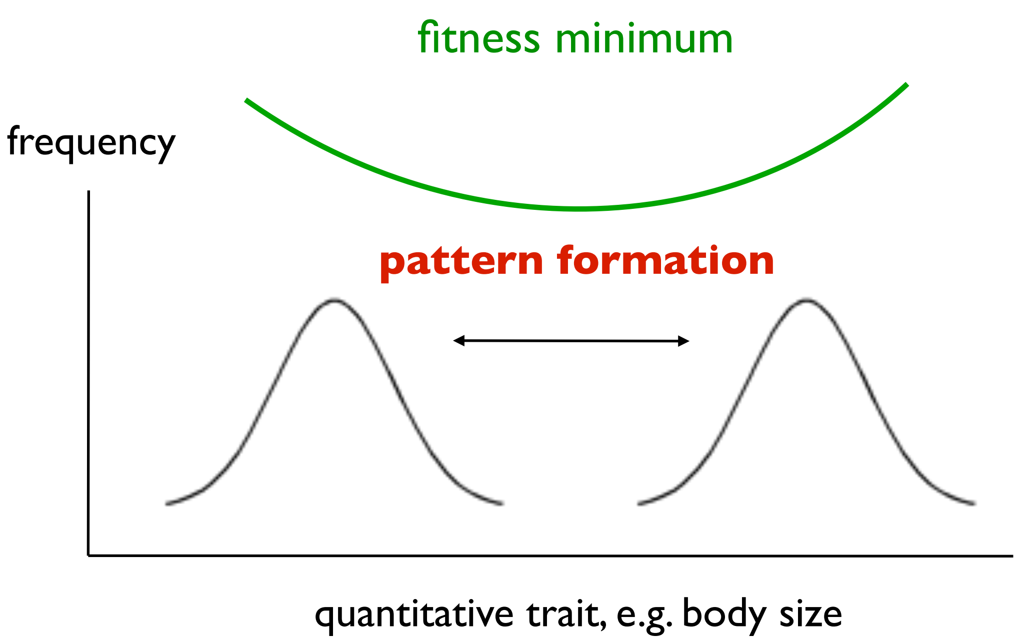
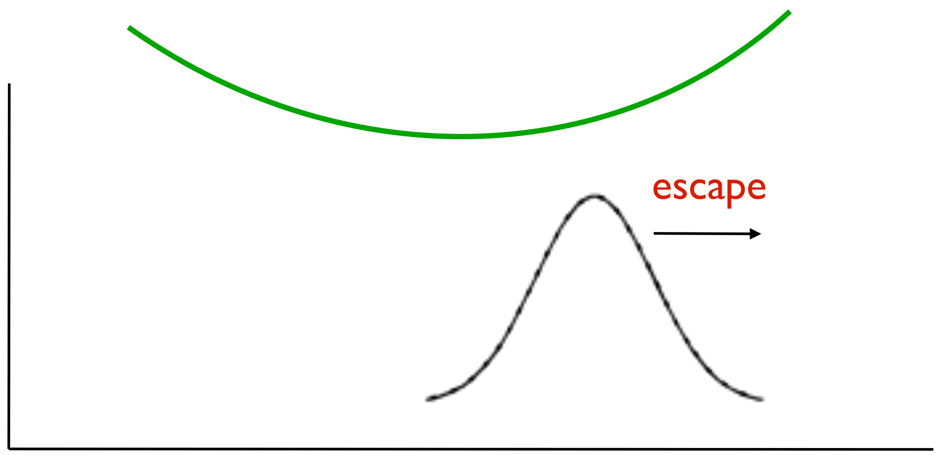
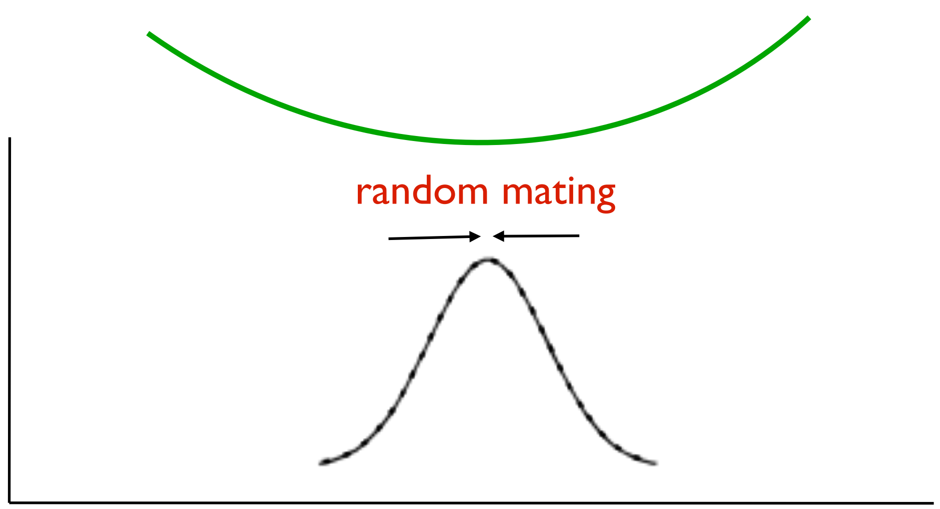


Theoretical Problems

Ecology: fitness minima are unstable



Population genetics: recombination prevents divergence



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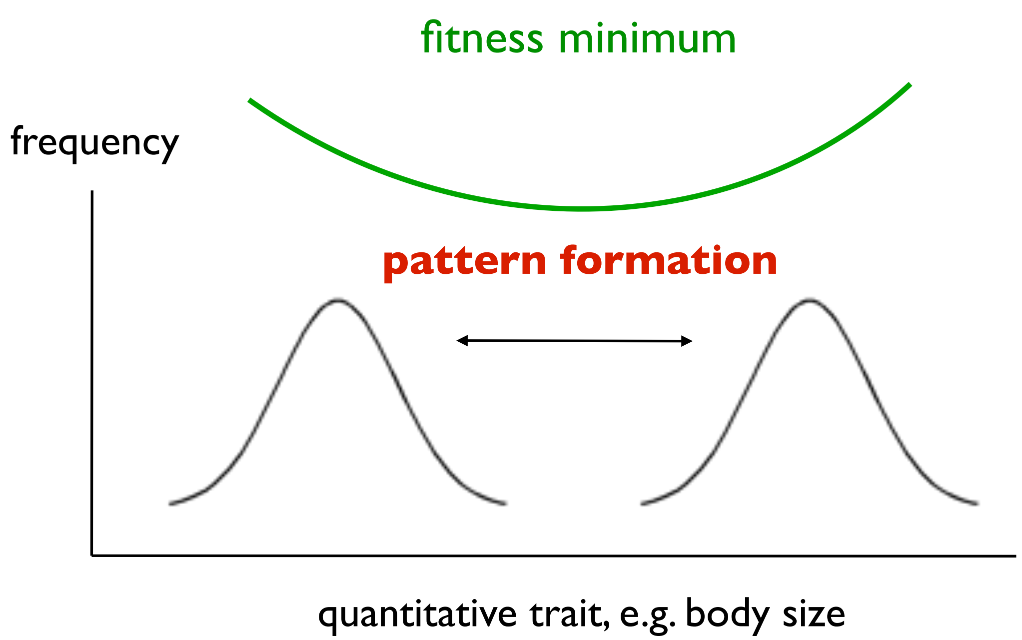

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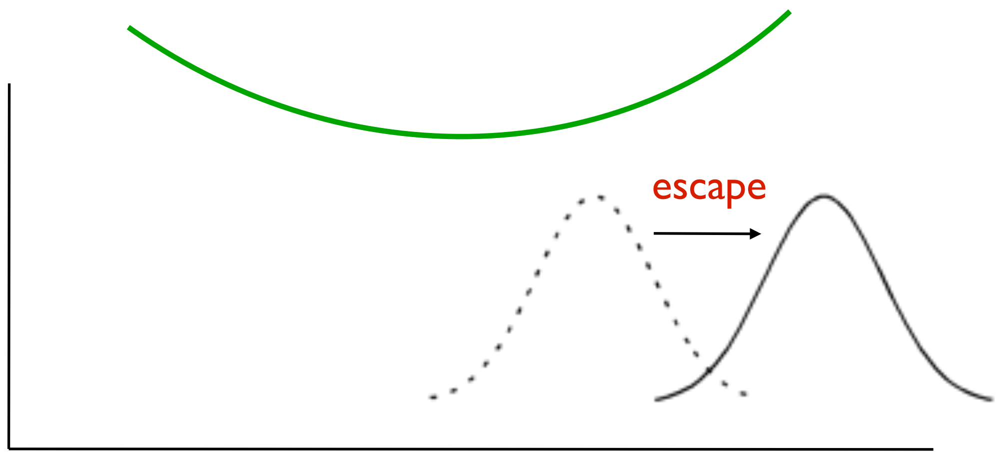

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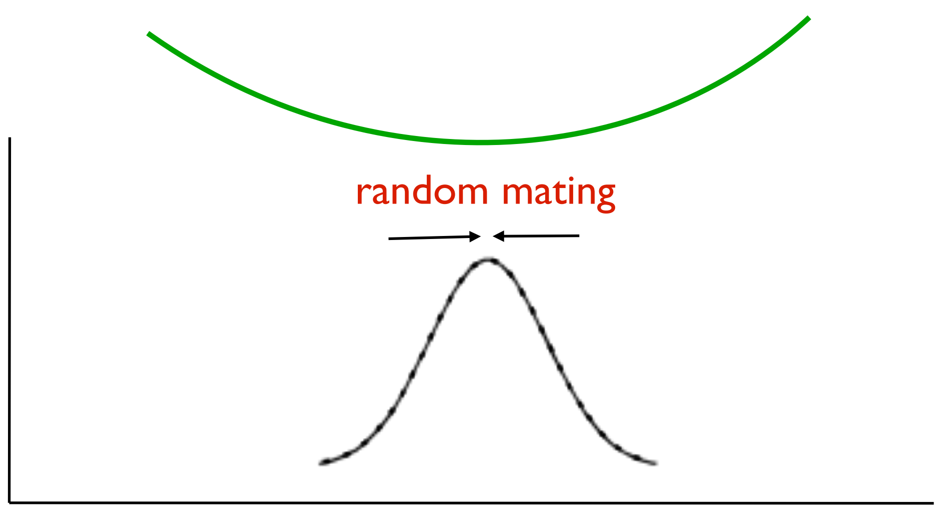

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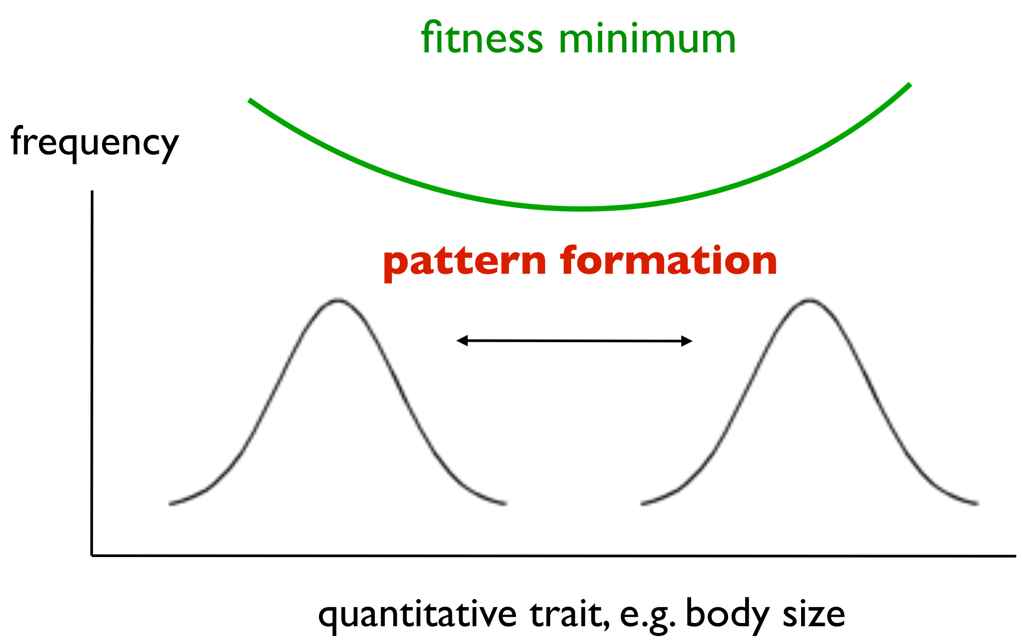

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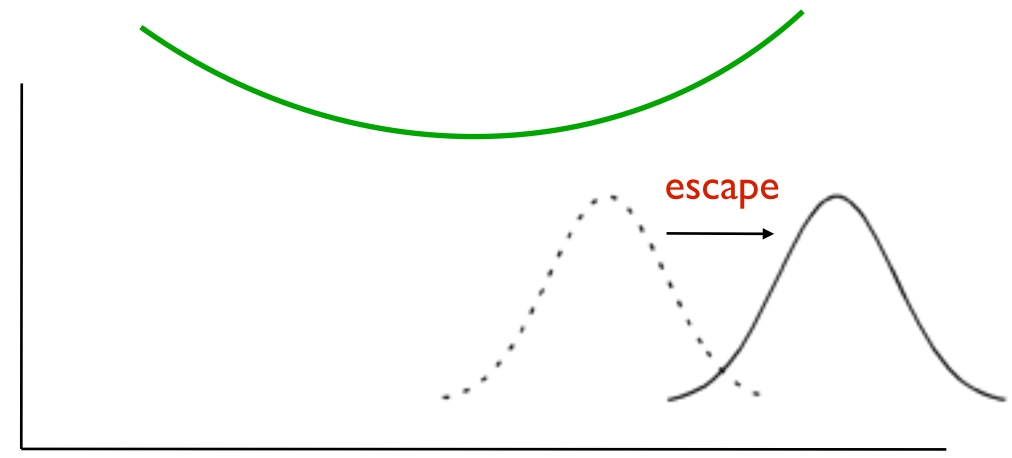

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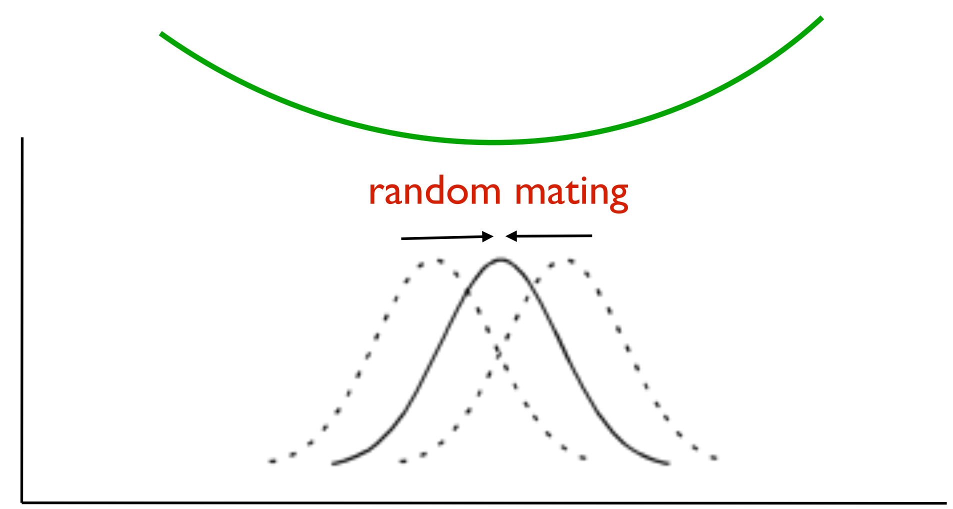
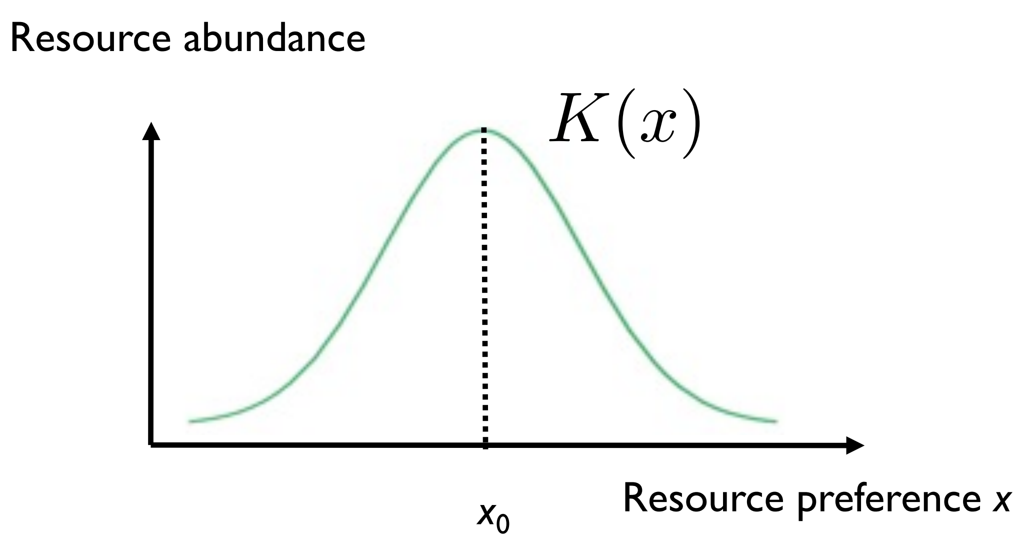
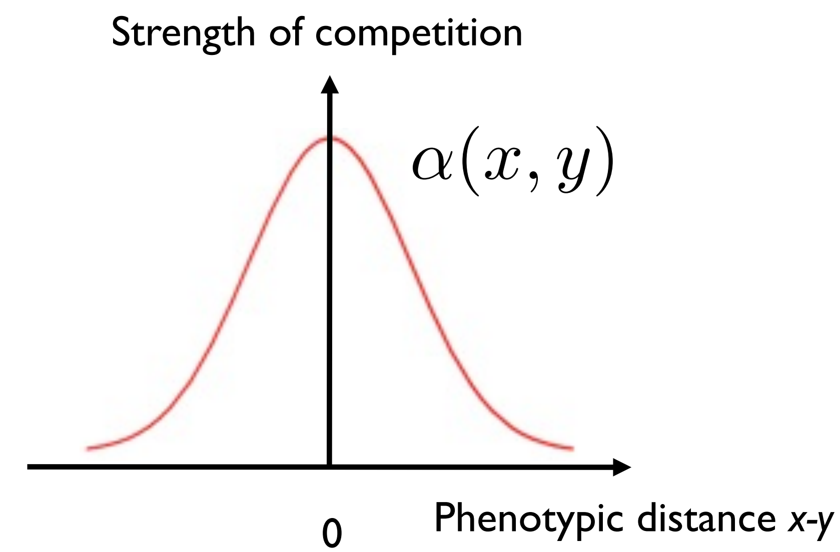


