Adaptive Speciation: Theory and Evolutionary Experiments

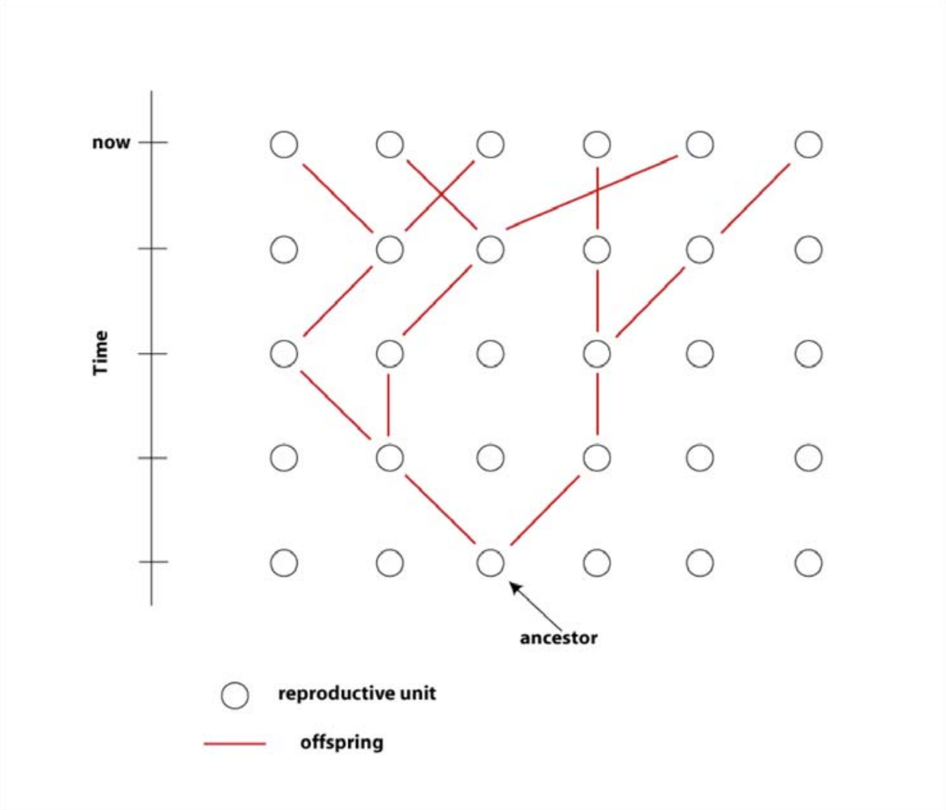
Michael Doebeli
University of British Columbia

How many species?

10,000,000 – 100,000,000

(Extant species represent ca. 1% of all species that ever existed…)

Yet, a single ancestor…



Speciation (evolutionary diversification) is rampant…

Species:

- Morphologically distinct group of organisms
- Reproductively isolated group of organisms
- Genetically cohesive group of organisms
- …

Traditional explanations of speciation are based on biogeographical patterns

Allopatric speciation:

The splitting of a lineage is a consequence of geographical isolation; intuitively appealing; thought to be the dominant mode of speciation, yet mechanisms not well understood

Sympatric speciation:

The splitting of a lineage occurs under conditions of ecological contact; has been deemed unlikely because of theoretical difficulties

Example of allopatric speciation:

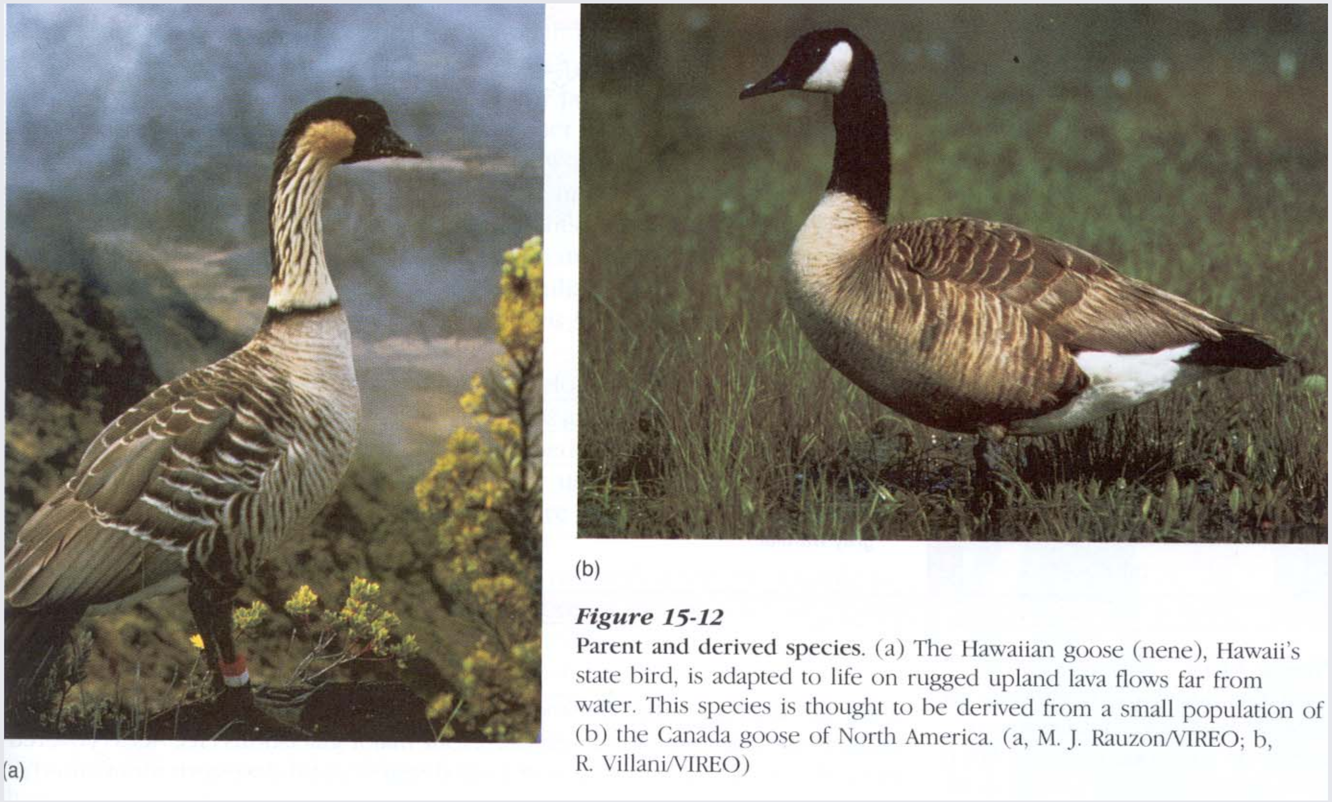


Figure 15-12

Parent and derived species. (a) The Hawaiian goose (nene), Hawaii's state bird, is adapted to life on rugged upland lava flows far from water. This species is thought to be derived from a small population of (b) the Canada goose of North America. (a, M. J. Rauzon/VIREO; b, R. Villani/VIREO)

Traditional explanations of speciation are based on biogeographical patterns

Allopatric speciation:

The splitting of a lineage is a consequence of geographical isolation; intuitively appealing; thought to be the dominant mode of speciation, yet mechanisms not well understood

Sympatric speciation:

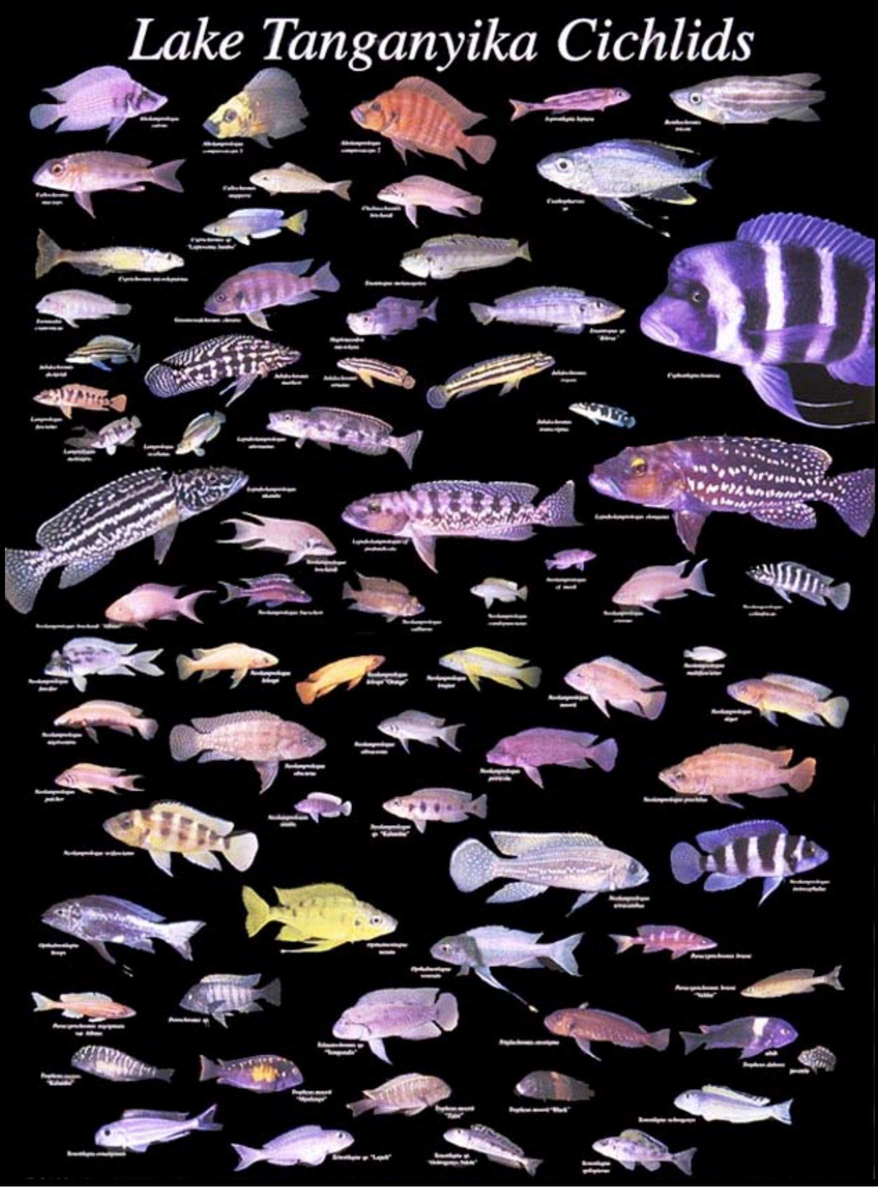
The splitting of a lineage occurs under conditions of ecological contact; has been deemed unlikely because of theoretical difficulties