Adaptive diversification due to resource competition





individuals with phenotype *x*

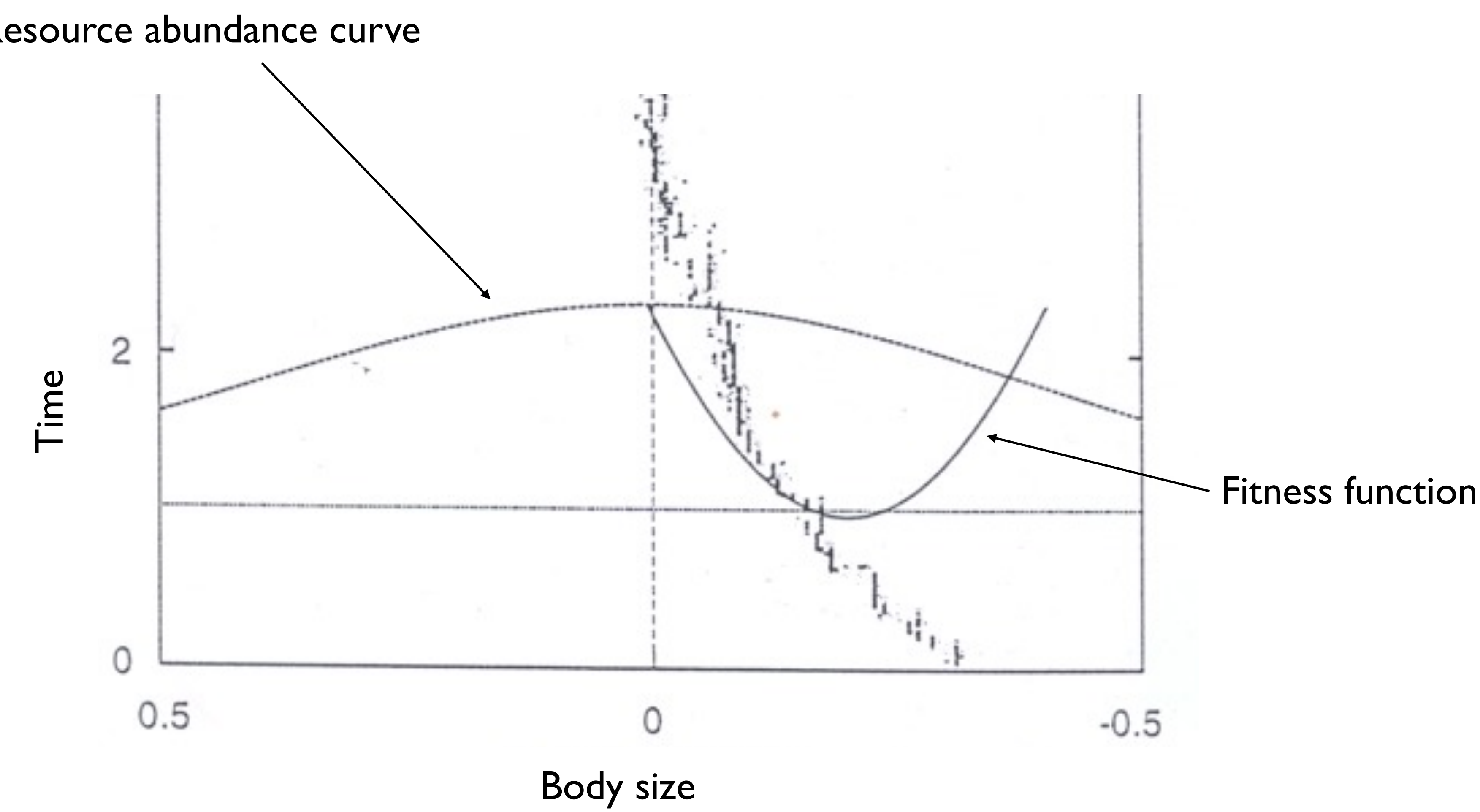
- per capita birth rate: $b = 1$ (constant), asexual reproduction with small mutations

- per capita death rate:

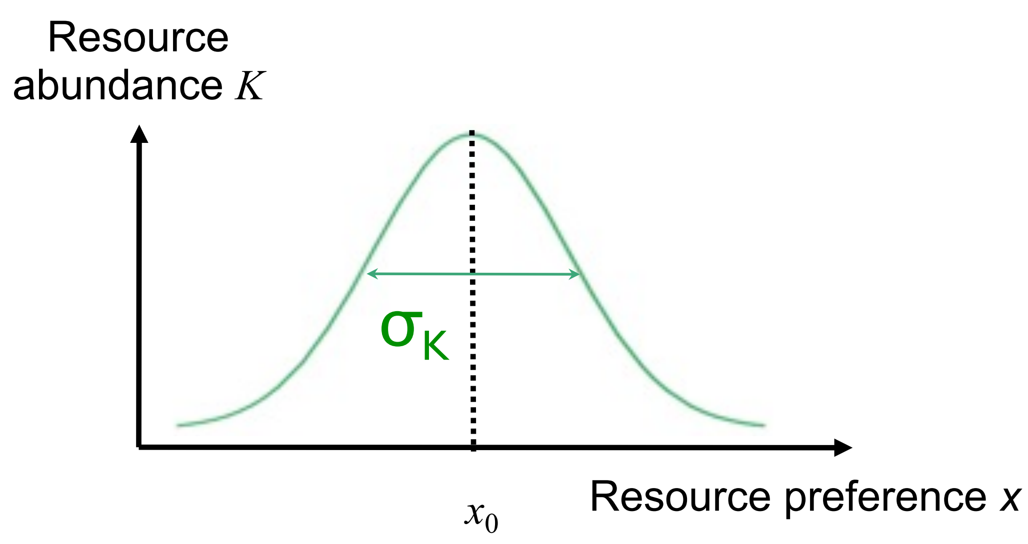
$$\frac{b}{K(x)} \sum_y \alpha(x - y)$$

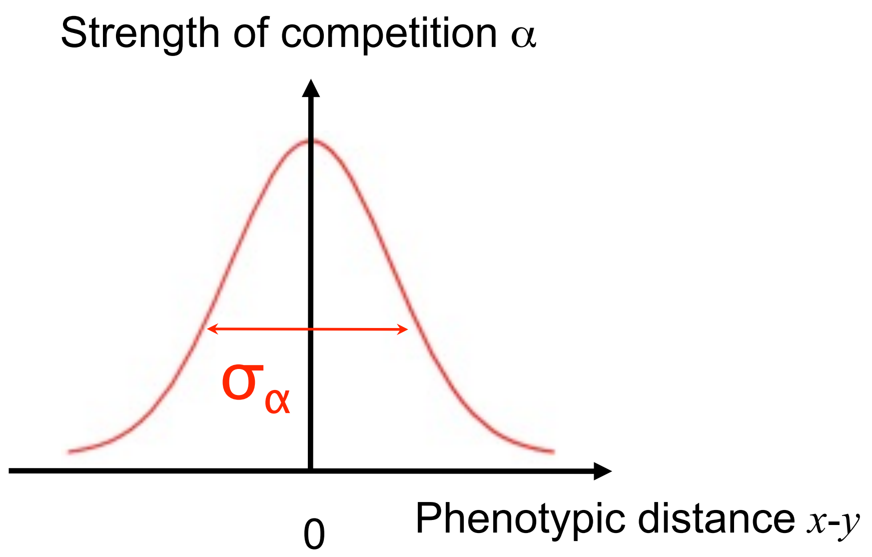
depends on phenotype and on the phenotypes of the other individual in the population (rare phenotypes have lower death rates than common phenotypes)

First, mean phenotype evolves to maximum of resource curve…

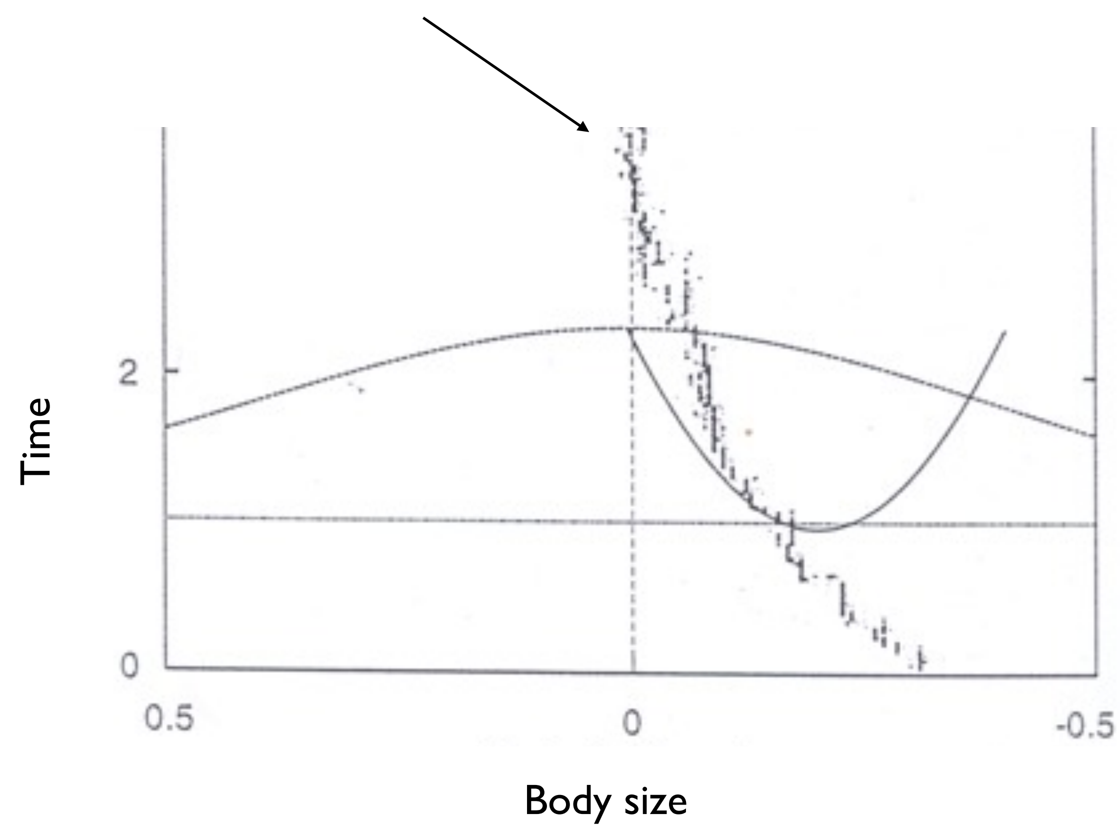


Dependence on ecological parameters

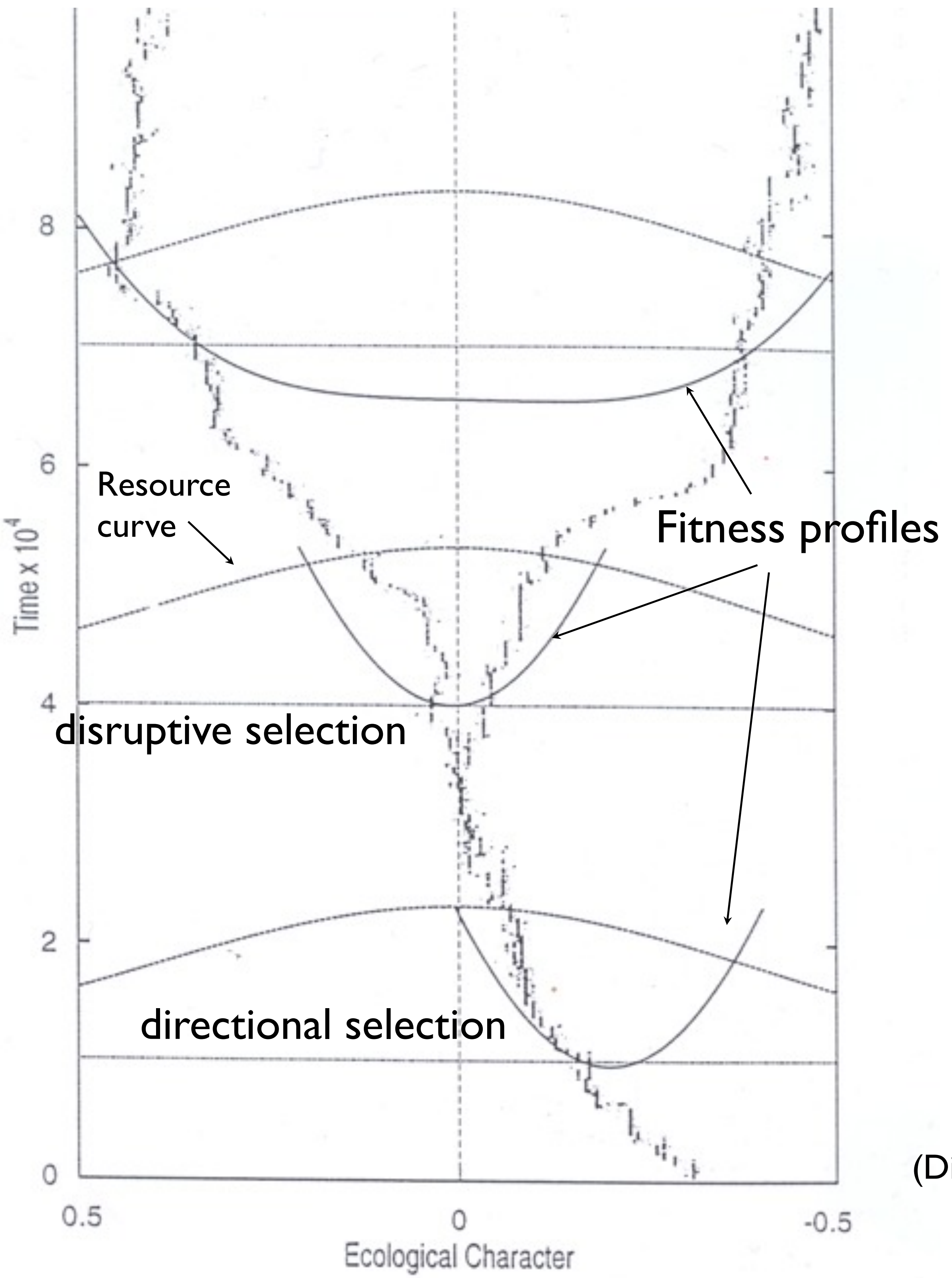




$\sigma_K < \sigma_\alpha$: the population remains at the maximum of the resource abundance curve



$\sigma_K > \sigma_\alpha$: ***Evolutionary branching***



(Dieckmann & Doebeli, *Nature*, 1999)

Adaptive Dynamics (Hans Metz)

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Logistic dynamics of monomorphic resident *x*:

$$\frac{dN(x)}{dt} = N(x)\left(1 - \frac{N(x)}{K(x)}\right)$$

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Per capita growth rate of rare mutant y in monomorphic resident *x*

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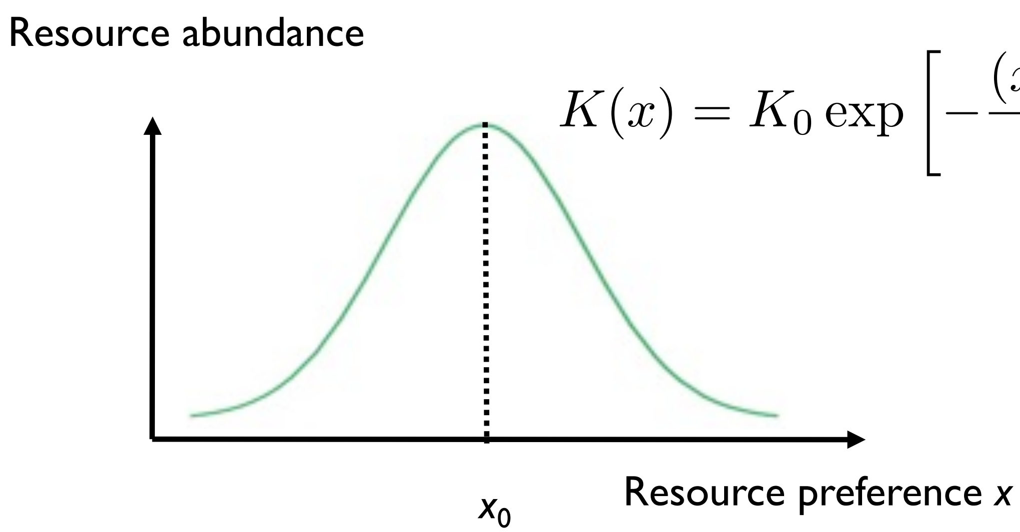
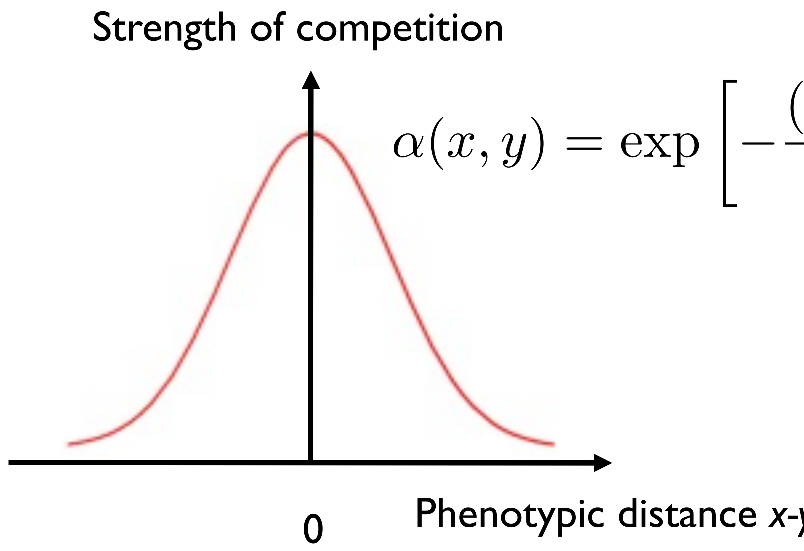
Evolutionary stability:

$$\left.\frac{\partial^2 f}{dy^2}(x^*, y)\right|_{y=x^*}$$

Gaussian case:



$$K(x) = K_0 \exp\left[-\frac{(x-x_0)^2}{2\sigma_K^2}\right]$$



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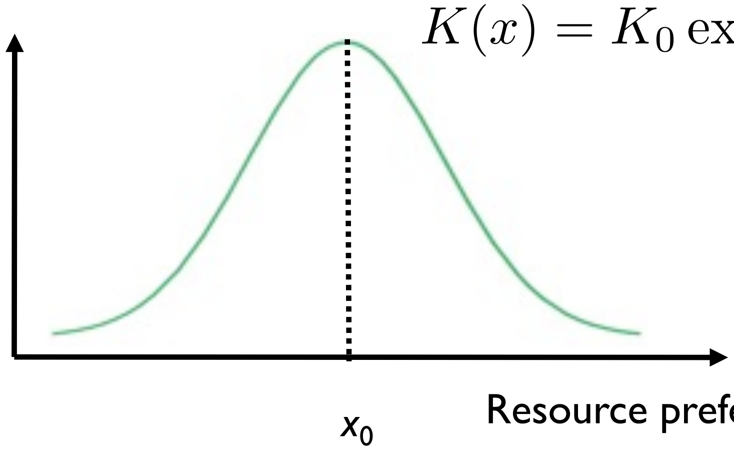

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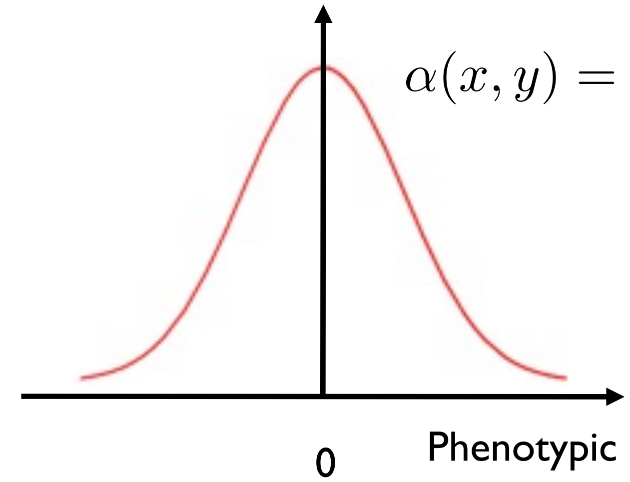

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$$= \frac{1}{\sigma_\alpha^2} - \frac{1}{\sigma_K^2}$$

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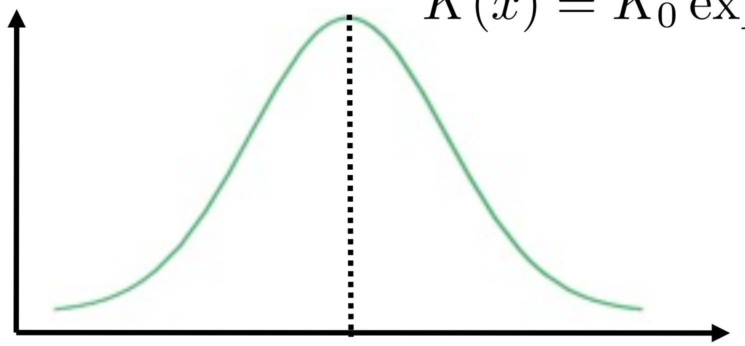

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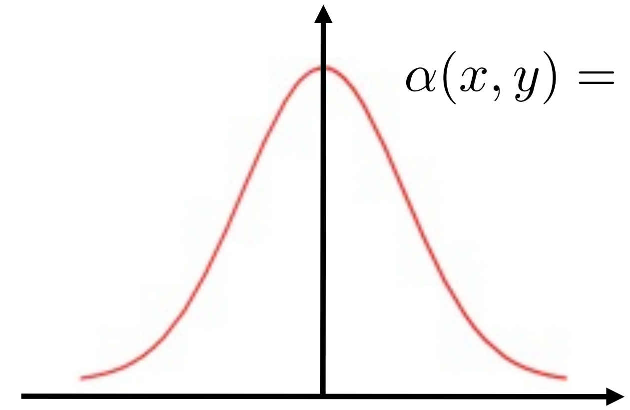

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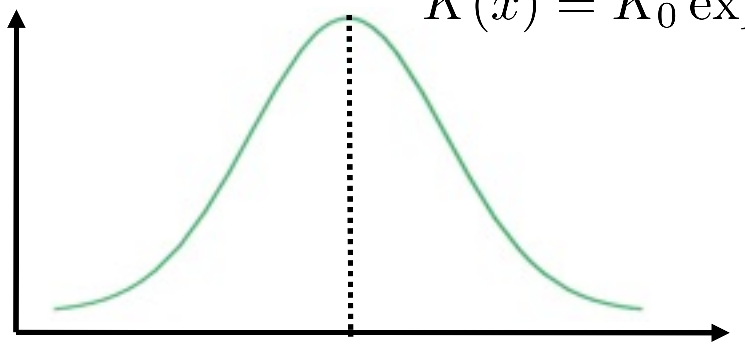
Resource abundance



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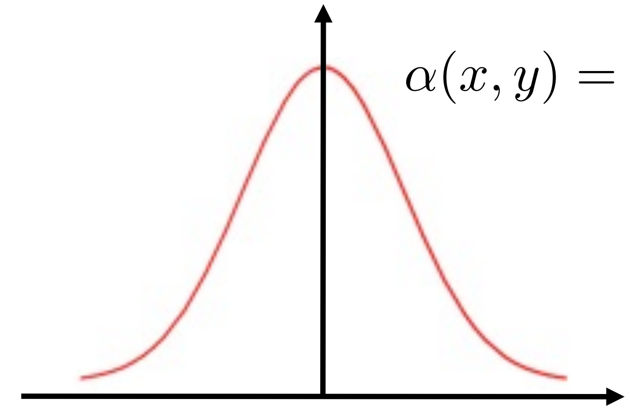
Strength of competition



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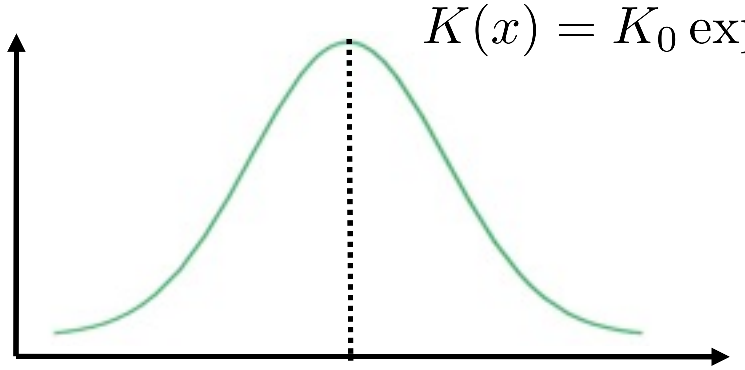

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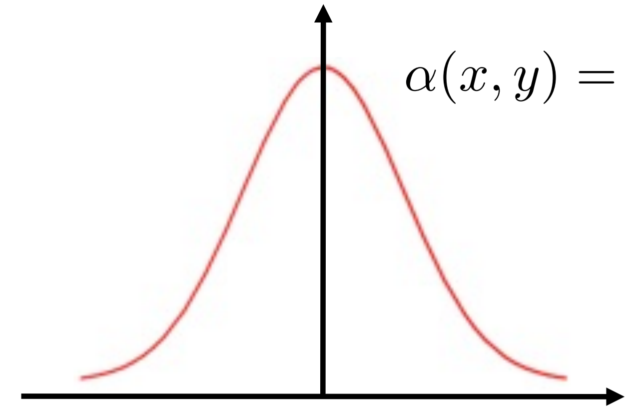

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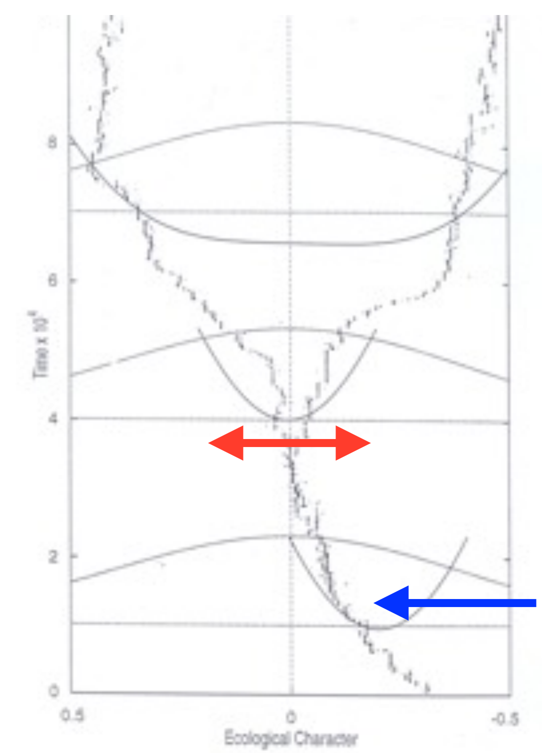
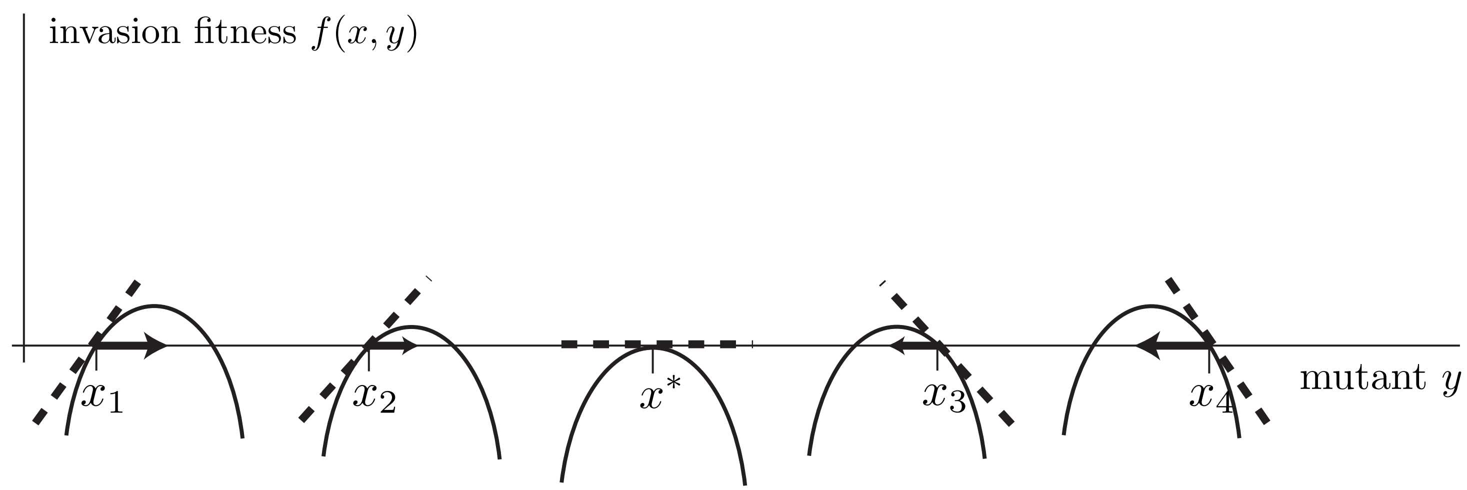


Evolutionary branching occurs if an attractor of adaptive dynamics represents a fitness minimum

Two generic evolutionary scenarios

Convergence stable and evolutionarily stable strategy



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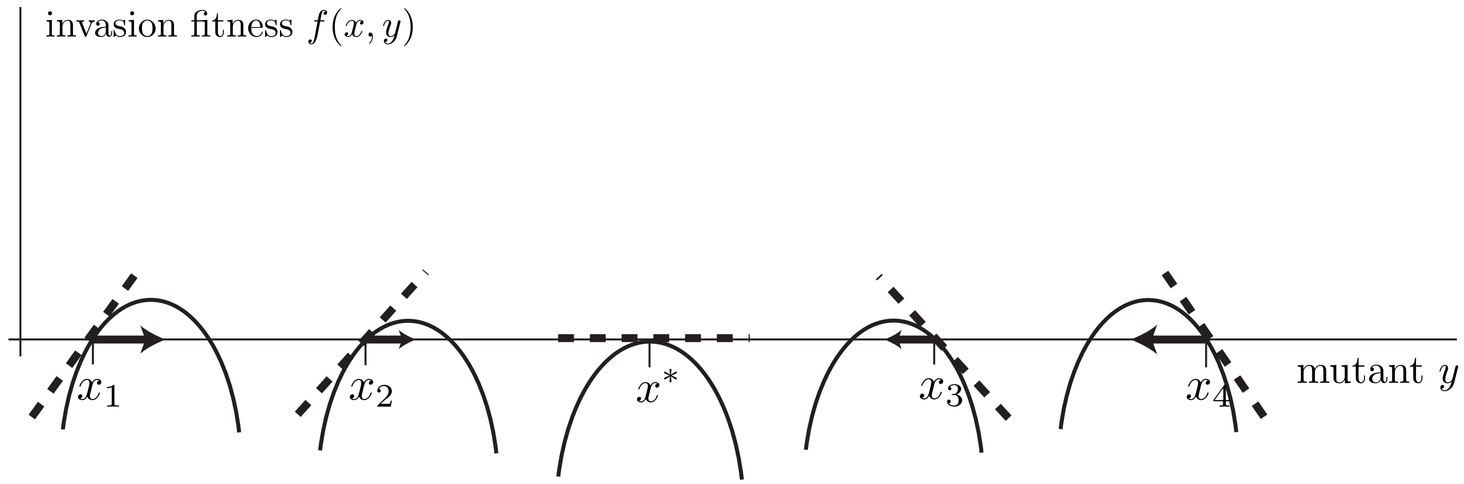
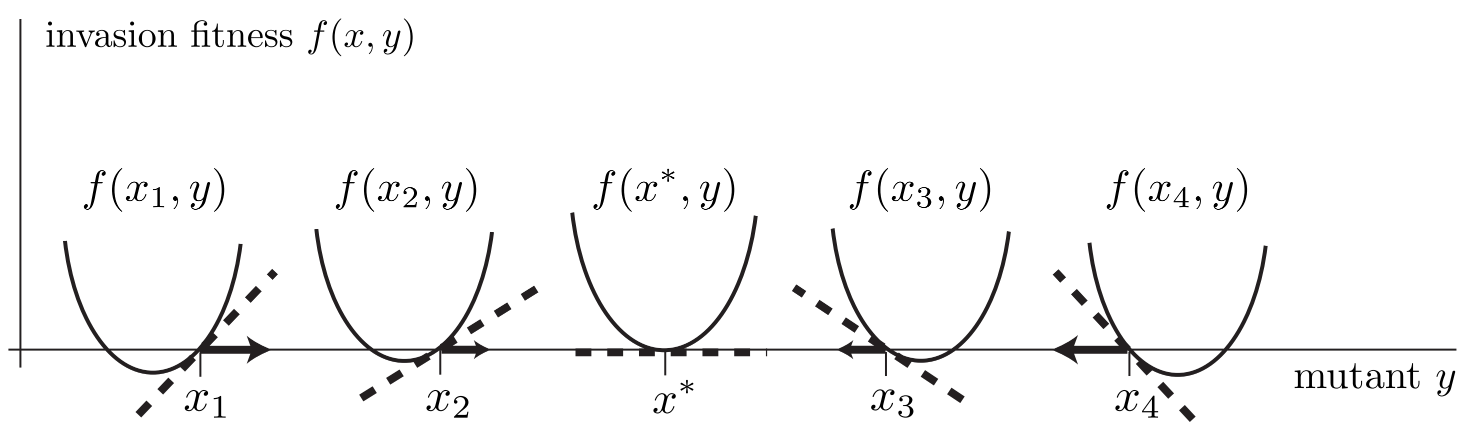
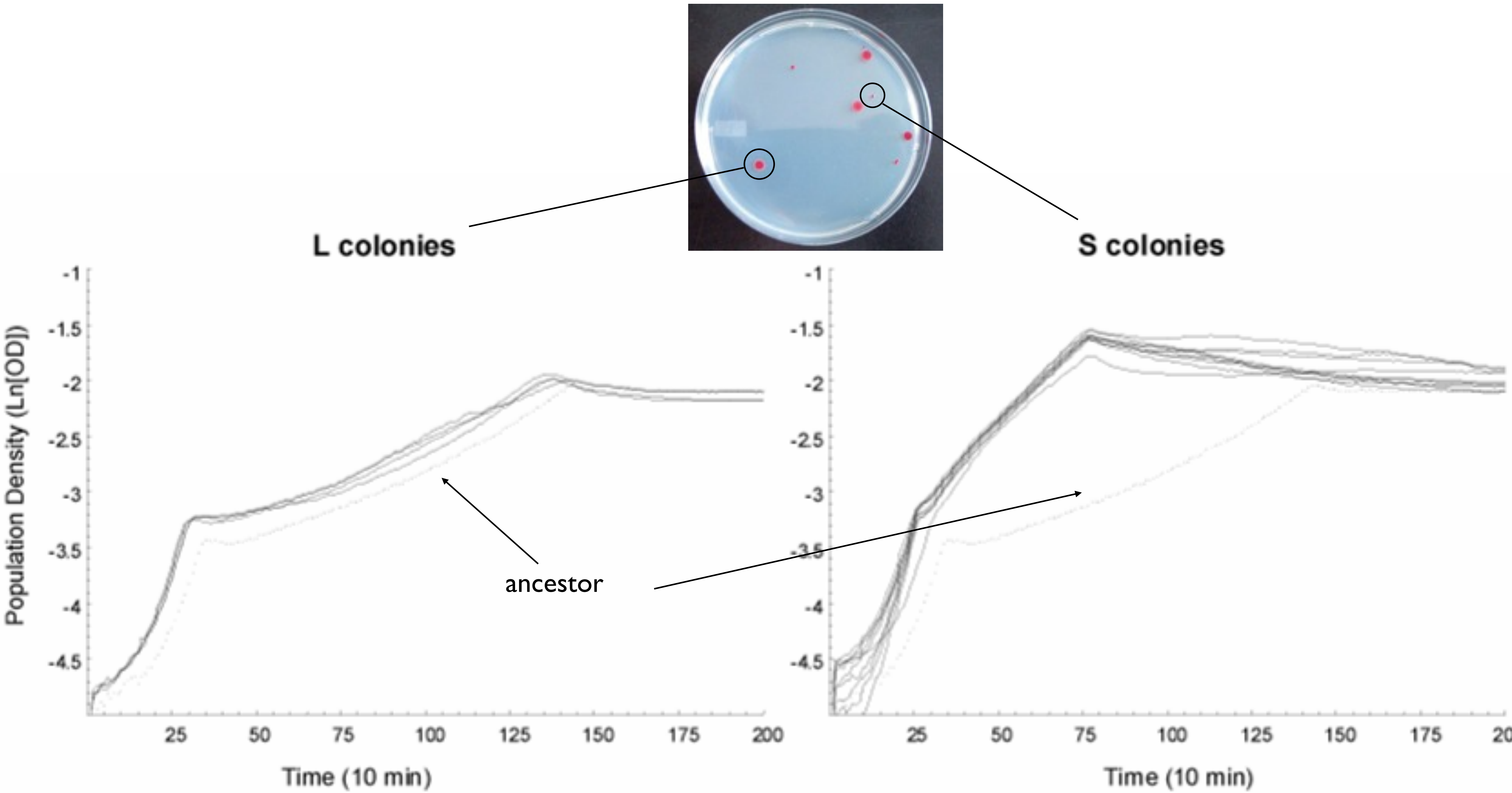