Classical view:

“[ ]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)

A large amount of diversity (ca. 2000 species) evolved in a short period (< 500,000 years) in Great African Rift Lakes in the absence of geographical barriers …



Adaptive speciation:

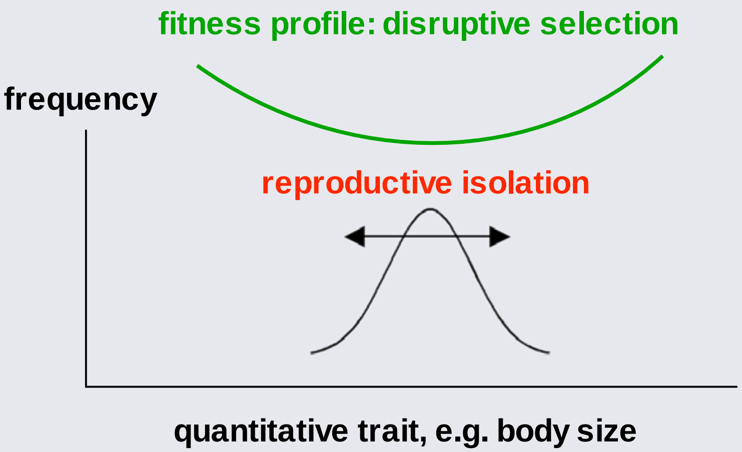
Lineage splitting as an adaptive response to biological interactions

Outline of talk:

a. Theory of adaptive speciation

b. Experimental evolution of adaptive diversification in *E. Coli*

Adaptive Speciation
(sympatric speciation)



fitness profile: disruptive selection

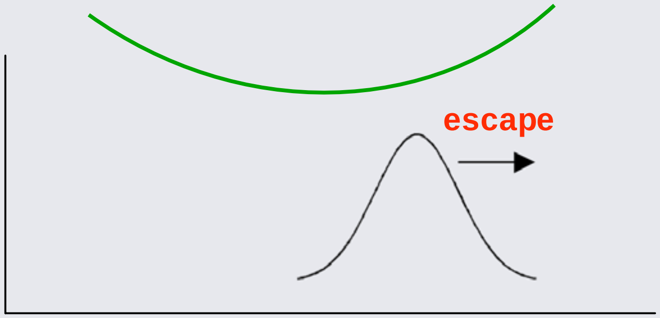
frequency

reproductive isolation

quantitative trait, e.g. body size

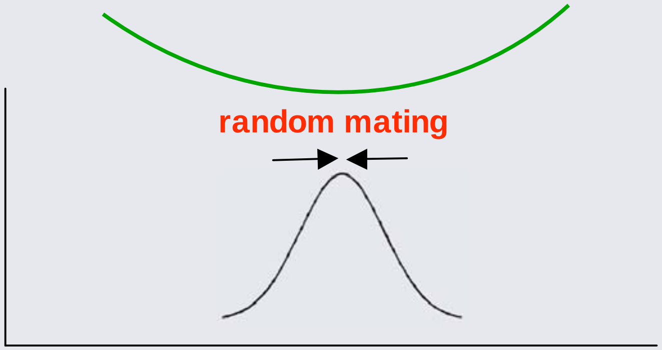
Theoretical Problems

Ecology: fitness minima are unstable



escape

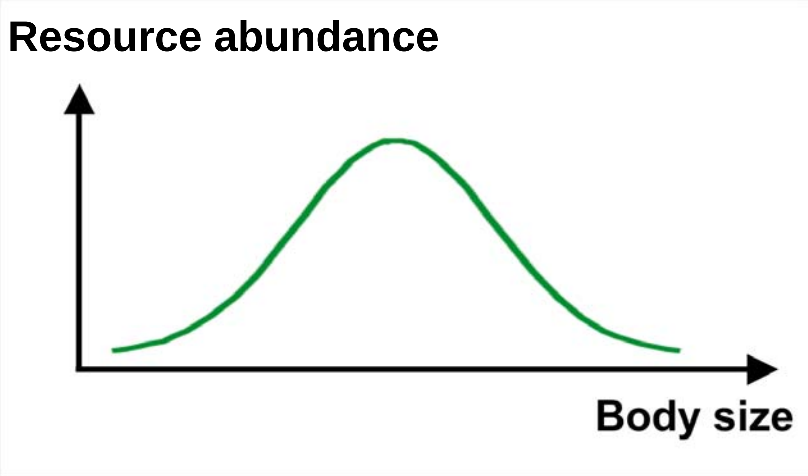
Population genetics: recombination prevents divergence

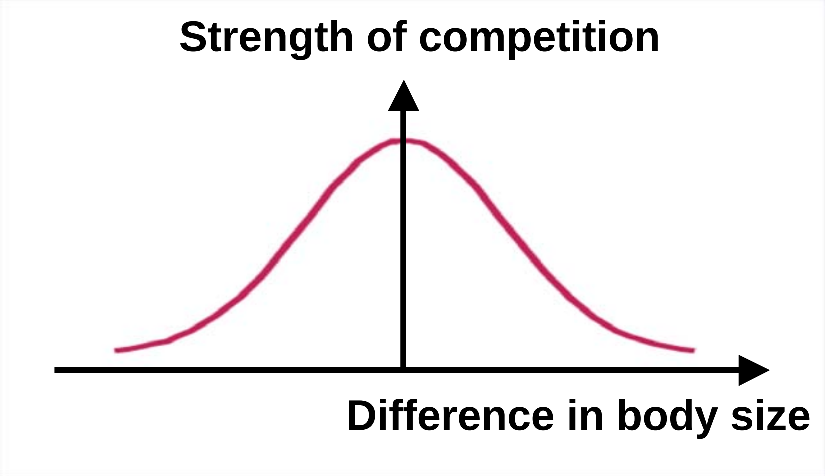


random mating

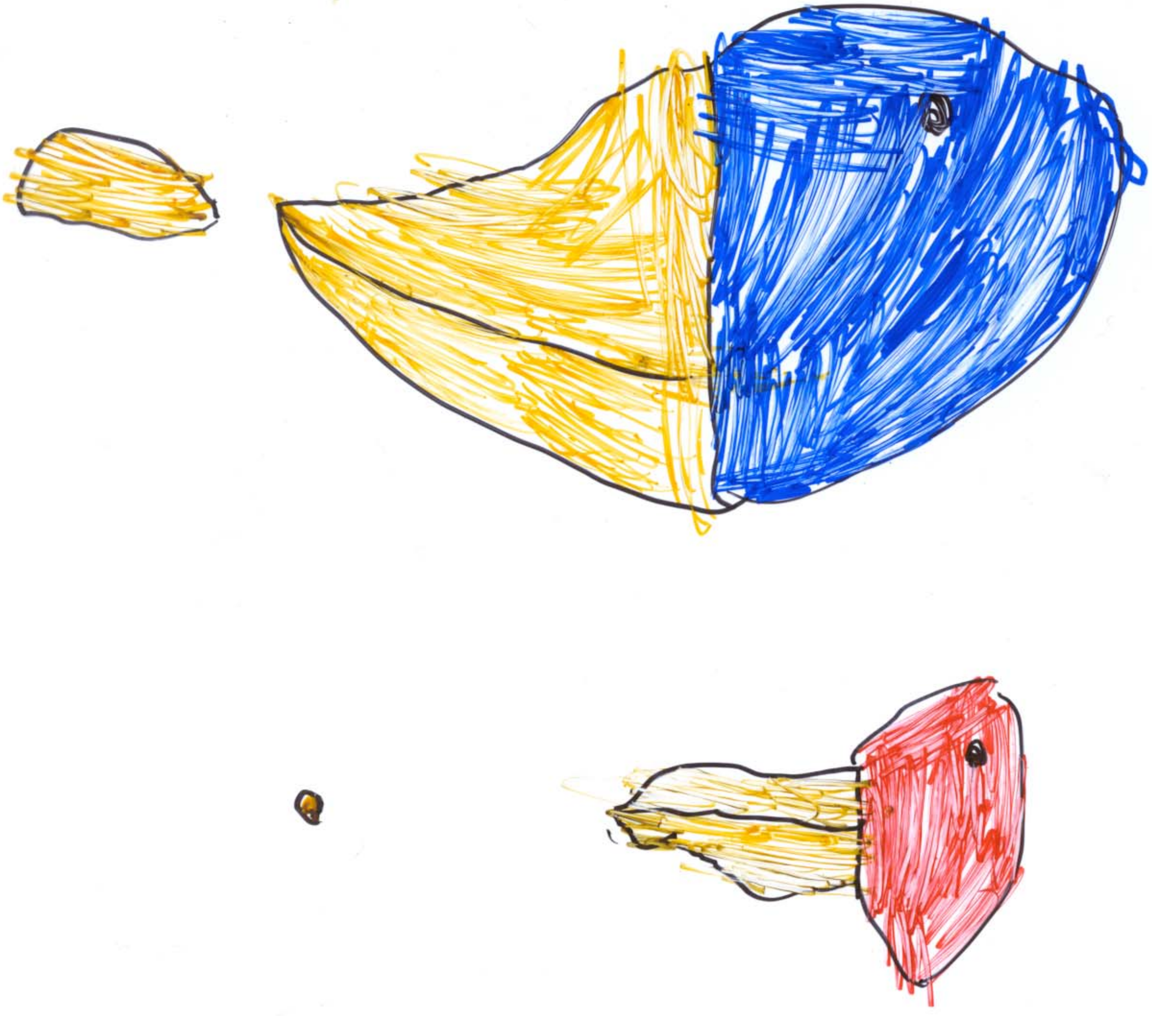
Adaptive speciation in models for resource competition

Two ecological assumptions:

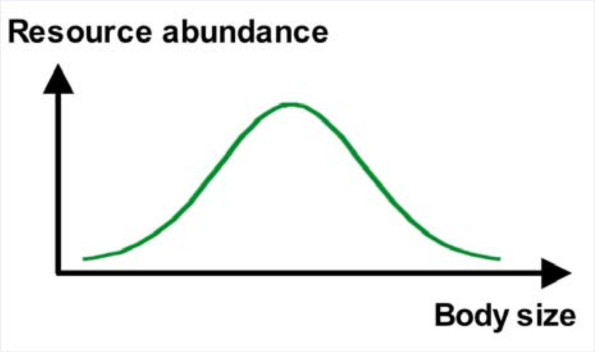


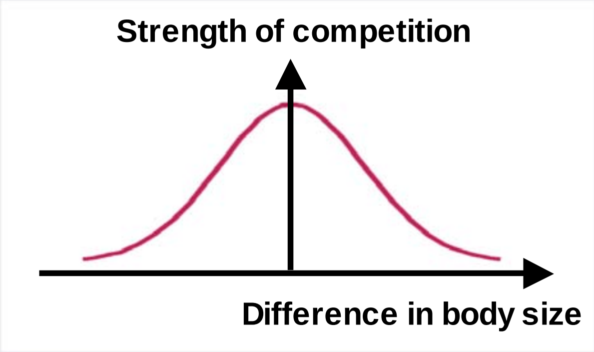


Imagine beak size in birds…



Adaptive speciation in models for resource competition



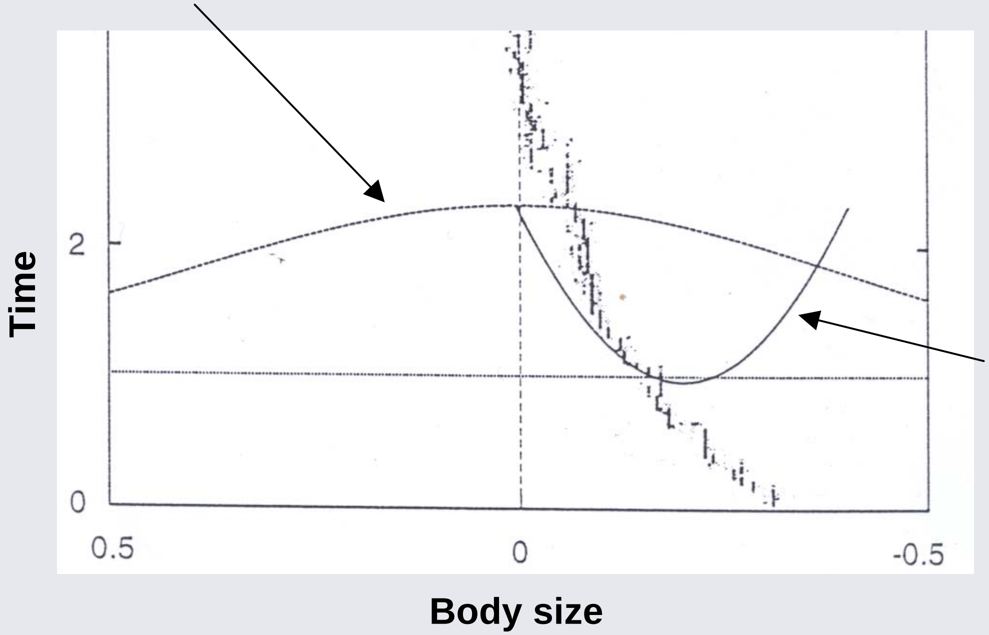


(Imagine beak size in birds…)

Individual-based model:

- Individuals described by their trait value (body size) x
- Individuals give birth at a constant rate and die at a rate determined by resource abundance and by frequency-dependent competition (common phenotypes have higher death rate than rare phenotypes)
- Phenotypes breed true (asexual reproduction) with small mutations

First, mean phenotype evolves to maximum of resource curve:

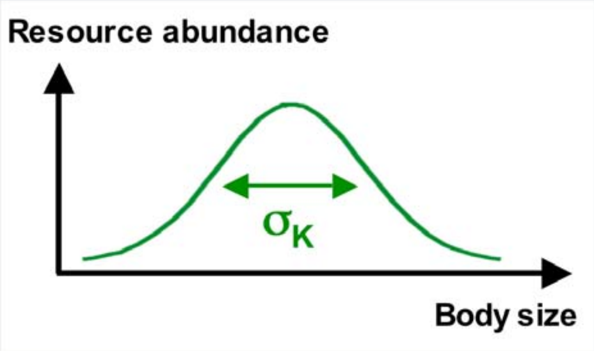


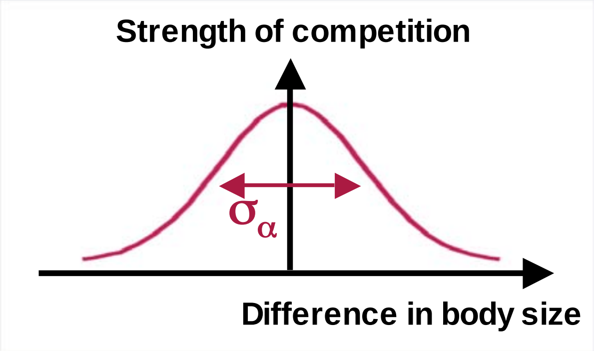
Resource abundance curve

Fitness function at time
given by horizontal line

What next?

Dependence on ecological parameters:

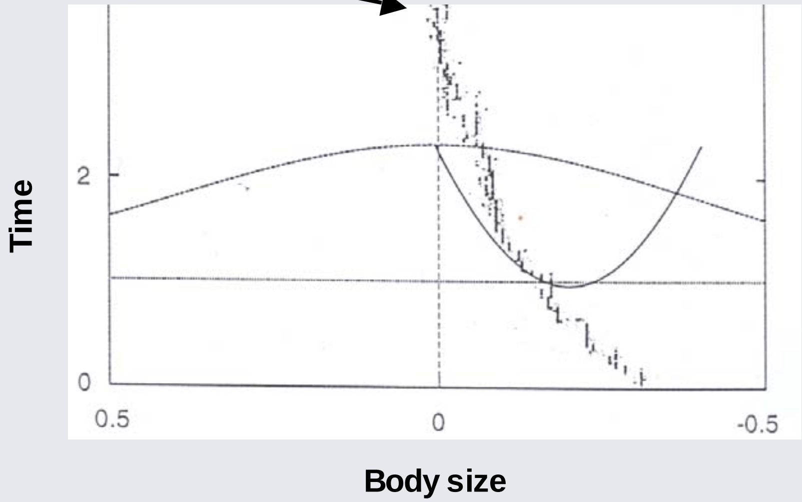




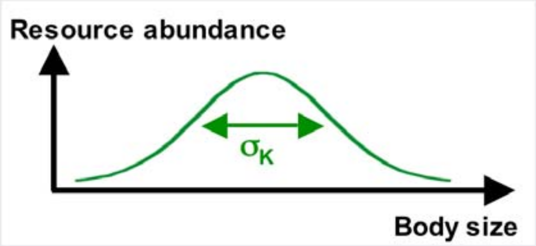
σ_K = width of resource abundance curve

σ_α = width of competition curve

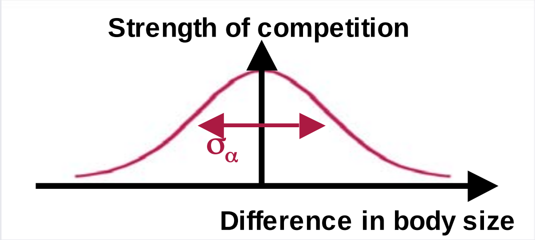
If $\sigma_K < \sigma_\alpha$ then the population is evolutionarily stuck at the maximum of the resource abundance curve:



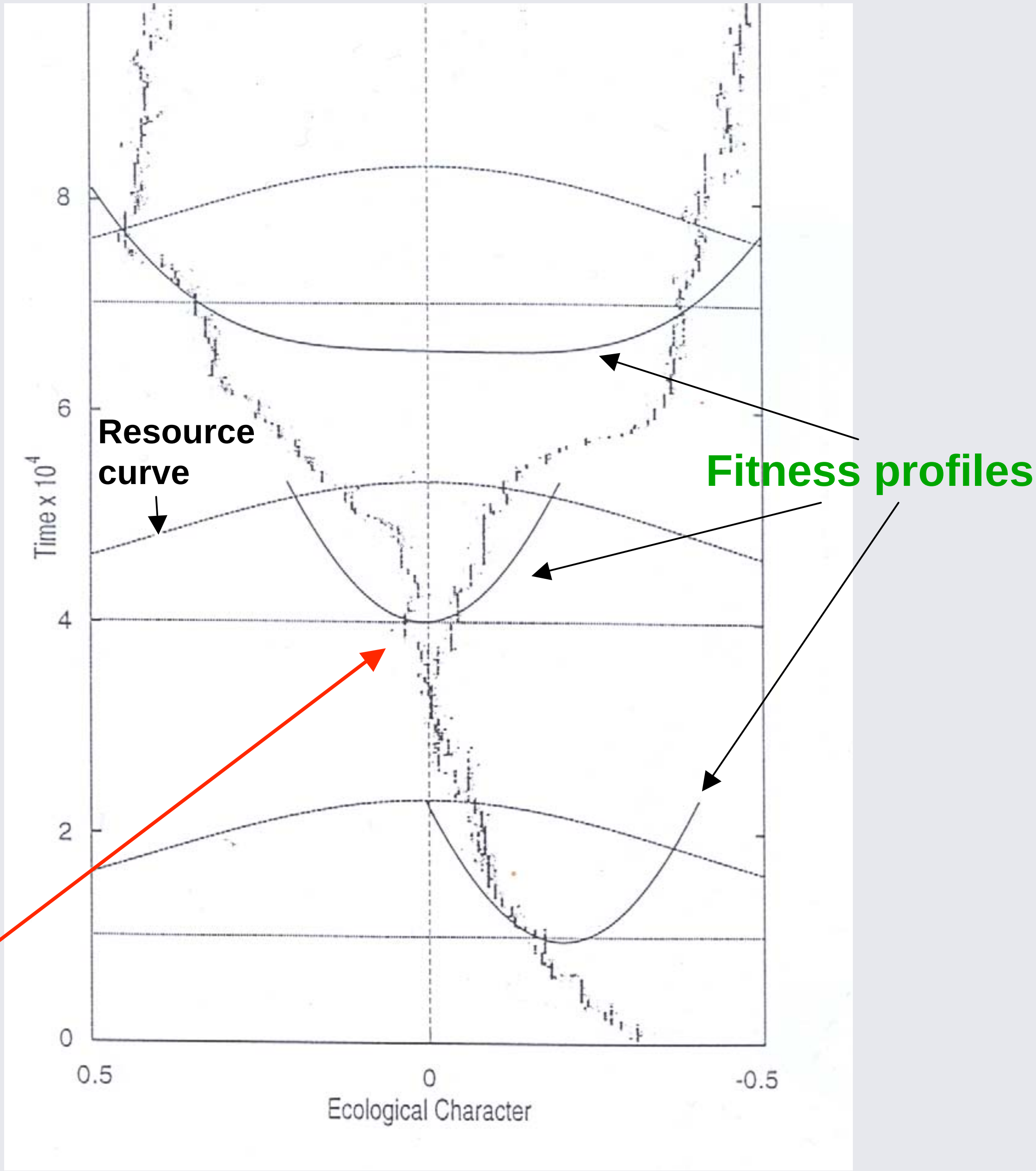
If $\sigma_K > \sigma_\alpha$: Evolutionary branching



σ_K = width of resource abundance curve



σ_α = width of competition curve



When the mean phenotype reaches the maximum of the resource abundance curve, competitive interactions generate disruptive selection

Adaptive dynamics (Metz et al.):

Mathematical framework for studying long-term evolutionary dynamics of quantitative traits

Invasion fitness:

$f(y,x)$ = long-term growth rate of rare mutant *y* in monomorphic resident *x*

Selection gradient:

$$D(x) = \frac{\partial f}{\partial y}(x, y)\,|_{y=x}$$

Adaptive dynamics:

$$\frac{dx}{dt} = \mu \cdot D(x)$$

(μ describes mutational process)

Adaptive dynamics (Metz et al.)

$$\frac{dx}{dt} = \mu \cdot D(x)$$

- $D(x) > 0 \Rightarrow$ selection for larger x

  $D(x) < 0 \Rightarrow$ selection for smaller x

- attractors for the adaptive dynamics (evolutionary attractors): points x^* in phenotype space with

$$D(x^*) = 0 \qquad \frac{dD}{dx}(x^*) < 0$$

Evolutionary branching occurs if an evolutionary attractor represents a fitness minimum, i.e. if

$$\left.\frac{\partial^2 f}{\partial y^2}(y, x^*)\right|_{y=x^*} > 0$$

Evolutionary branching points (stable fitness minima):

- “Singular” Points in phenotype space satisfying certain mathematical conditions
- Existence of such points can be checked in any adaptive dynamics model

Analytical result for symmetric resource competition:

Evolutionary branching (convergence to a fitness minimum and subsequent split into diverging lines) occurs when the width of the competition function is smaller than the width of the resource distribution, i.e., if

$$\sigma_K > \sigma_\alpha$$

On the ecology of speciation:

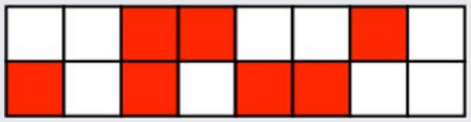
Evolutionary branching (evolutionary convergence to fitness minima) is a generic outcome of frequency-dependent interactions due to competition, predation, and mutualism.

(First models of evolutionary branching in the late 90’s; to date over 40 publications reporting evolutionary branching, many more on adaptive dynamics in general.)

Conclusion: **Selection for lineage splitting may often be a natural consequence of ecological interactions.**

Evolutionary branching in sexual populations: Speciation

- traits (e.g. body size) are determined by many diallelic additive loci:



trait value = # of 🟥 - alleles

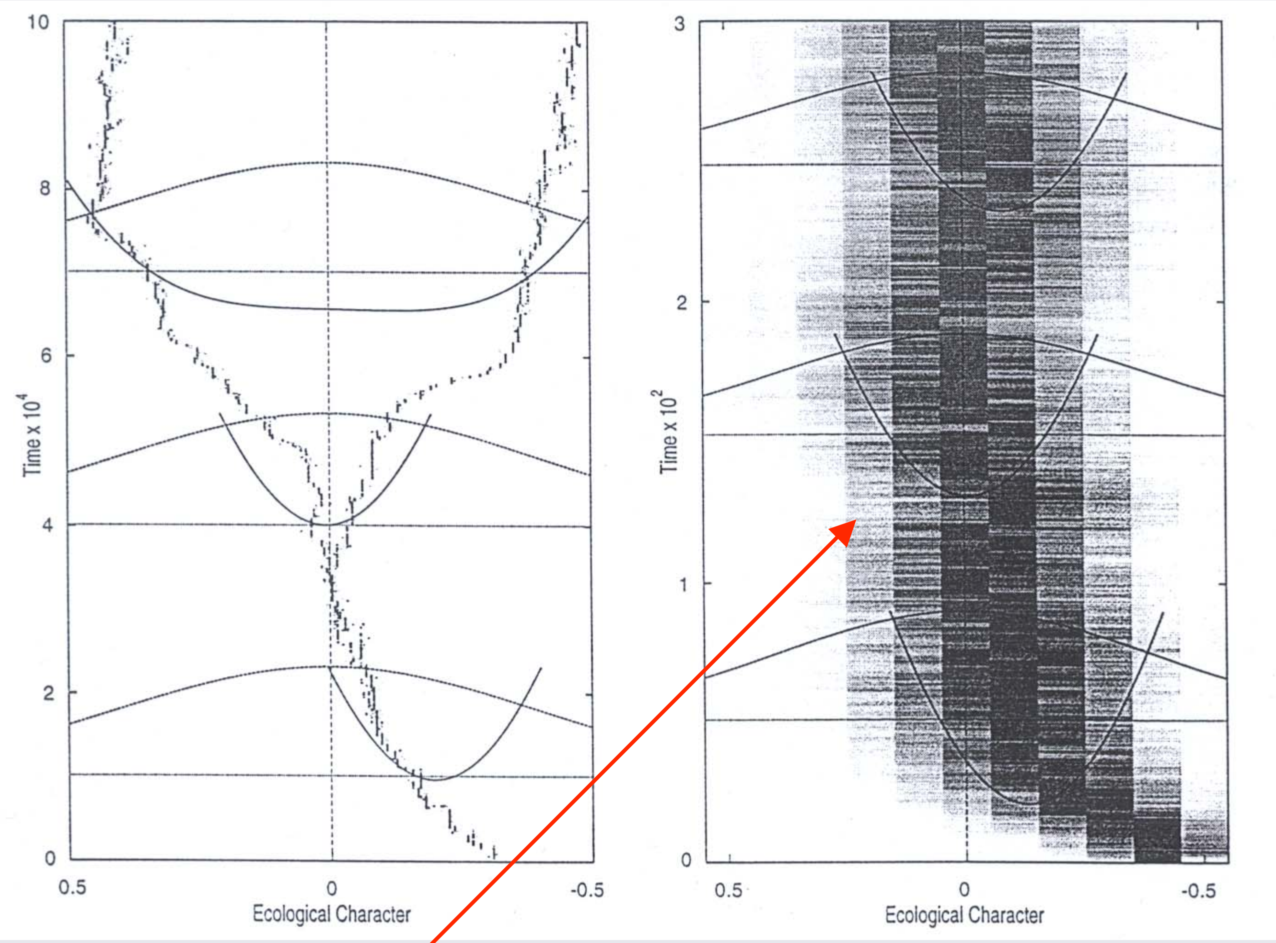
- individuals are given by their genotype

- death rates are determined by the ecological interactions

- if an individual gives birth to an offspring it chooses a partner according to its mode of mating (random or assortative), and the offspring genotype is generated using Mendelian segregation and free recombination

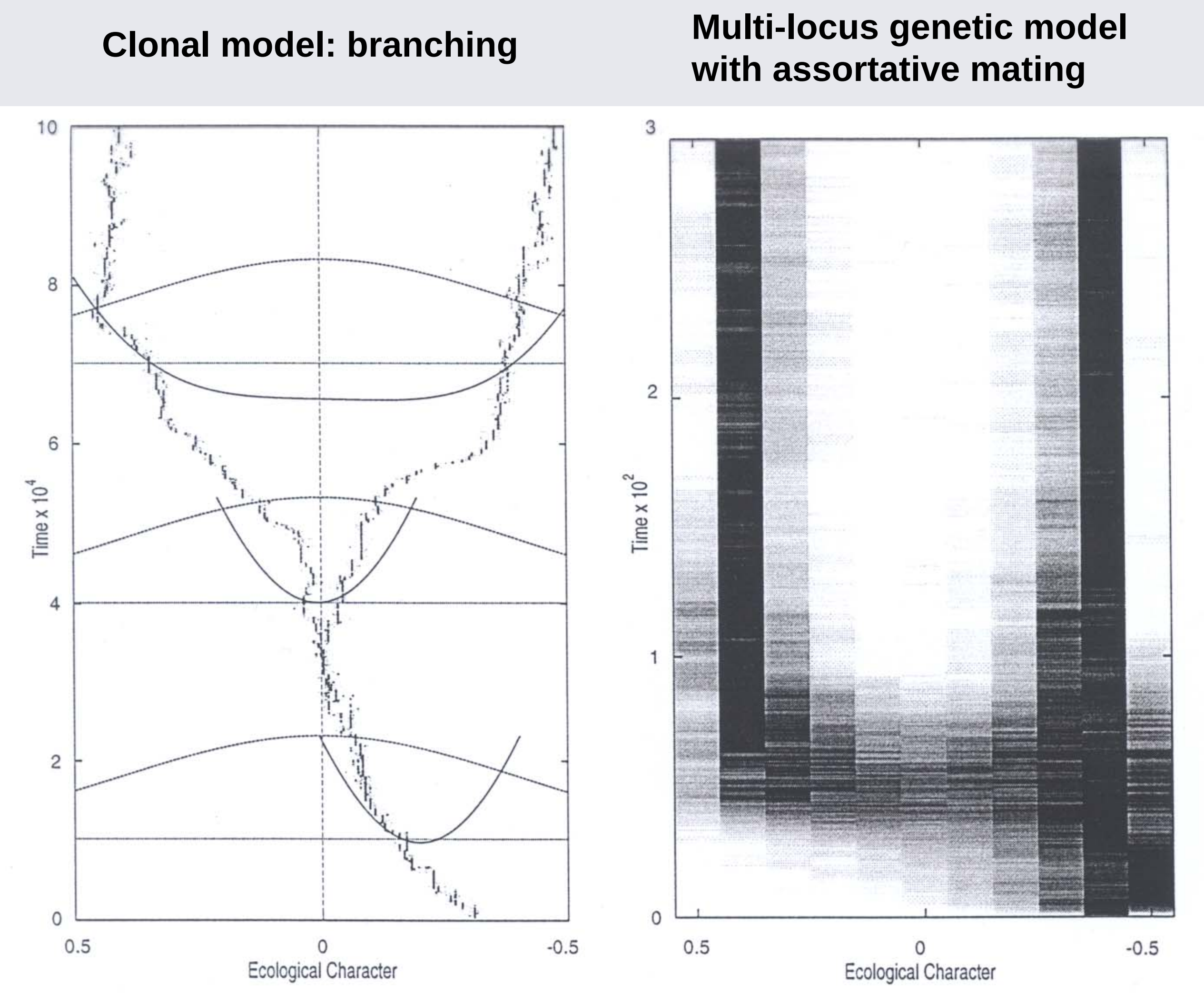
Clonal model: branching

Multi-locus genetic model with random mating



No branching in randomly mating sexual populations (despite disruptive selection): recombination prevents divergence