Evolutionary branching point



Diversification in bacterial populations:



Gene expression analysis reveals two types of changes:

1. Genes that are differentially expressed between Large and Small
    - growth in anaerobic conditions (low glucose concentration)
2. Genes that are differentially expressed between ancestor and both evolved strains
    - growth in aerobic conditions (high glucose concentration)
    - transport efficiency during stationary phase

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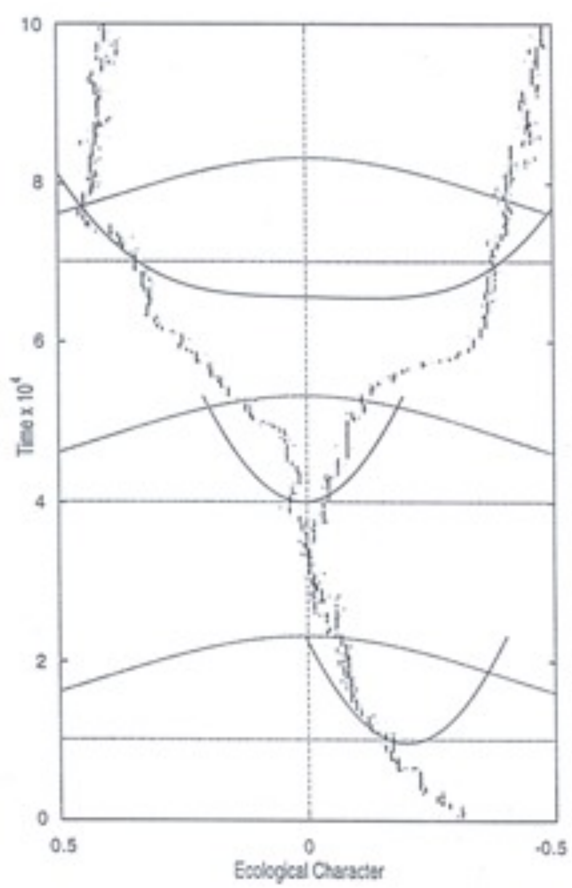
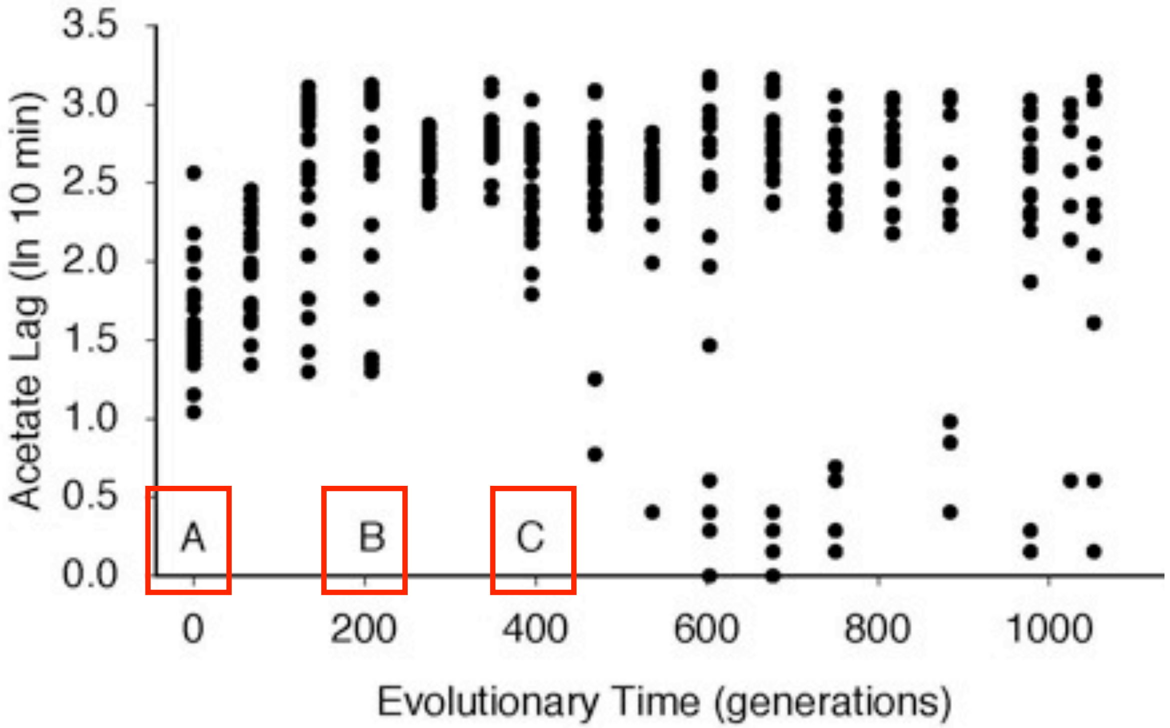


Evolutionary branching in switching lag:



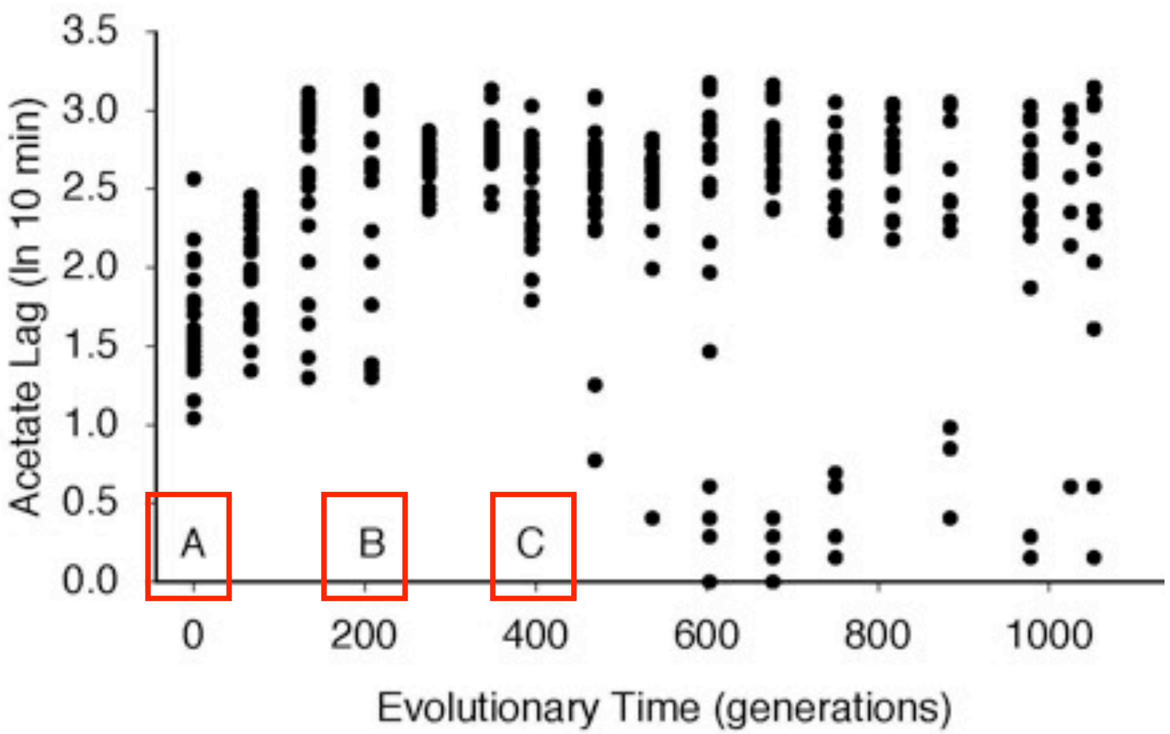
A: ancestral strain

B: midpoint

C: Most recent common ancestor (MRCA)

Evolutionary branching in switching lag:

Rediversification from different time points A, B, C in the "fossil record":



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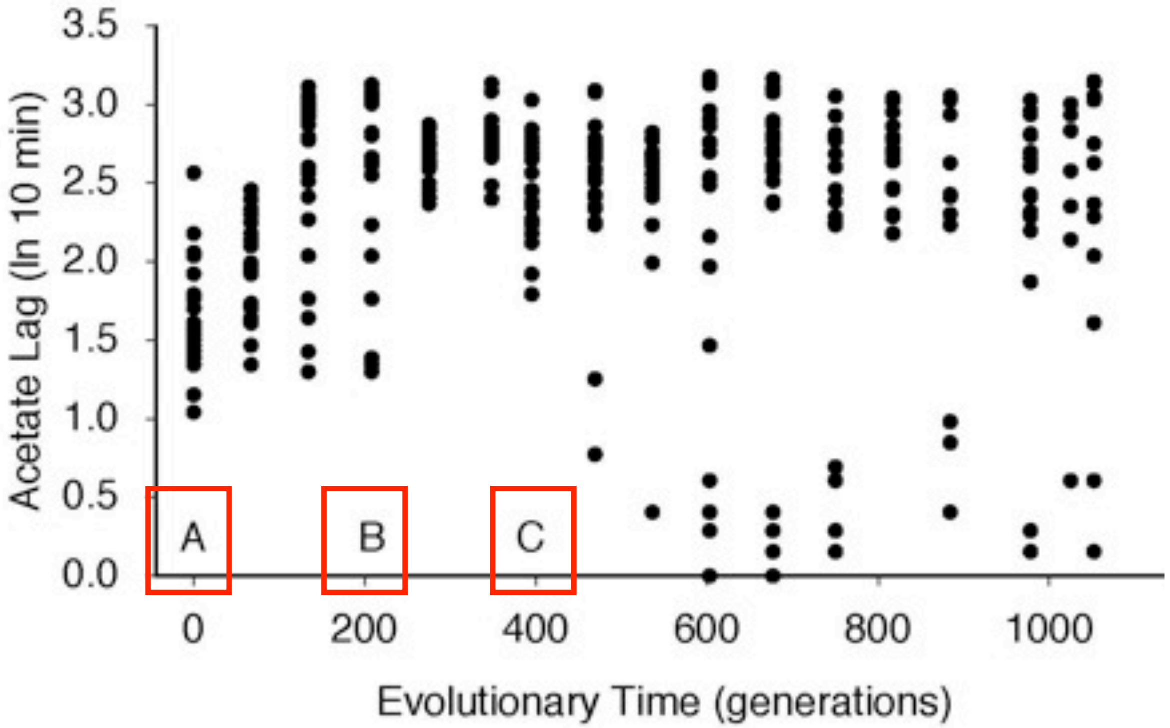

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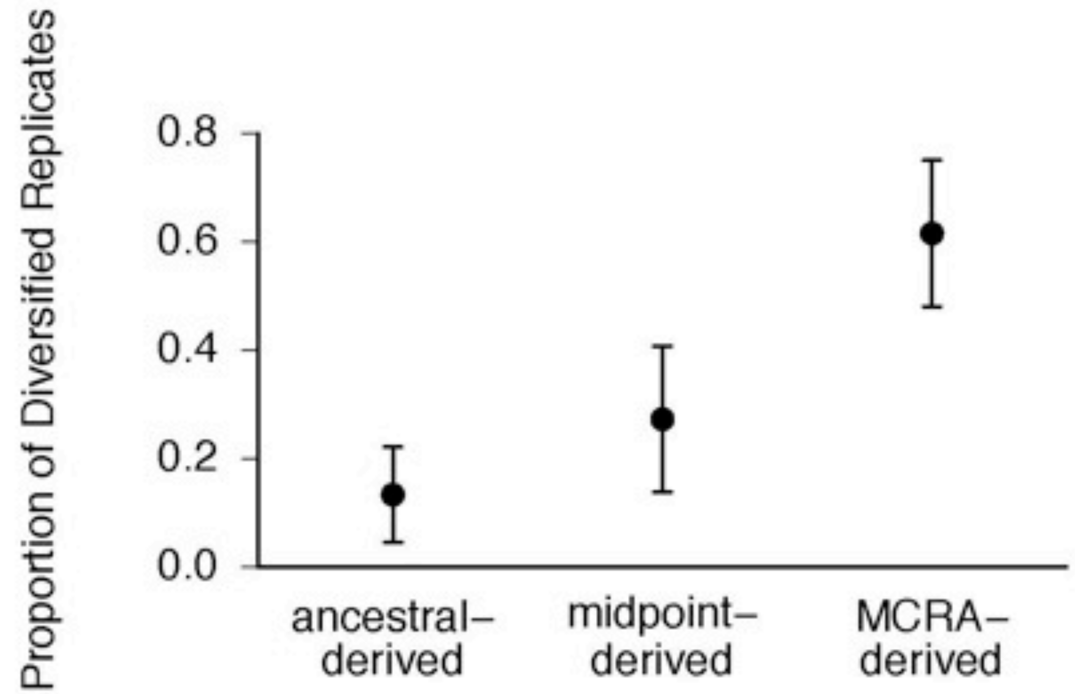
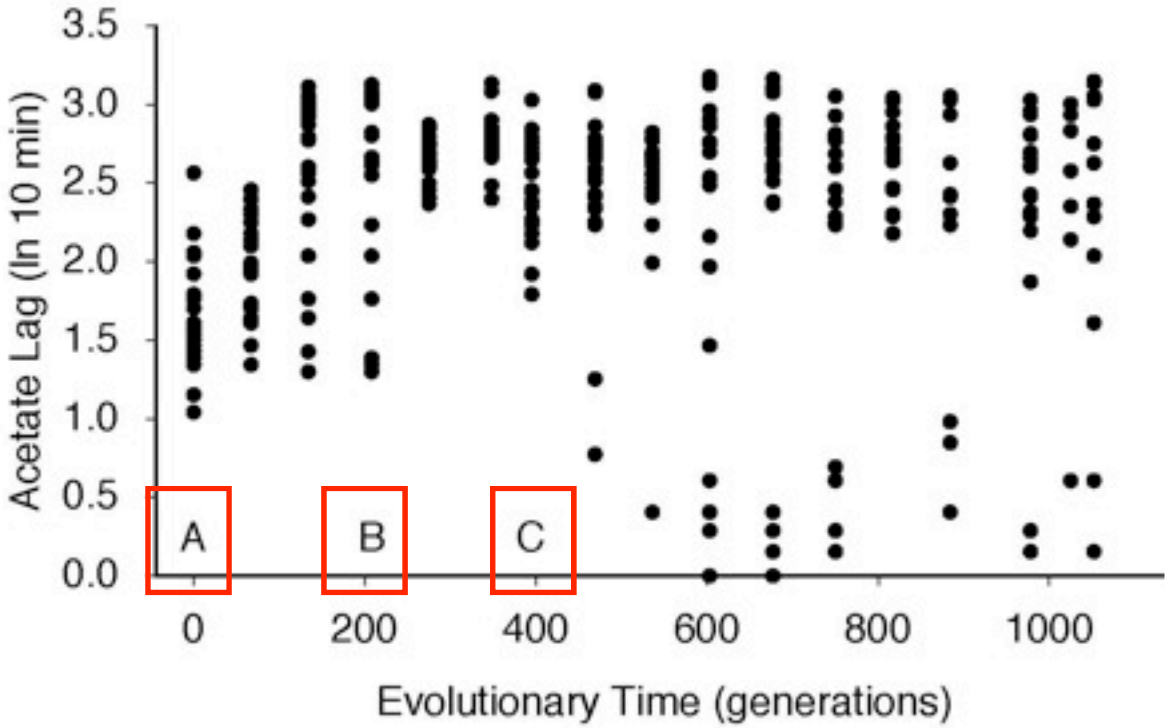


Likelihood of diversification increases over time

Evolutionary branching in switching lag:



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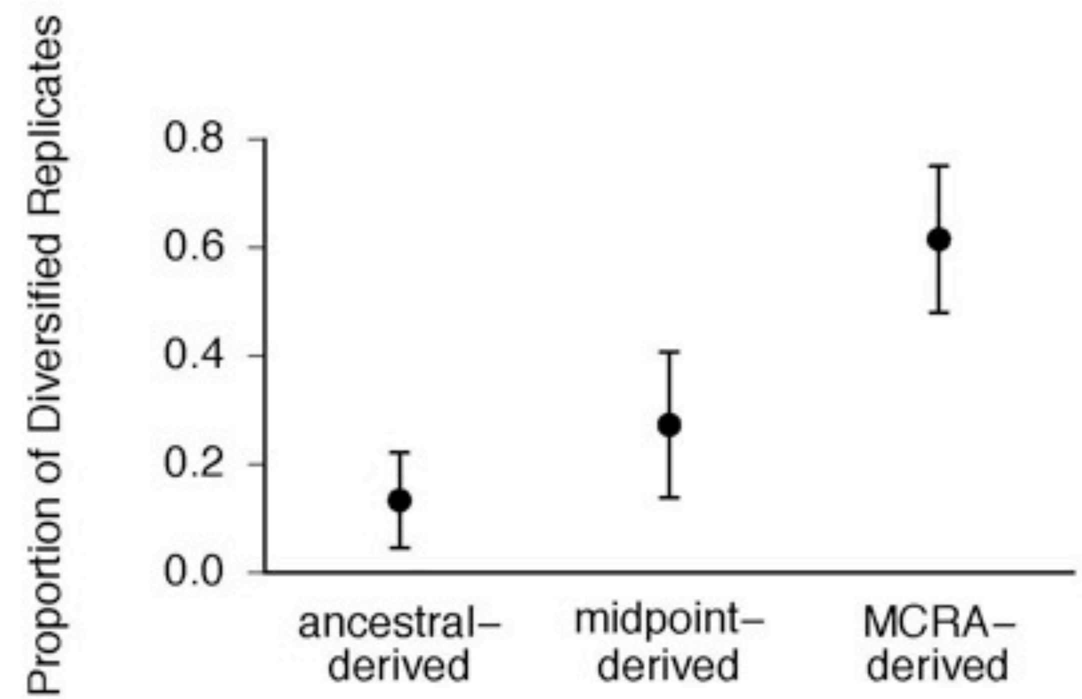

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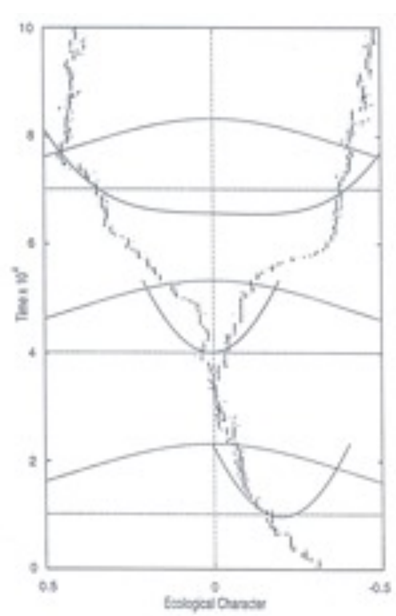
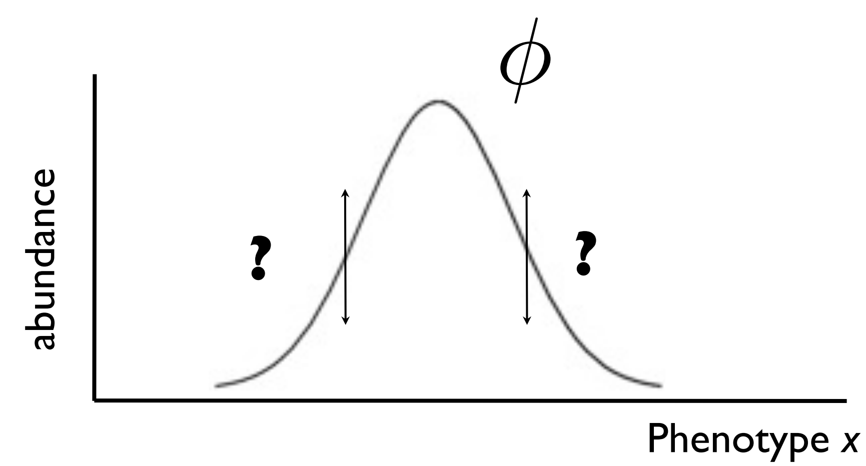


Likelihood of diversification increases over time

Adaptive dynamics assumption: mutations are rare and occur one at a time

PDE models: dynamics of continuous phenotype distributions (all types present at all a times)

$\phi(x, t)$: Phenotype distribution at time *t*



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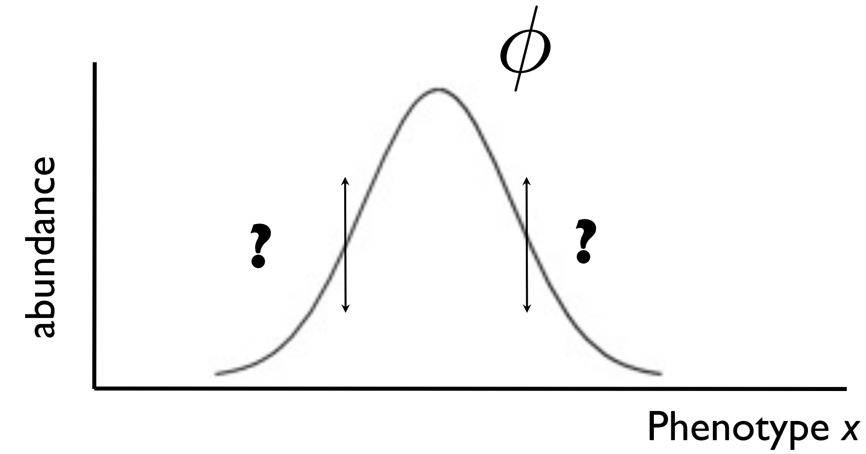

$$\frac{\partial \phi}{\partial t} = b\phi(x)\left(1 - \frac{(\alpha * \phi)(x)}{K(x)}\right)$$

where: $$(\alpha * \phi)(x) = \int \alpha(x,y)\phi(y)dy$$

effective density at *x*

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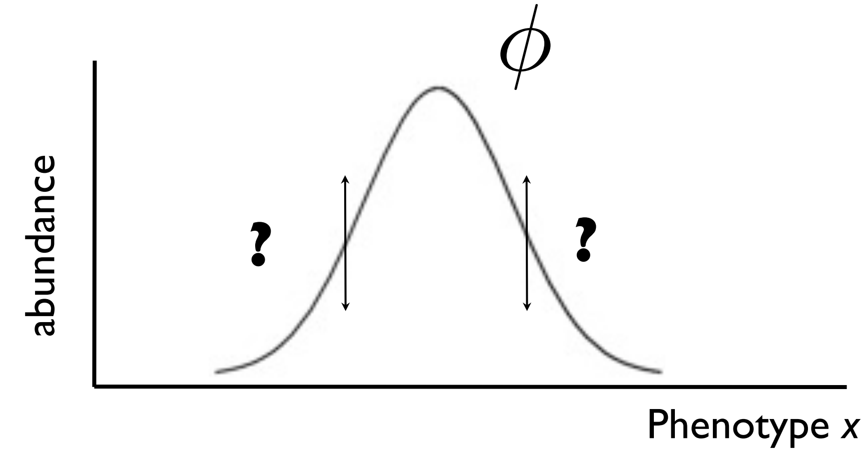

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effective density at *x*

Equilibrium distribution $\hat{\phi}$: $$(\alpha * \hat{\phi})(x) = K(x)$$

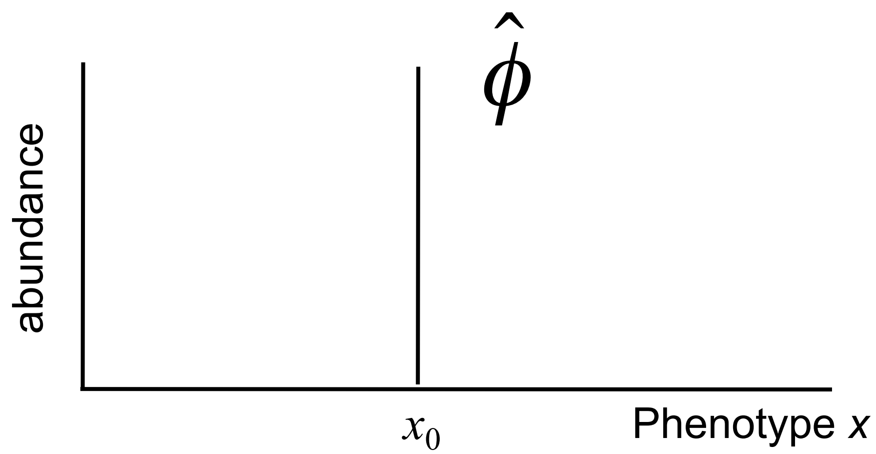
Gaussian case:

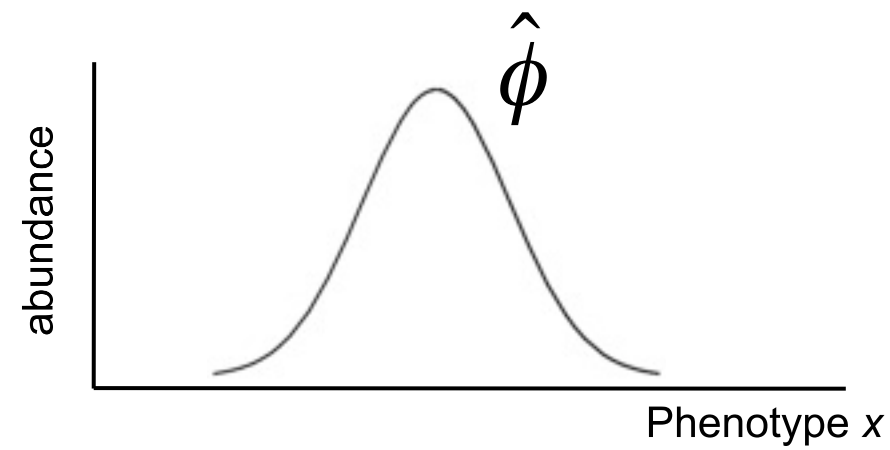
$$\alpha(x,y) = \exp\left[\frac{-(x-y)^2}{2\sigma_\alpha^2}\right] \qquad K(x) = \exp\left[\frac{-(x-x_0)^2}{2\sigma_K^2}\right]$$

Gaussian solution $\hat{\phi}$ with variance $\sigma_K^2 - \sigma_\alpha^2$

$\sigma_K^2 < \sigma_\alpha^2$

$\sigma_K^2 > \sigma_\alpha^2$





Phase transition, but no pattern formation…

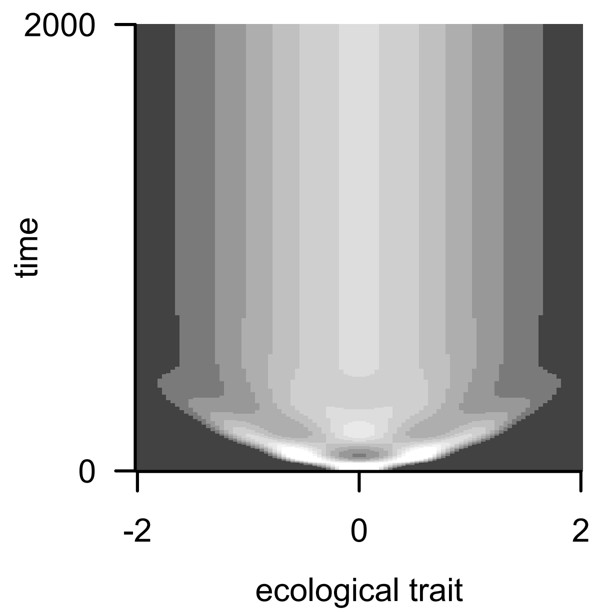
Gaussian case is structurally unstable

$$\alpha(x,y) = \exp\left[-\frac{(x-y)^{2+\epsilon}}{2\sigma_\alpha^{2+\epsilon}}\right]$$

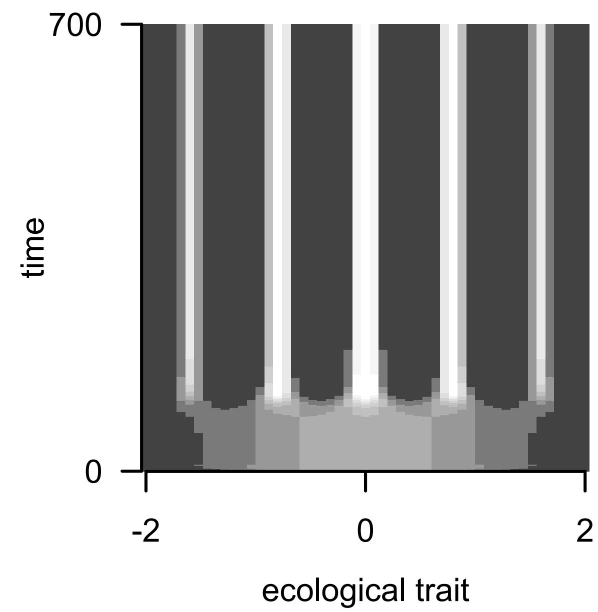
$$K(x) = \exp\left[-\frac{(x)^{2+\delta}}{2\sigma_K^{2+\delta}}\right]$$

Gaussian case: $\epsilon = \delta = 0$

Quartic case: $\epsilon = \delta = 2$

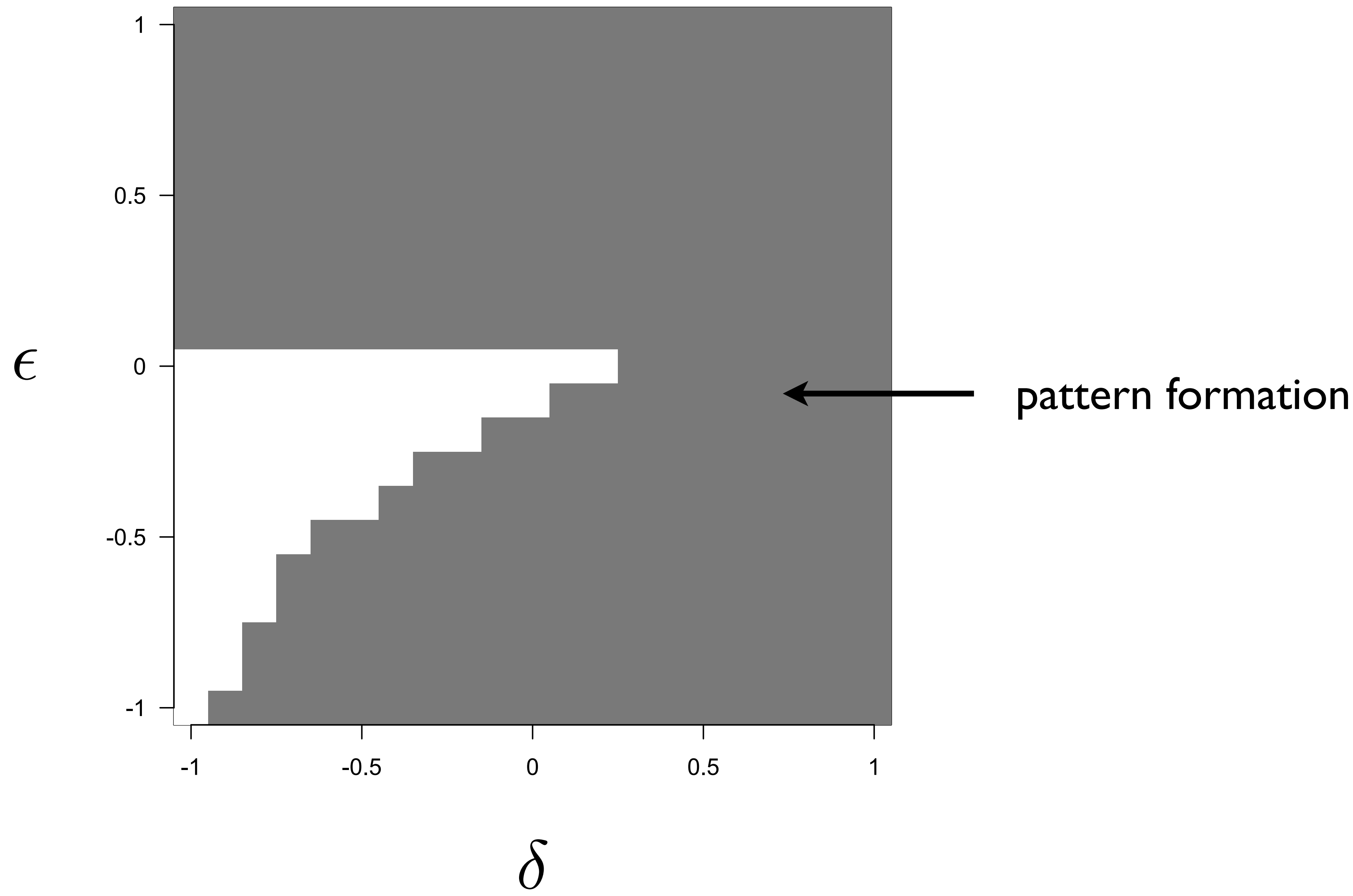


Gaussian equilibrium



Pattern formation

$$\alpha(x,y) = \exp\left[-\frac{(x-y)^{2+\epsilon}}{2\sigma_\alpha^{2+\epsilon}}\right] \qquad K(x) = \exp\left[-\frac{(x)^{2+\delta}}{2\sigma_K^{2+\delta}}\right]$$