Assortative mating: mating partners are chosen based on their ecological character; individuals with similar ecological trait values (e.g. similar body size) are preferred


Clonal model: branching

Multi-locus genetic model with assortative mating

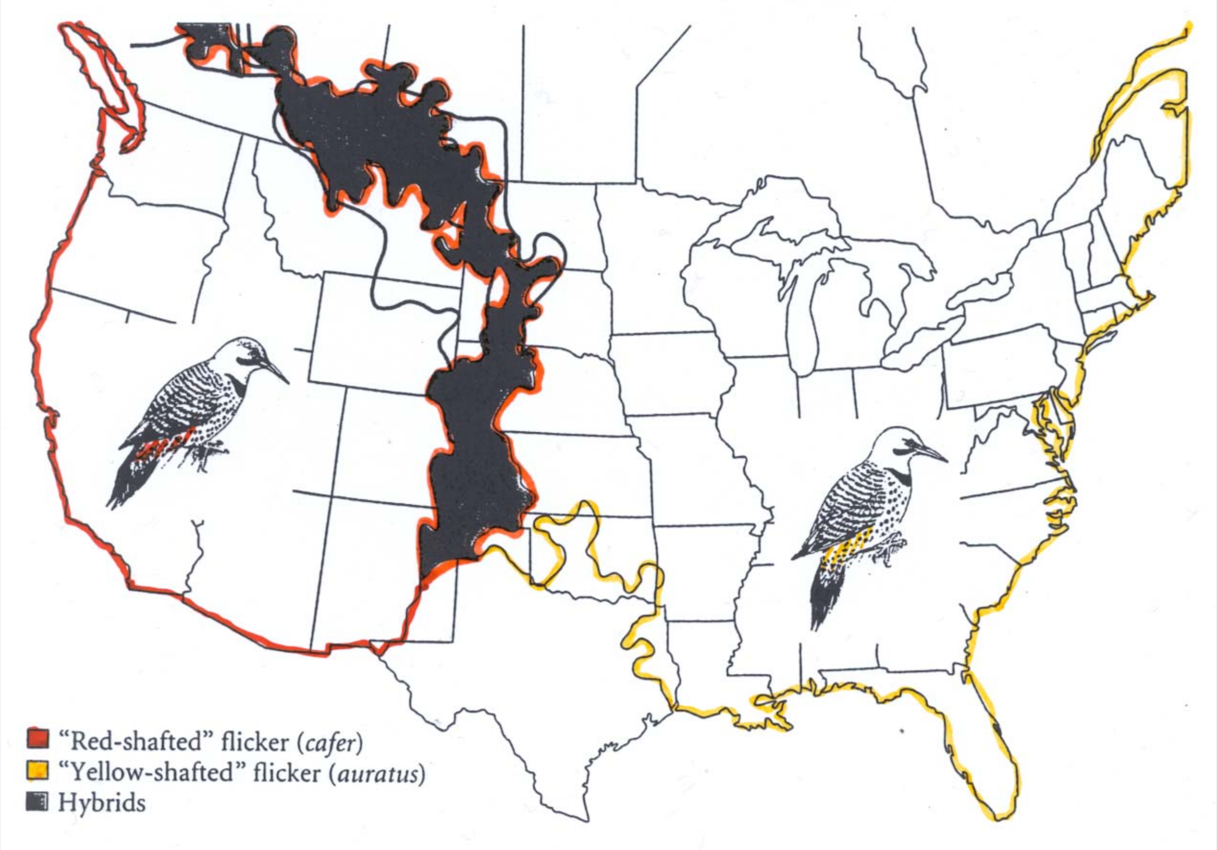
With assortative mating evolutionary branching (i.e. adaptive speciation) is possible in sexual populations

On the population genetics of adaptive speciation:

Evolutionary branching in sexual populations is made possible by the evolution of various assortative mating mechanisms (direct and indirect assortative mating, preference mating, etc.).

Evolution of reproductive isolation is a solution to an adaptation problem posed by ecology, i.e. a response to ecological selection for lineage splitting.

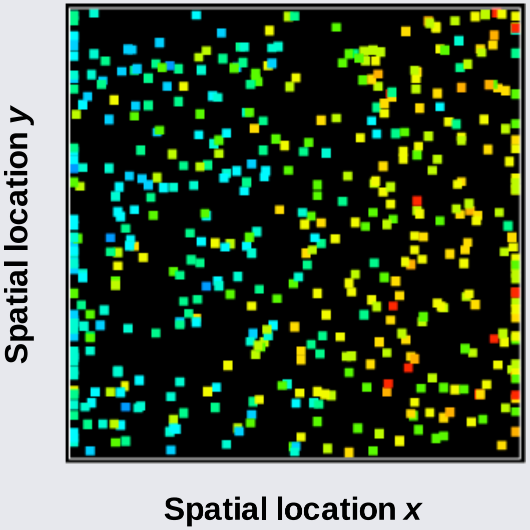
Combining pattern and process: adaptive speciation in spatially structured populations



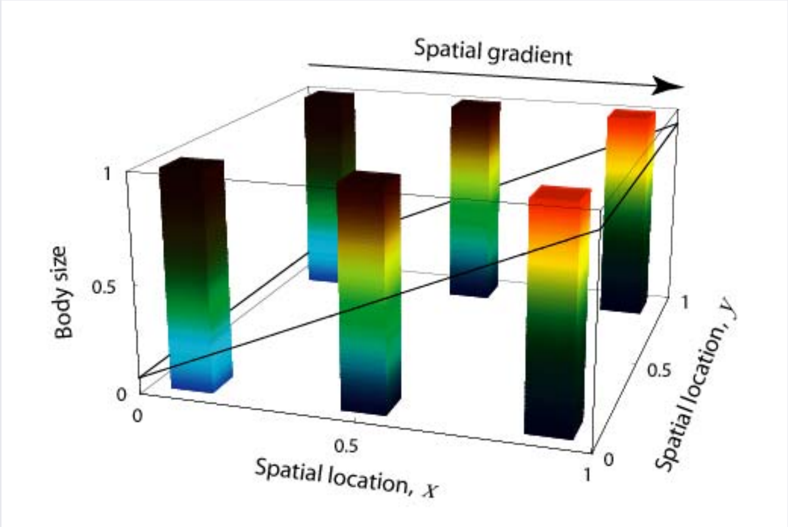
Does spatial segregation imply allopatric speciation?

Individual-based model for spatially structured populations:

Individuals move around in a continuous spatial arena:



The optimal body size varies linearly along the *x*-axis (linear environmental gradient):

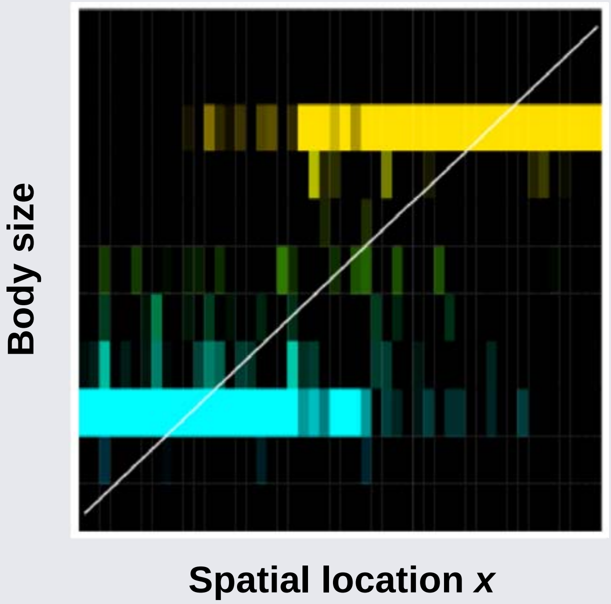


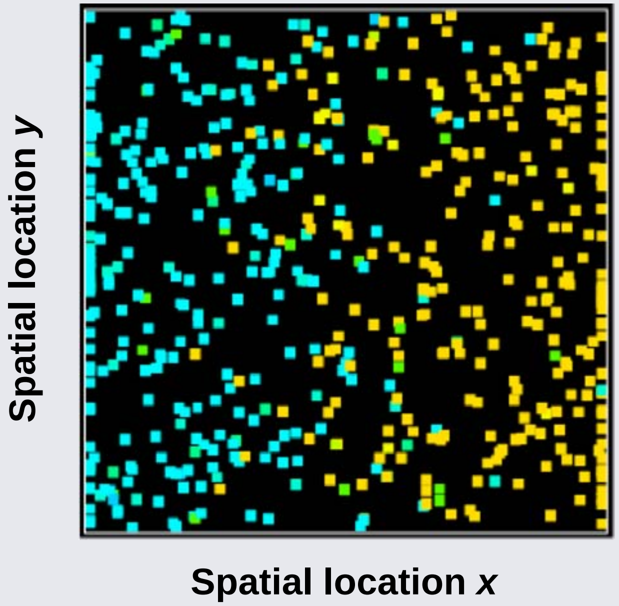
Different colors = different phenotypes

Diversification along environmental gradient:

Spatial segregation due to adaptive speciation

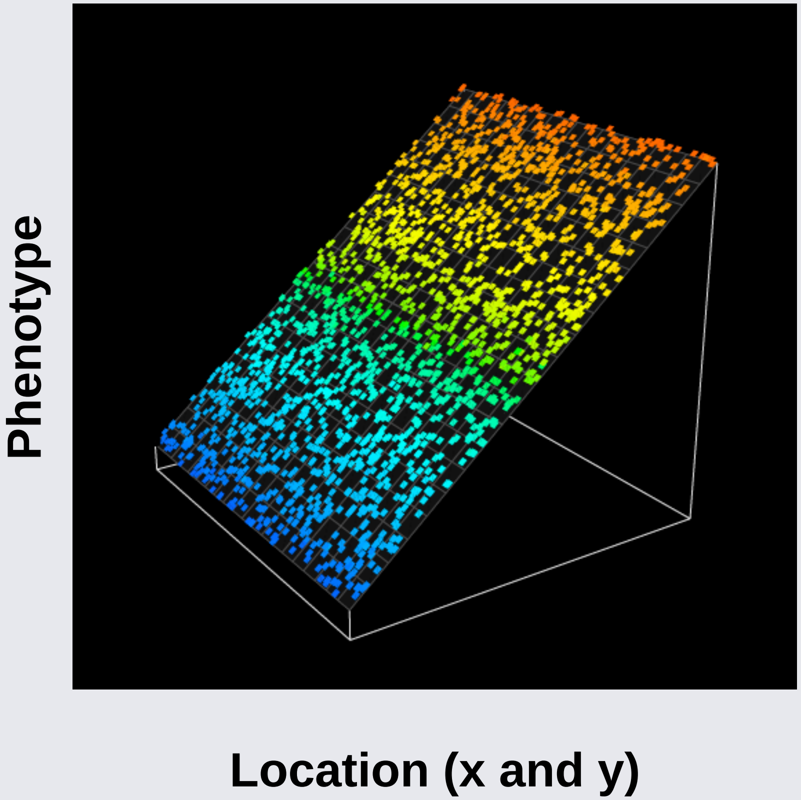
Initial state (monomorphic population)



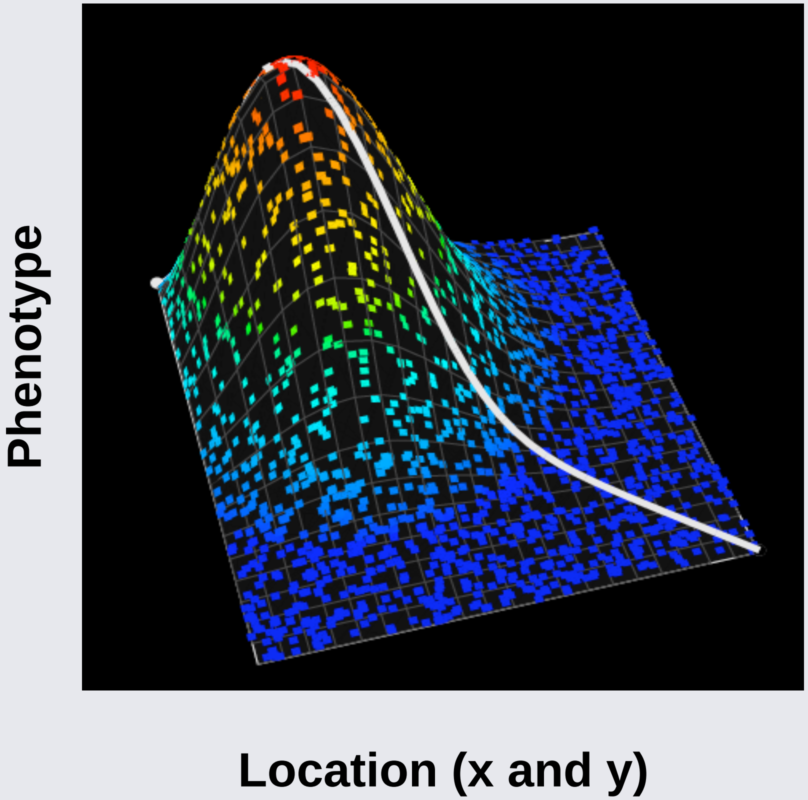


Assortative mating

Linear resource gradient:

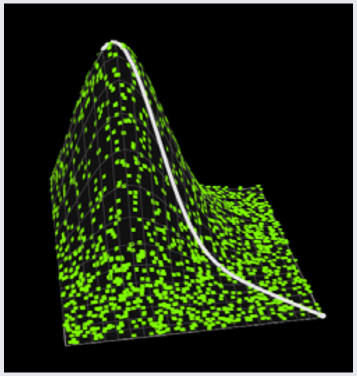


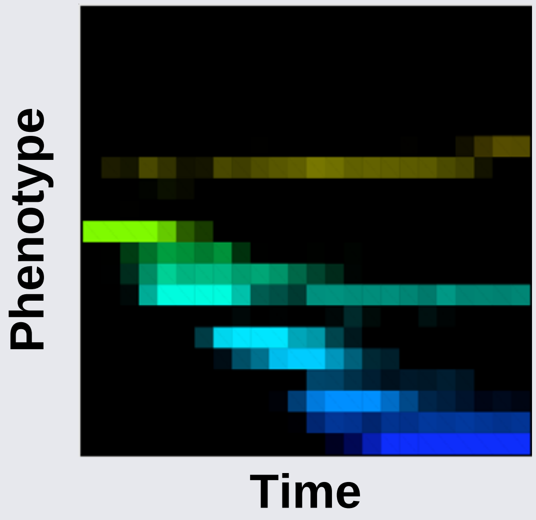
More complicated resource landscapes:

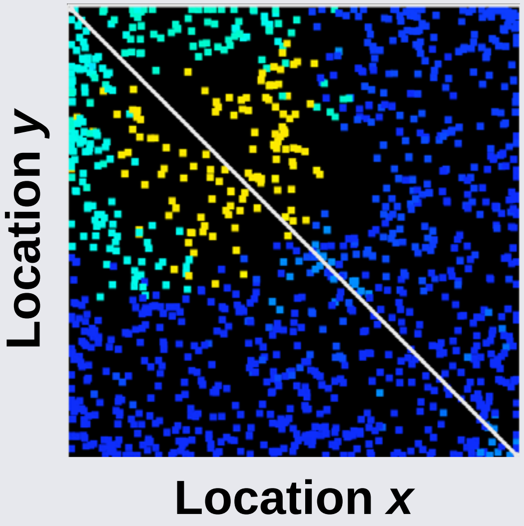


Spatial isolation after adaptive speciation

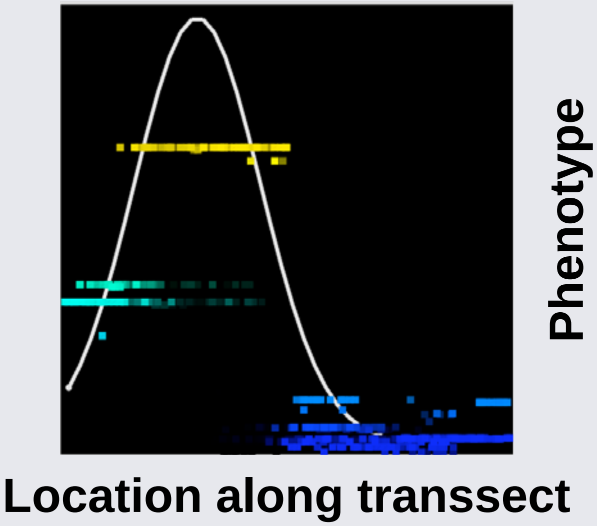
Initial conditions:







No contact between sister species along transsect



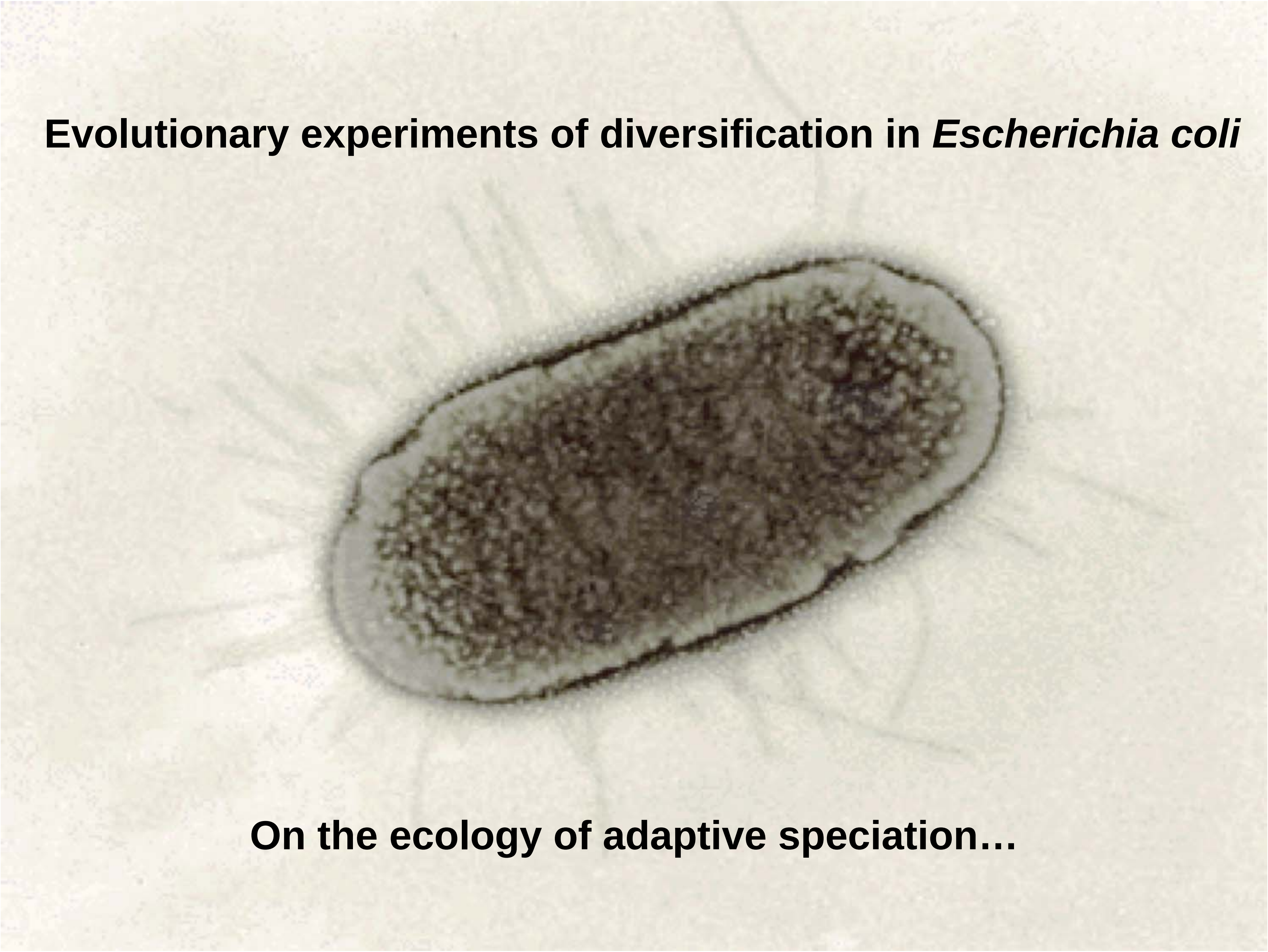
Conclusions from theory:

Evolutionary branching (evolutionary convergence to fitness minima) and adaptive speciation are generic outcomes of frequency-dependent ecological interactions (competition, predation, mutualism)

Spatial structure facilitates evolutionary branching

Adaptive speciation along environmental gradients (an intrinsically ‘sympatric’ process) leads to ‘allopatric’ patterns of species abundance

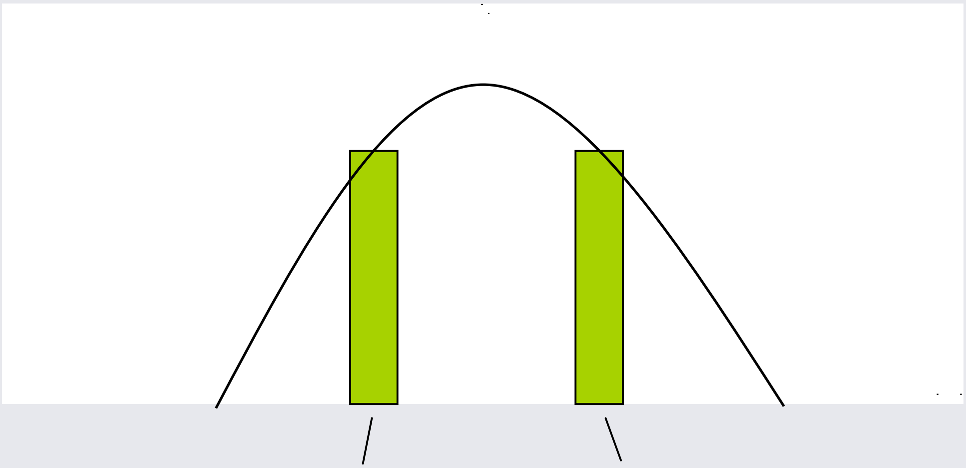
Evolutionary experiments of diversification in *Escherichia coli*



On the ecology of adaptive speciation…

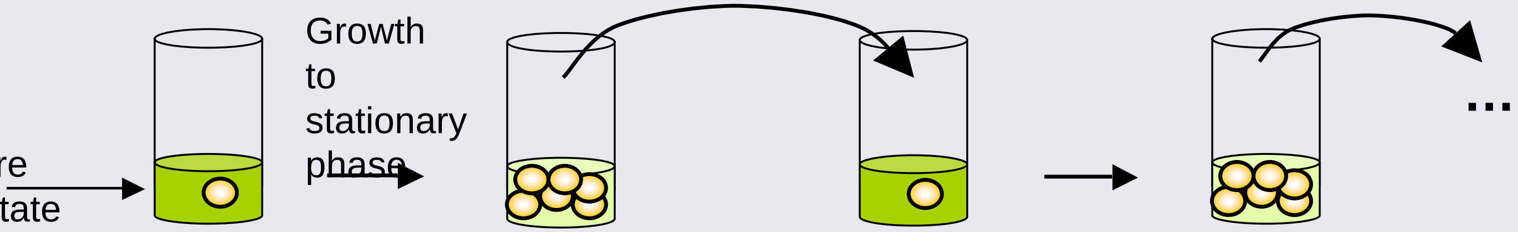
Experimental tests of adaptive diversification with *Escherichia Coli B*

Discrete Resource spectrum:



Carbon source: **50% Glucose** **50% Acetate**

12 experimental lines propagated in serial batch cultures for ~1,000 generations:



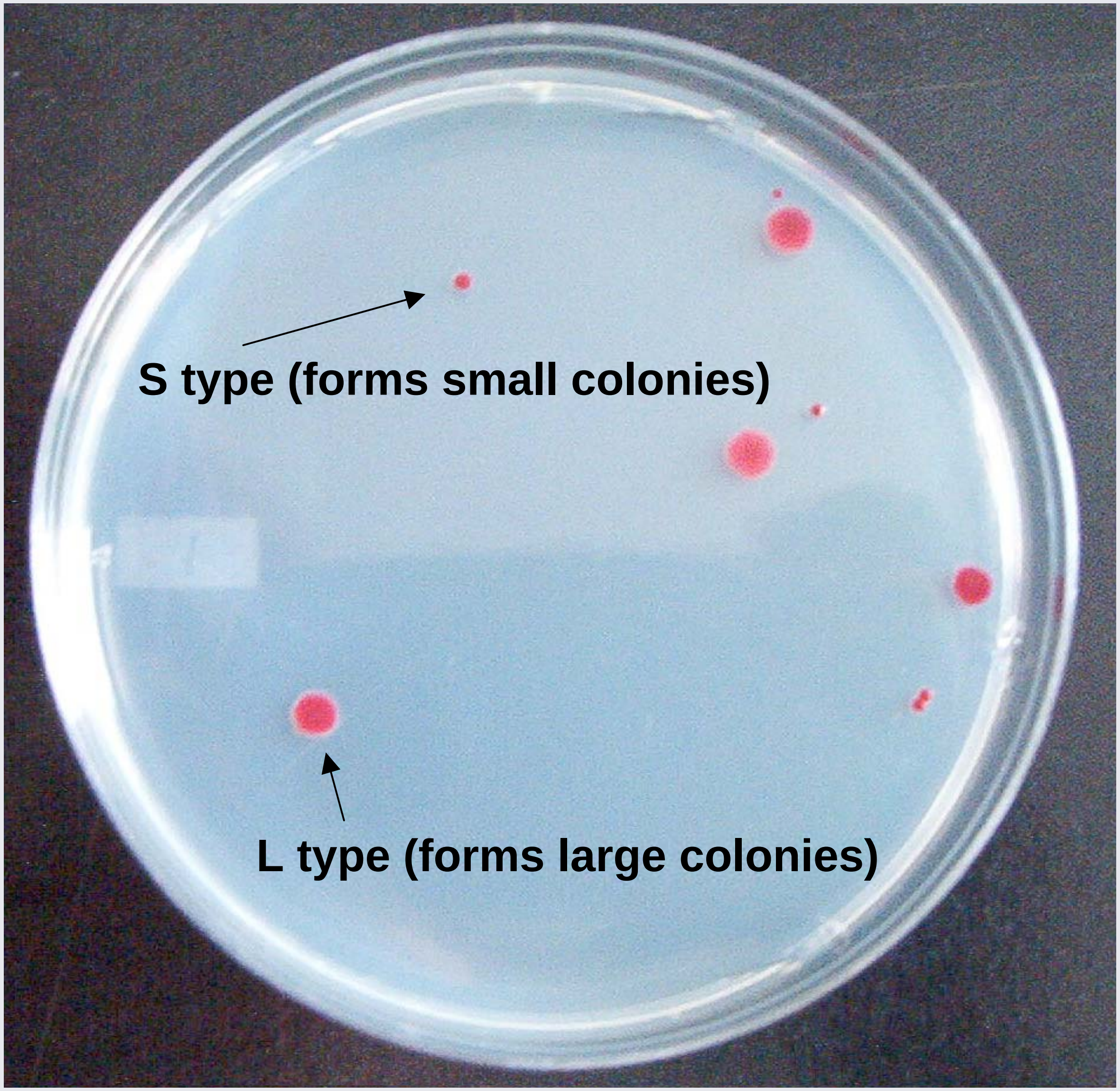
inoculate

Growth to stationary phase

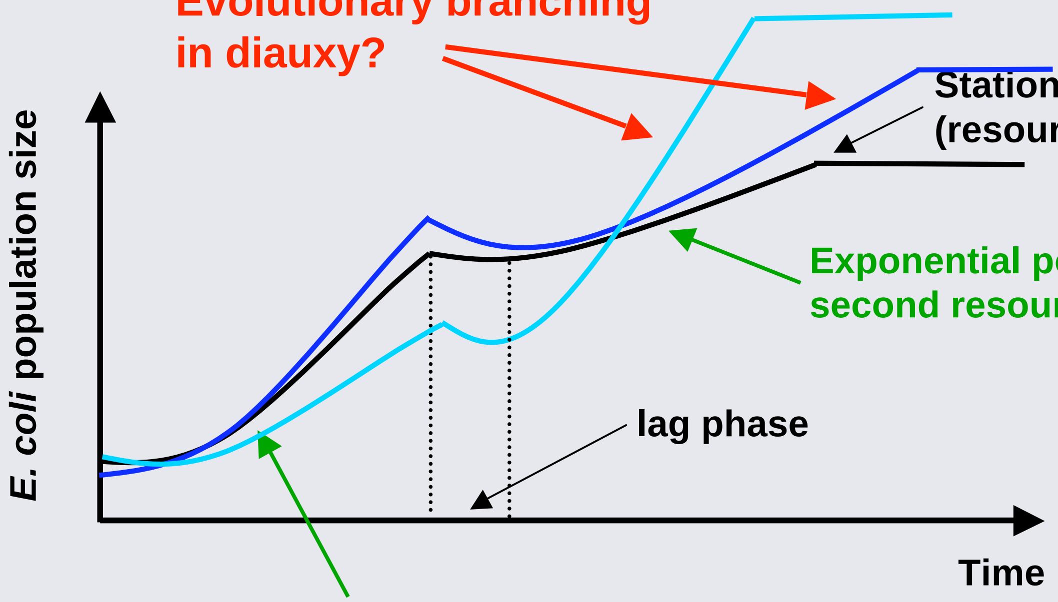
50/50 mixture of glucose/acetate

…

Diversification in colony morphology in 9 out of 12 microcosms:



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



Evolutionary branching in diauxy?