Sexual model

- Asexual model:

$$\frac{\partial \phi}{\partial t} = b\phi(x)\left(1 - \frac{(\alpha * \phi)(x)}{K(x)}\right) = b\phi(x) - b\phi(x)\frac{(\alpha * \phi)(x)}{K(x)}$$

asexual birth term

death term

Sexual model

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asexual birth term — death term

- Sexual model: same death term

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asexual birth term: $b\phi(x)$

death term: $b\phi(x)\frac{(\alpha * \phi)(x)}{K(x)}$

- Sexual model: same death term
- Sexual birth term: $b\beta(x)$

Mating probability between phenotypes *x* and *y* is proportional to Gaussian function:

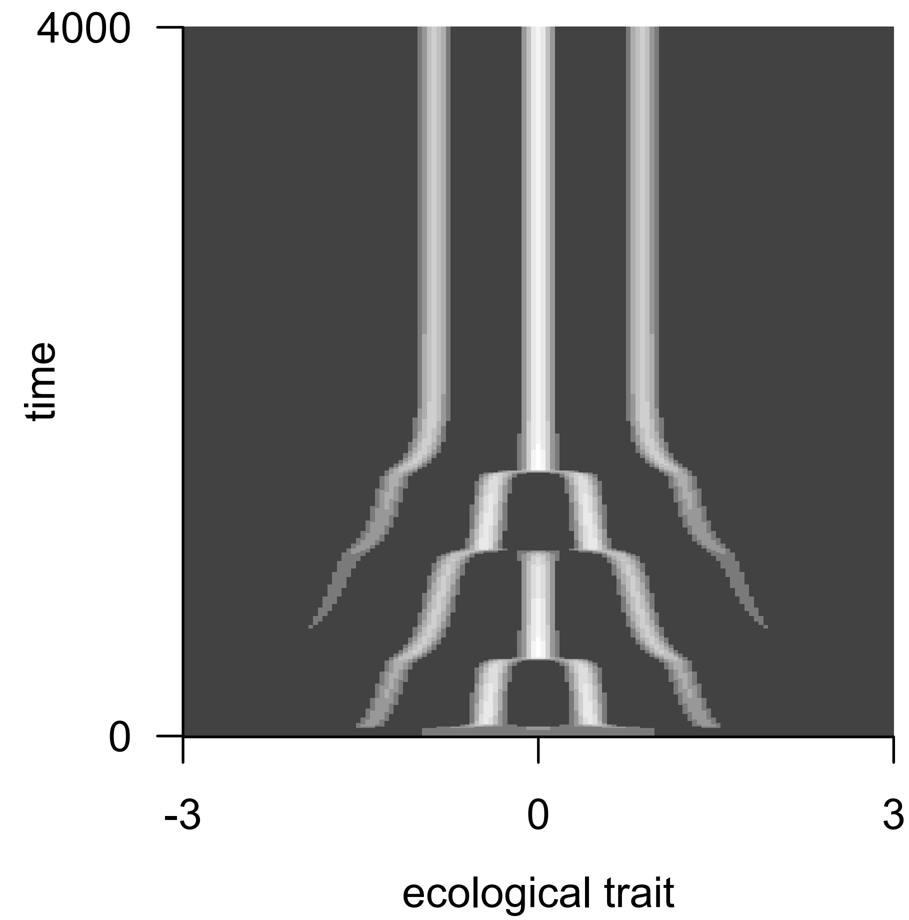
$$A(x,y) = \exp\left[\frac{-(x-y)^2}{2\sigma_A^2}\right]$$

σ_A : Strength of assortment

Mating between *x* and *y* produces a Gaussian offspring distribution mean (*x*+*y*)/2

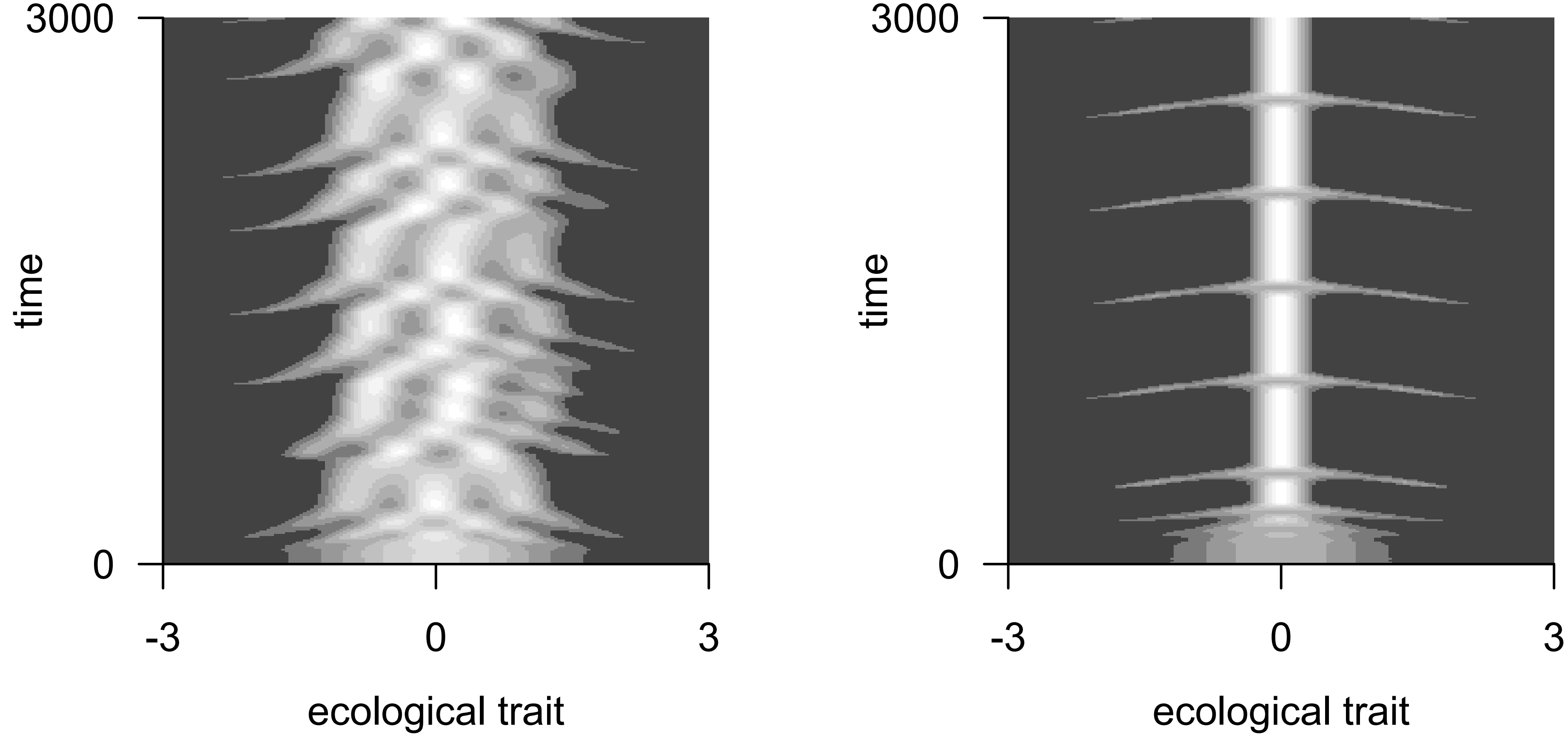
Sexual model with assortative mating:

Pattern formation even with Gaussian competition kernel and carrying capacity
(Guassian equilibrium unstable!)



Sexual model with assortative mating:

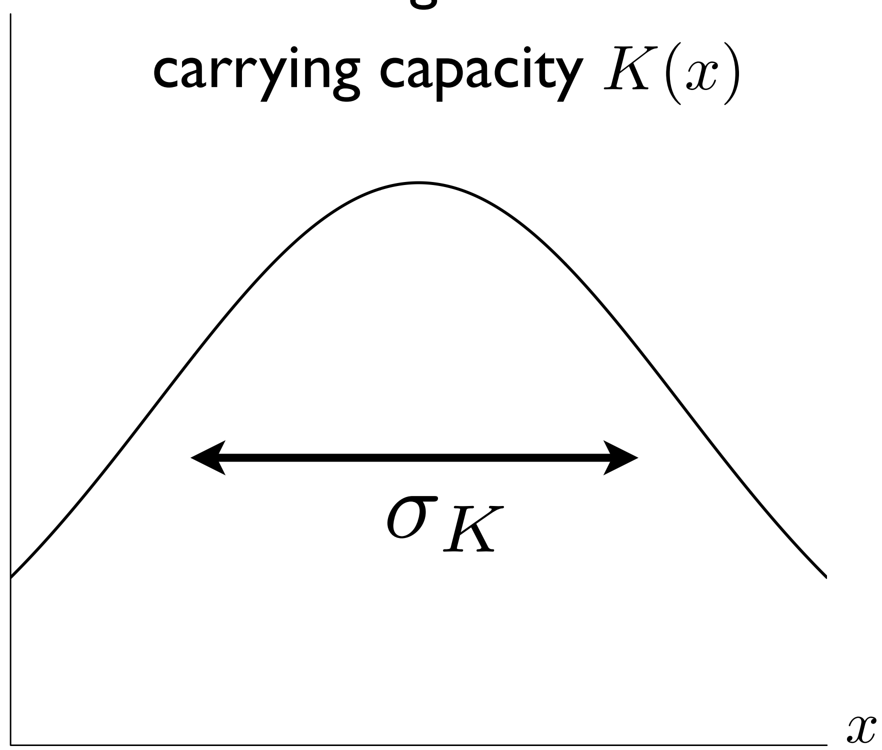
Non-equilibrium dynamics (Gaussian kernels)



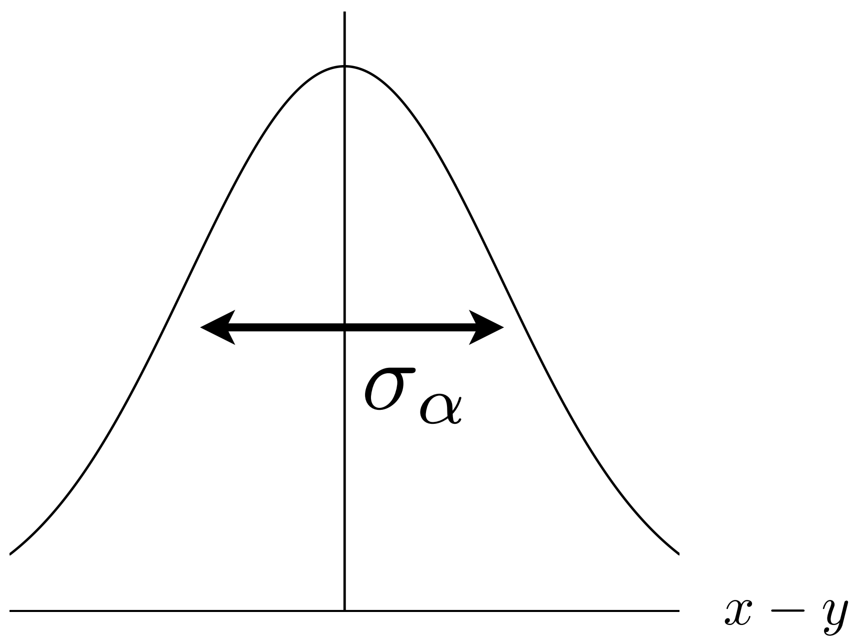
Phenotypic complexity: diversity in high-dimensional phenotype spaces

1-dimensional: $$\frac{\partial \phi}{\partial t} = b\phi(x)\left(1 - \frac{(\alpha * \phi)(x)}{K(x)}\right)$$

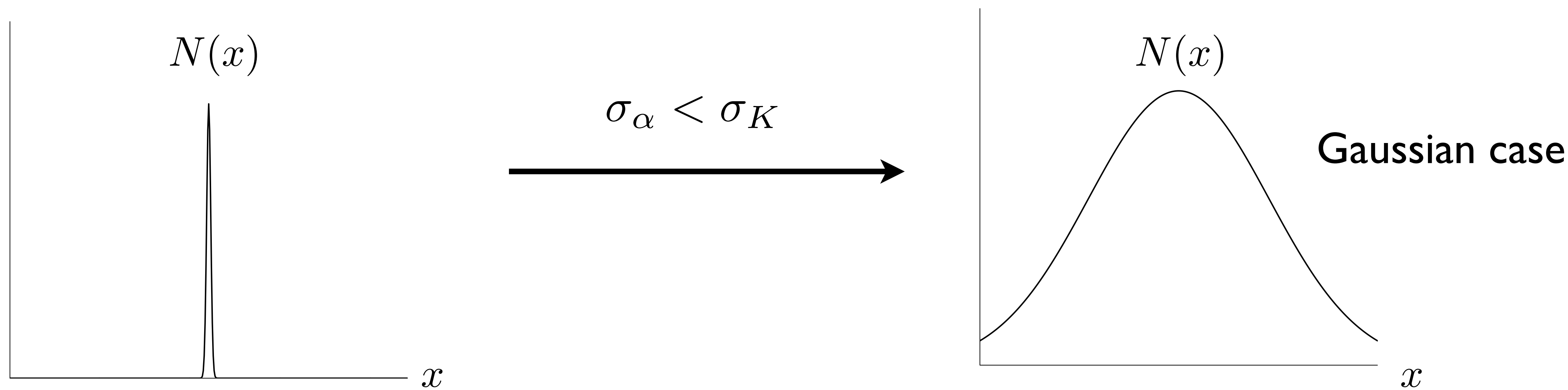
stabilizing selection:
carrying capacity $K(x)$



frequency dependence:
competition kernel $\alpha(x,y)$



maintenance of variation in the phenotype distribution *N(x)* if



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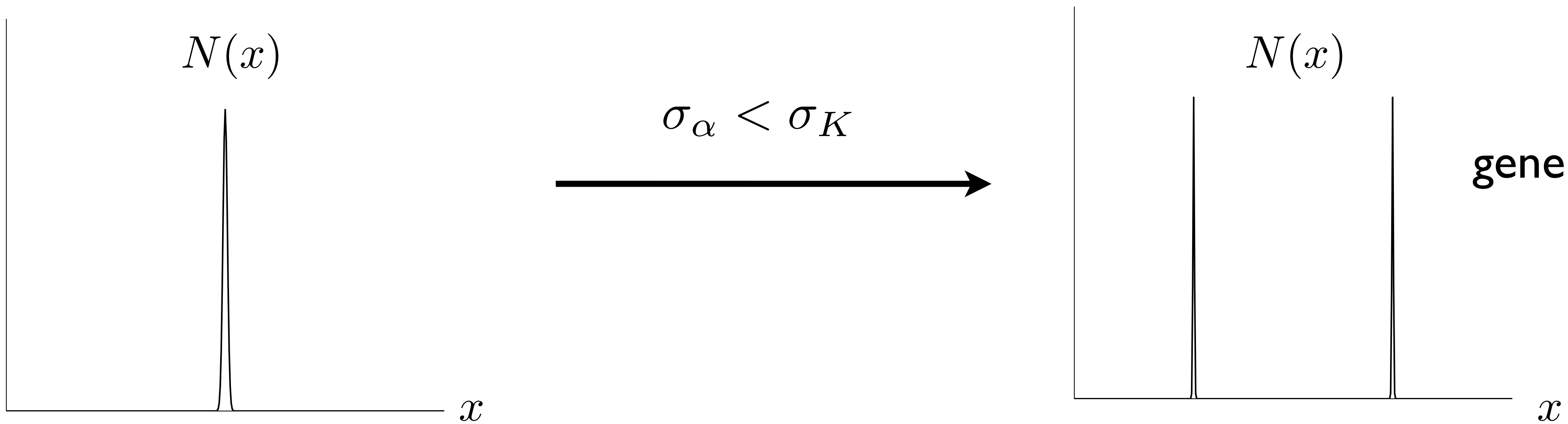
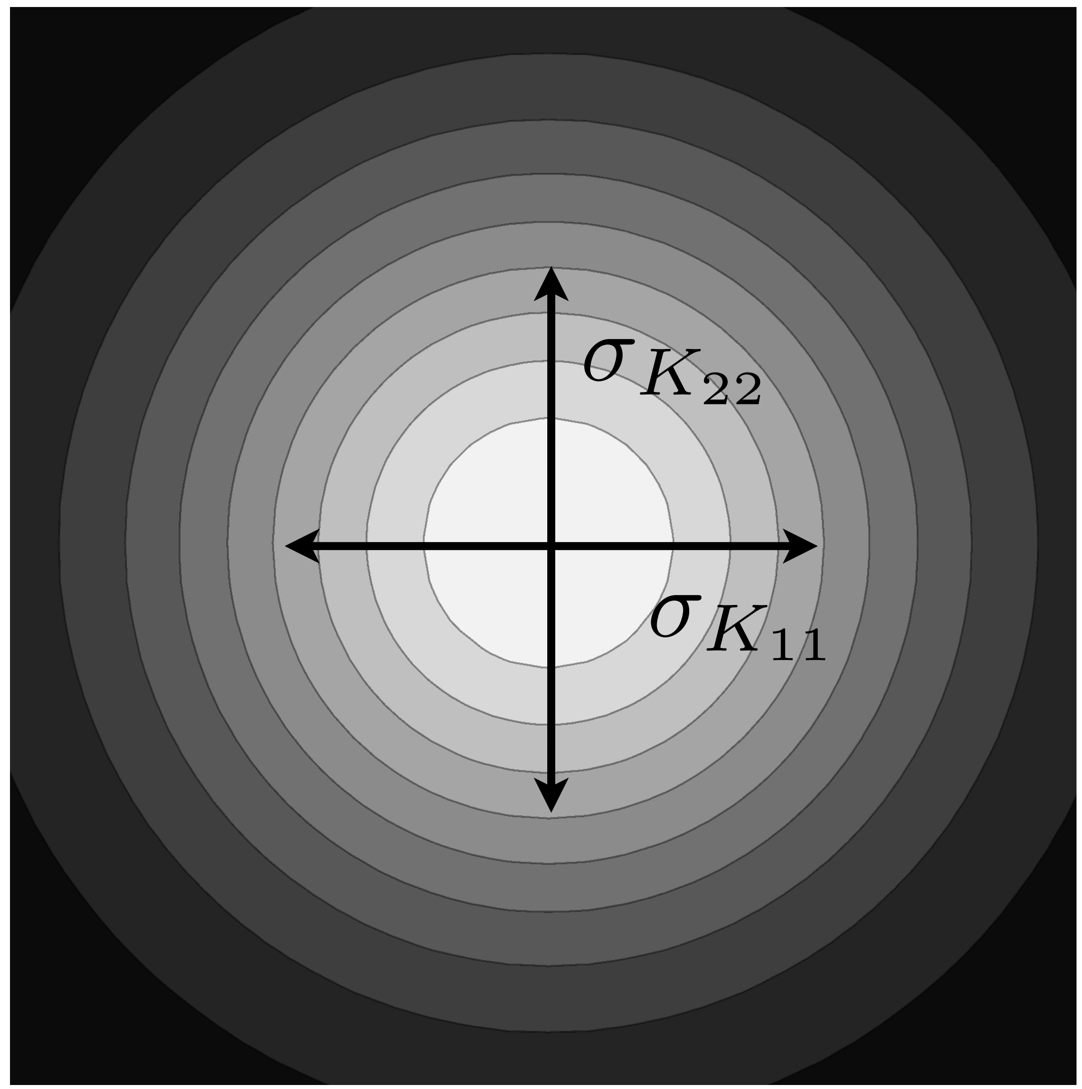


generic case

two phenotypic dimensions (x_1, x_2)

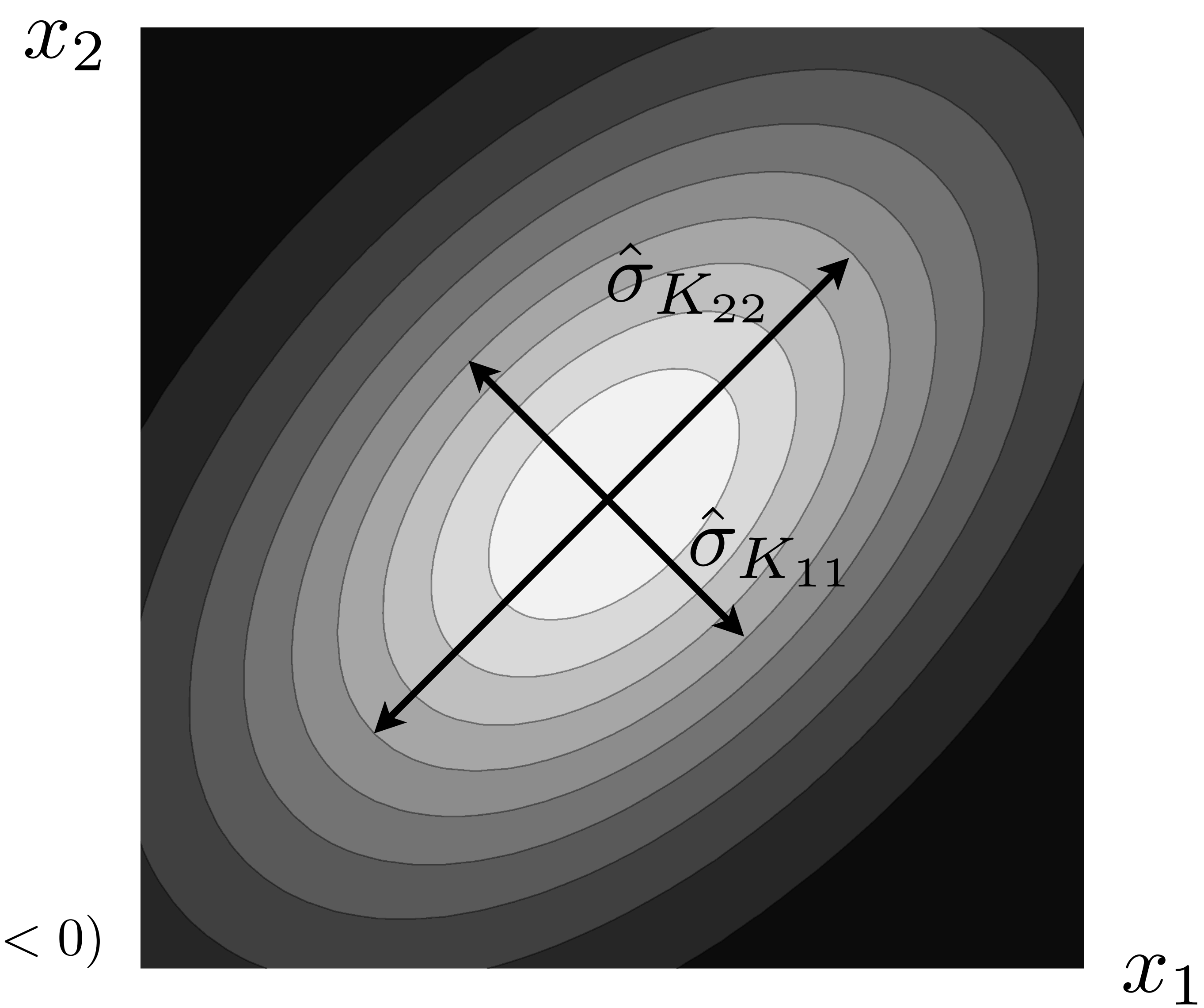
carrying capacity $$K(x_1, x_2) = \exp\left[-\frac{x_1^2}{2\sigma_{K_{11}}^2}\right] \cdot \exp\left[-\frac{x_2^2}{2\sigma_{K_{22}}^2}\right]$$



$(\sigma_{K_{11}} = \sigma_{K_{22}})$

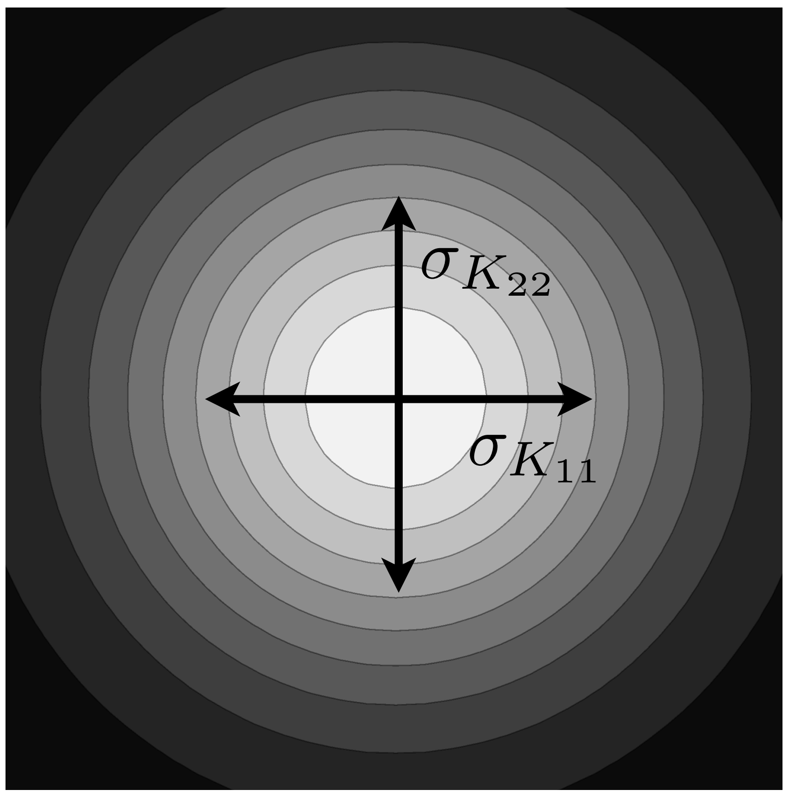
"separable" case: no interactions between phenotypes "non-separable" case: interactions between phenotypes

$$K(x_1, x_2) = \exp\left[-\frac{x_1^2}{2\sigma_{K_{11}}^2}\right] \cdot \exp\left[-\frac{x_2^2}{2\sigma_{K_{22}}^2}\right] \cdot \exp\left[-\frac{x_1 x_2}{2\sigma_{K_{12}}}\right]$$

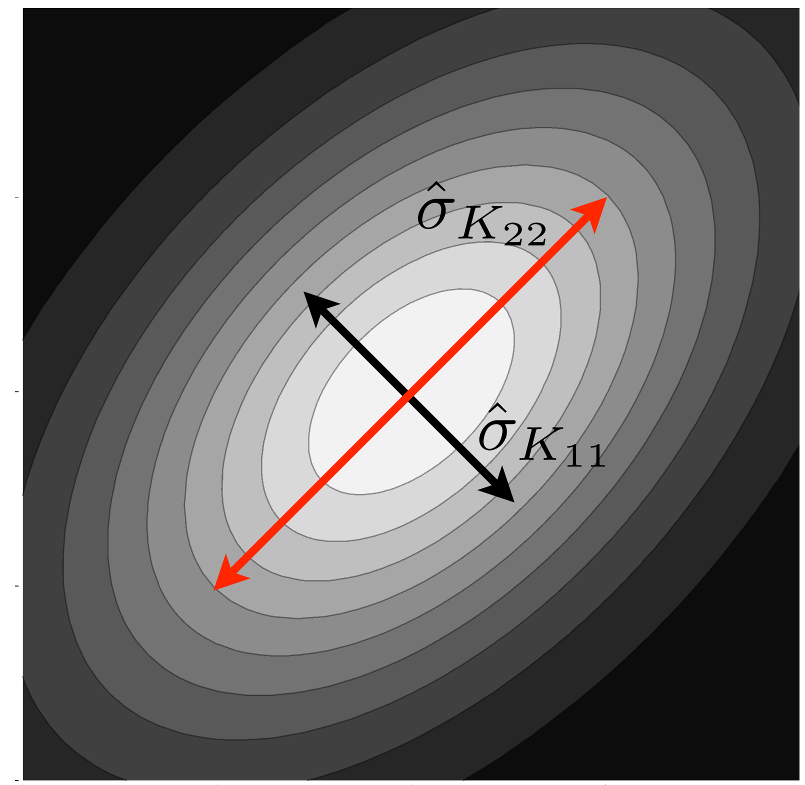


$(\sigma_{K_{12}} < 0)$

separable
(no interactions)

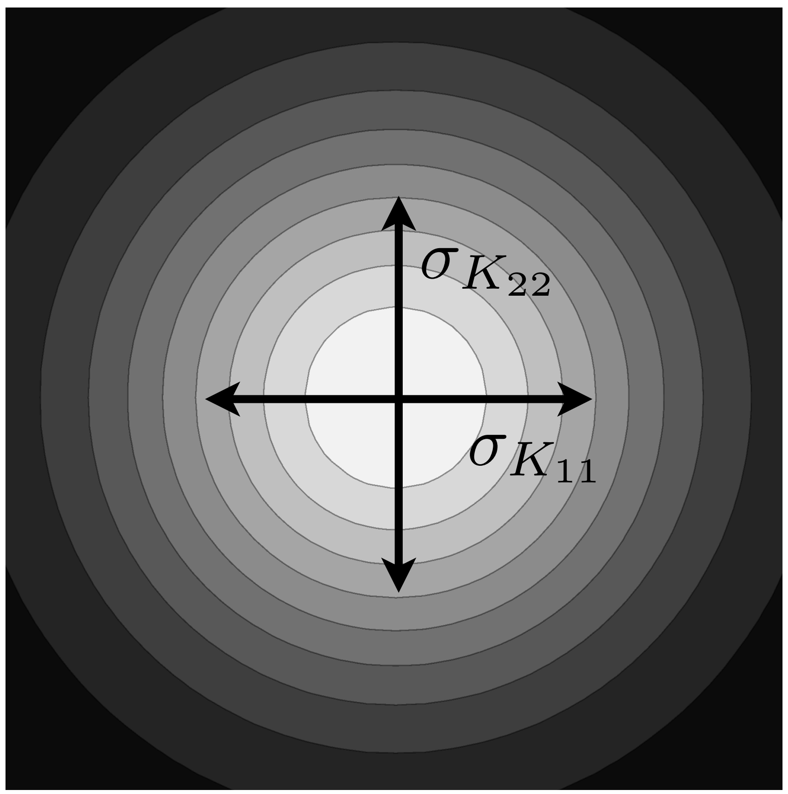


non-separable
(phenotype interactions)



$$\sigma_{K_{22}} < \hat{\sigma}_{K_{22}}!$$

separable
(no interactions)



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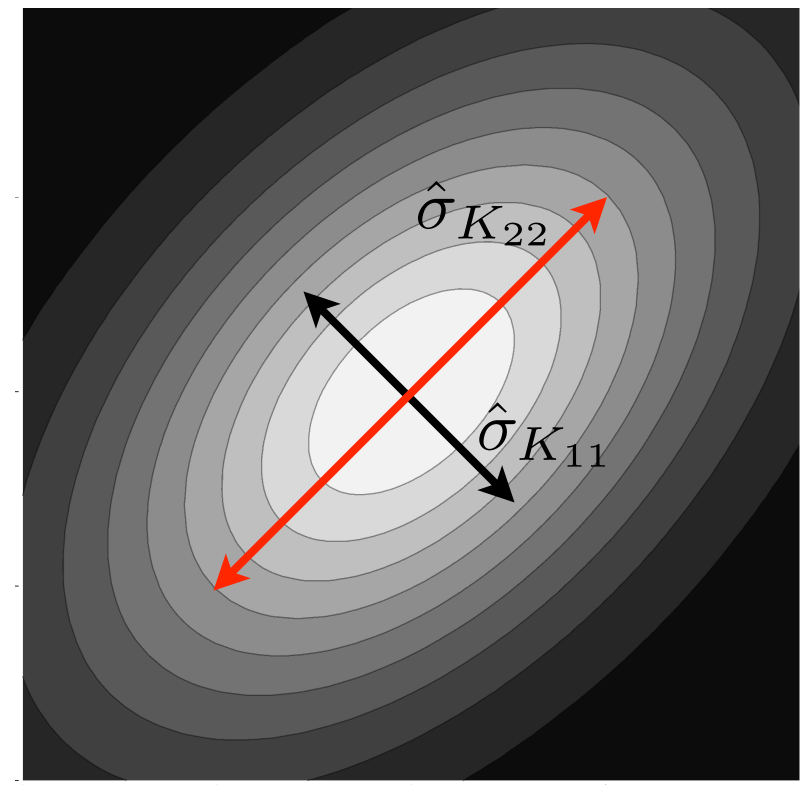
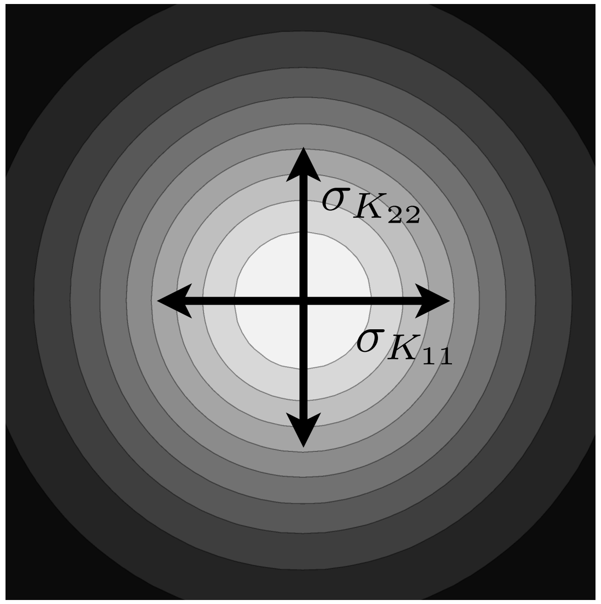


$$\sigma_{K_{22}} < \hat{\sigma}_{K_{22}}!$$

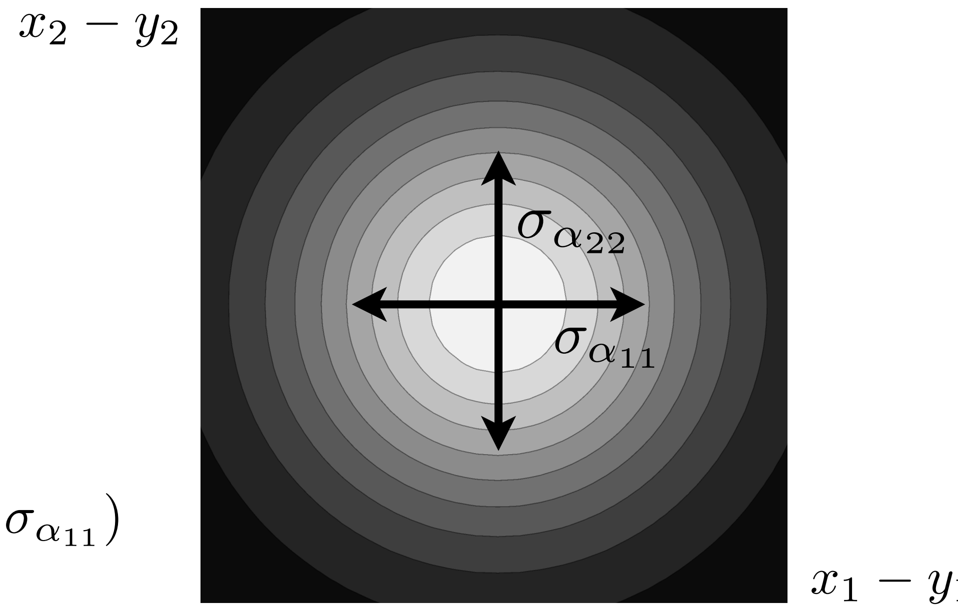
(occurs for *any* interaction between x_1 and x_2...)

“on the brink of diversification”: widths the same in all directions



separable carrying capacity

$$(\sigma_{K_{11}} = \sigma_{K_{22}} = \sigma_{\alpha_{11}} = \sigma_{\alpha_{11}})$$



separable competition kernel

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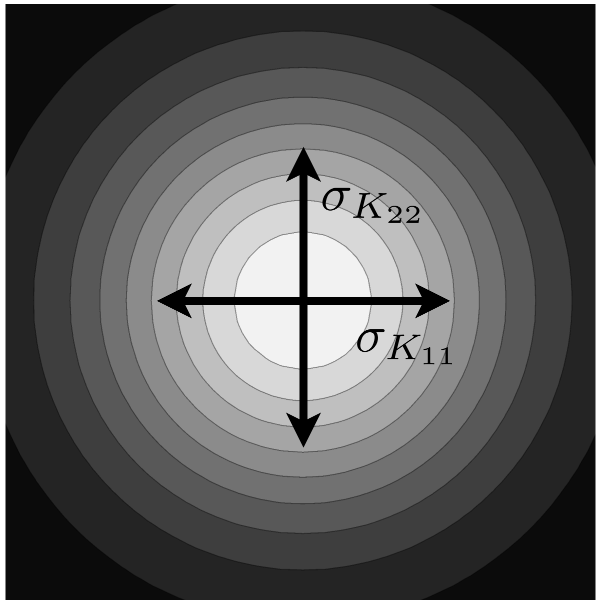

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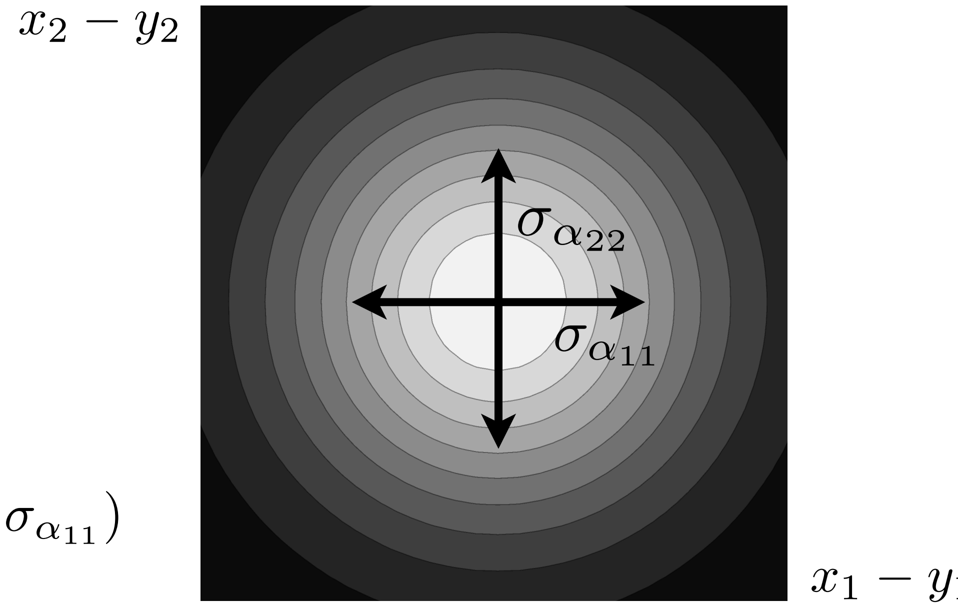

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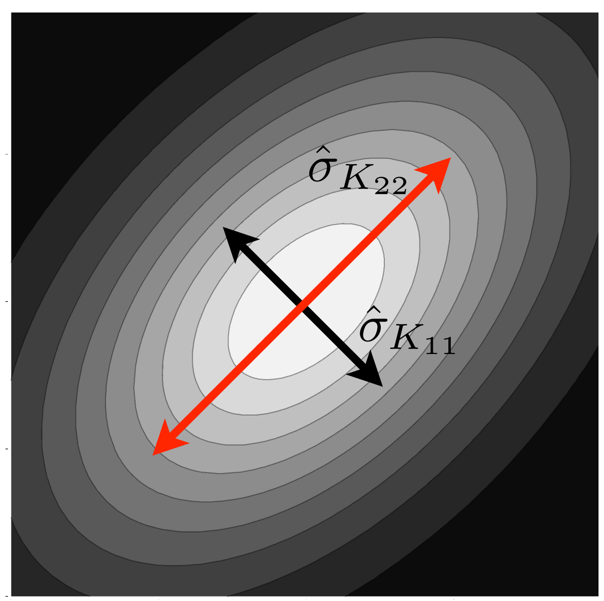

non-separable carrying capacity
(phenotype interactions)

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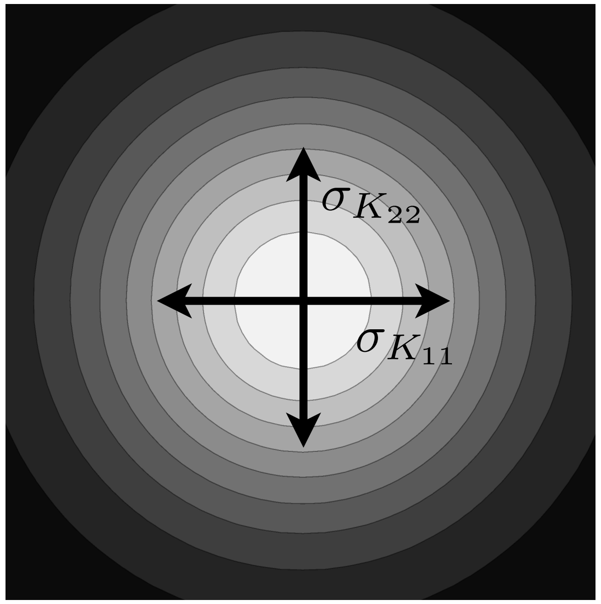
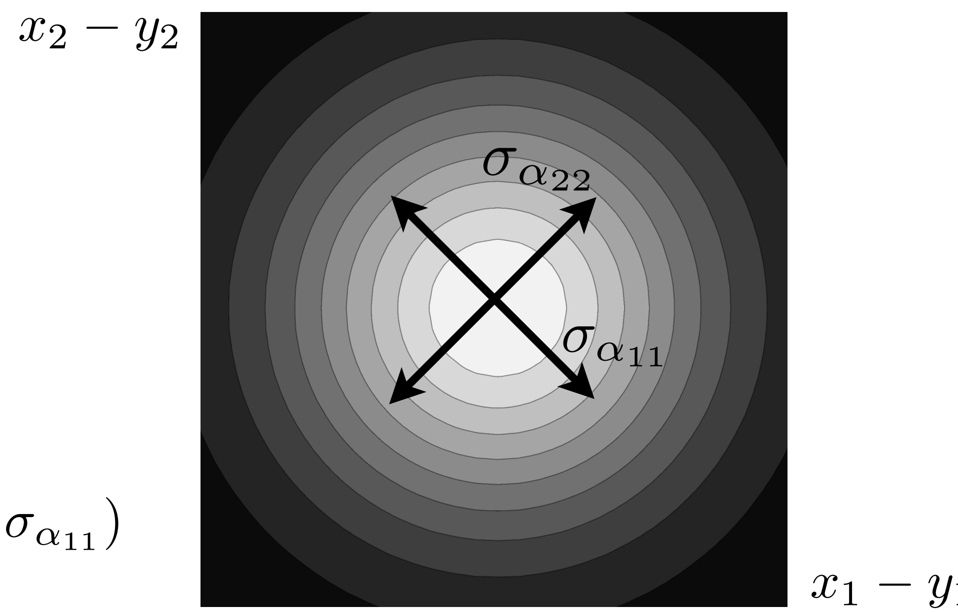


separable carrying capacity

$$(\sigma_{K_{11}} = \sigma_{K_{22}} = \sigma_{\alpha_{11}} = \sigma_{\alpha_{11}})$$



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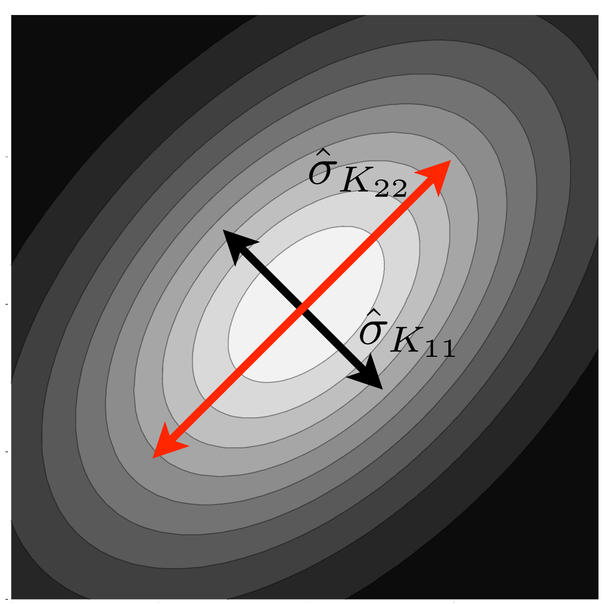

non-separable carrying capacity
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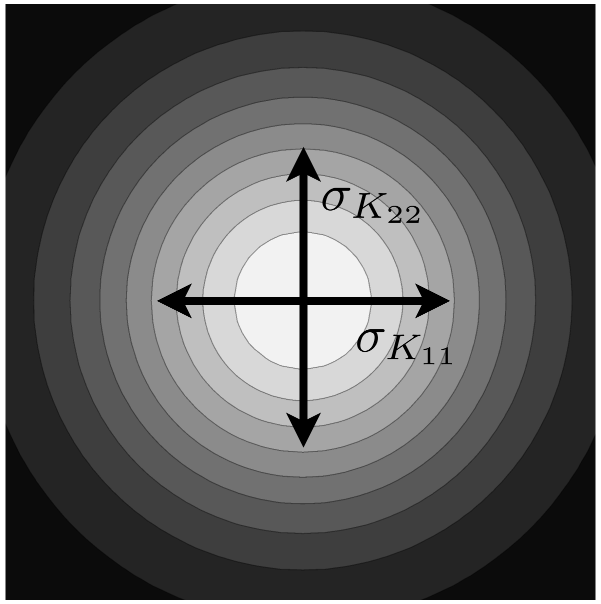

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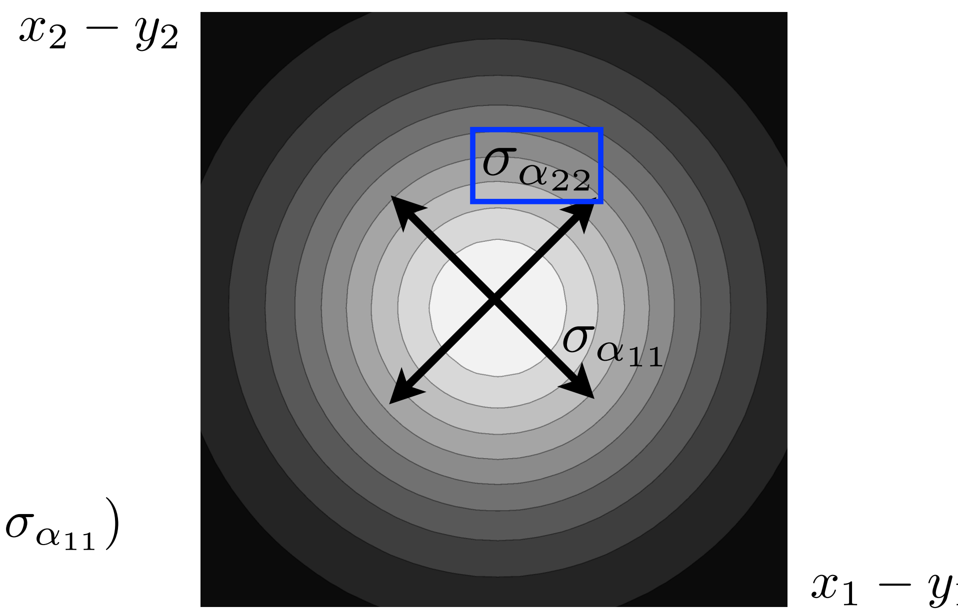

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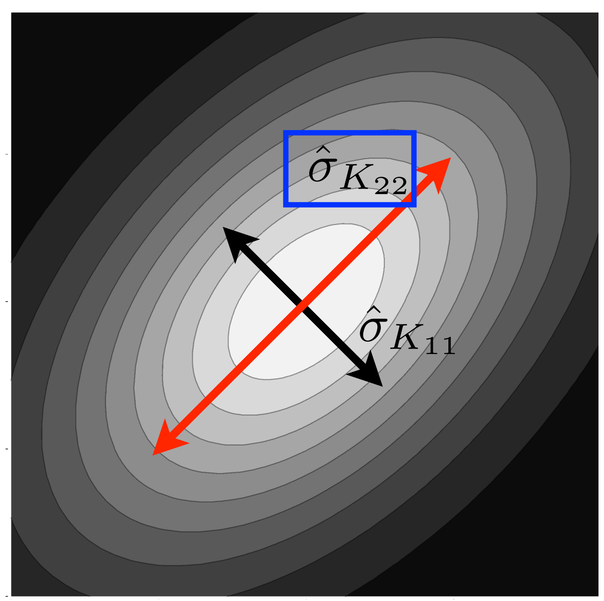


non-separable carrying capacity
(phenotype interactions)

$$\sigma_{\alpha_{22}} < \hat{\sigma}_{K_{22}} :$$

diversification (along diagonal)!

$n-$ dimensional phenotype $x = (x_1, \ldots, x_n)$

carrying capacity: $K(x) = \exp[-xKx^T]$

competition kernel: $\alpha(x, y) = \exp[-(x-y)A(x-y)^T]$

A, K: quadratic forms

Claim:

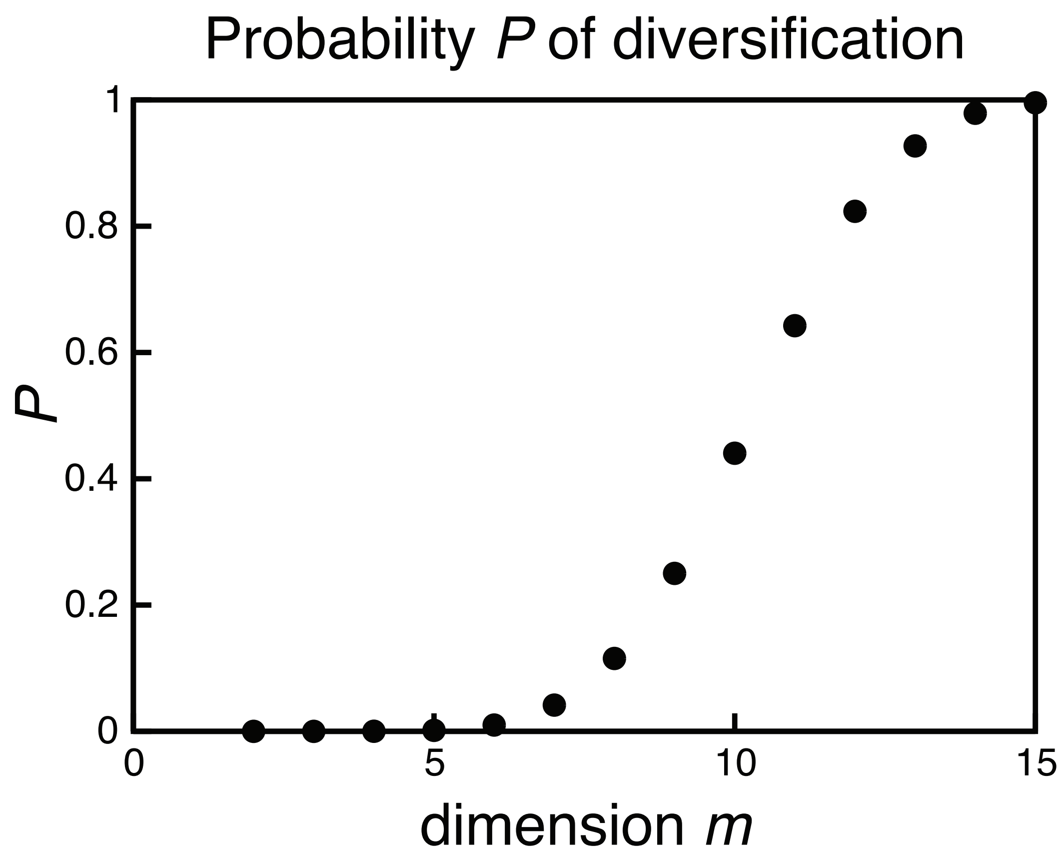
A, K symmetric, positive definite quadratic forms $\in \mathbb{R}^{n \times n}$
with diagonal elements $a_{ii} = k_{ii} \quad \forall i$

Then there is a coordinate system in which the quadratic forms are given by diagonal matrices $\hat{A}, \hat{K}$ such that $\hat{a}_{i_0} > \hat{k}_{i_0}$ for at least one index i_0

Example:

stabilizing selection dominates in each phenotypic direction *i* $(\sigma_{\alpha_{ii}} = 1.6 > \sigma_{K_{ii}} = 0.7)$

weak interactions strength between phenotypic components $(|\sigma_{K_{ij}}| \text{ large, random})$



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- "Adaptive Diversification", Princeton University Press, 2011

Thank you