Slow growth on glucose
Short switching lag and fast growth onto acetate

Fast growth on glucose
Long switching lag and slow growth on acetate

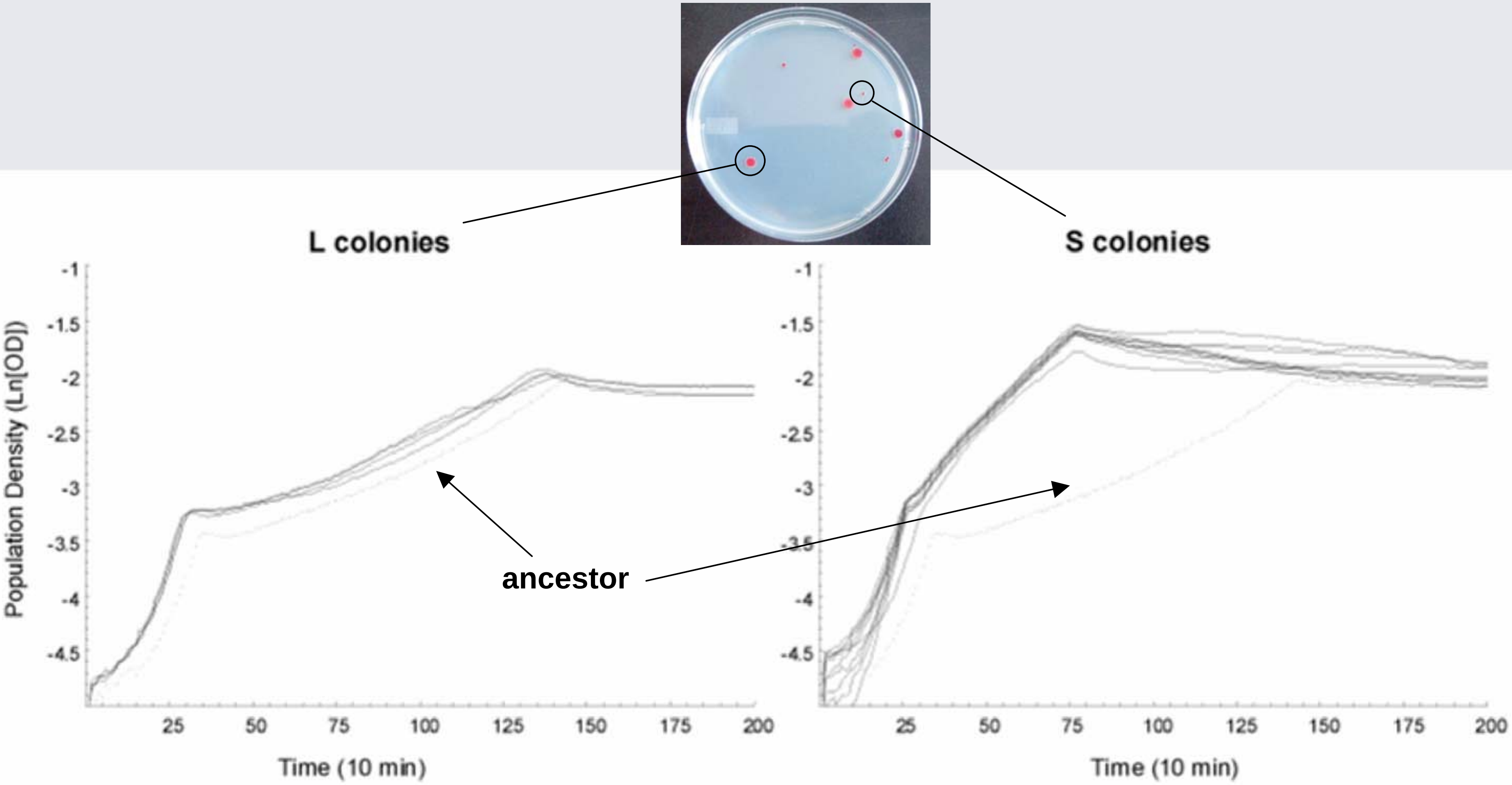
Stationary phase
(resources exhausted)

Exponential population growth on second resource (acetate)

lag phase

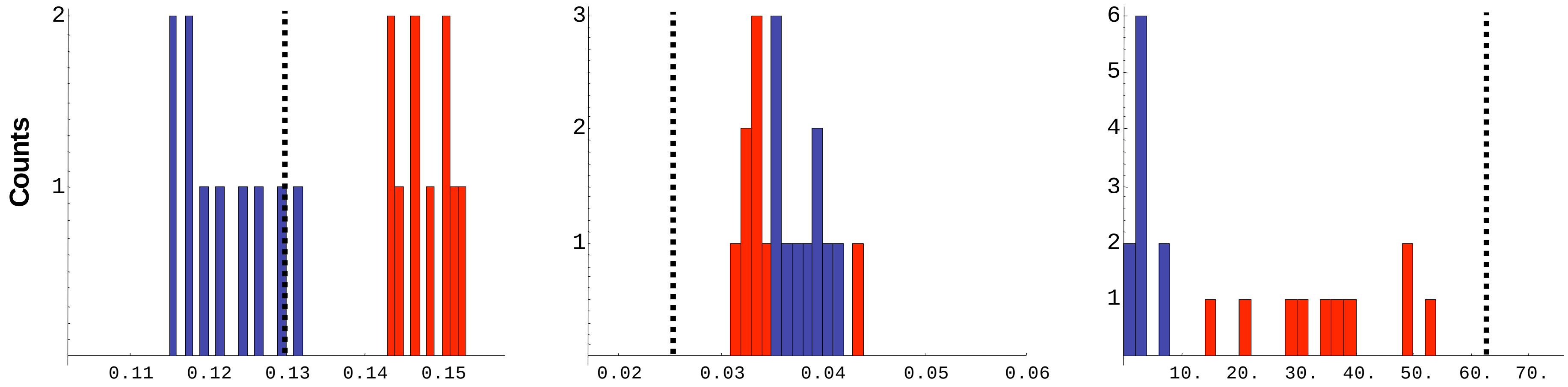
Exponential population growth on first resource (glucose)

Large (L) and Small (S) colonies exhibit different diauxy behavior (10:90 glucose/acetate):



Significant differences between Large (L) and Small (S) types in ecological parameters:

Population 33

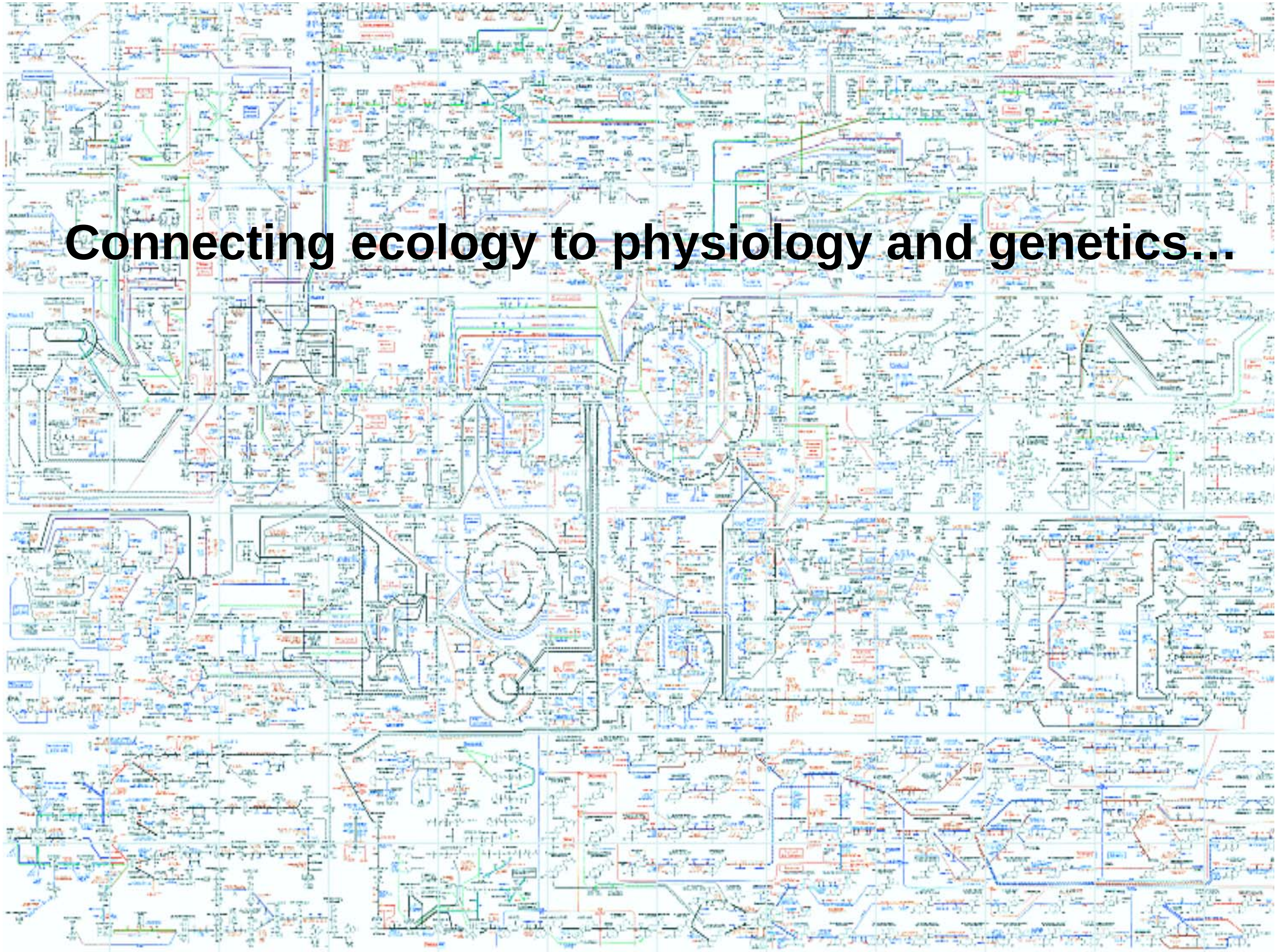


Growth rate in glucose

Growth rate in acetate

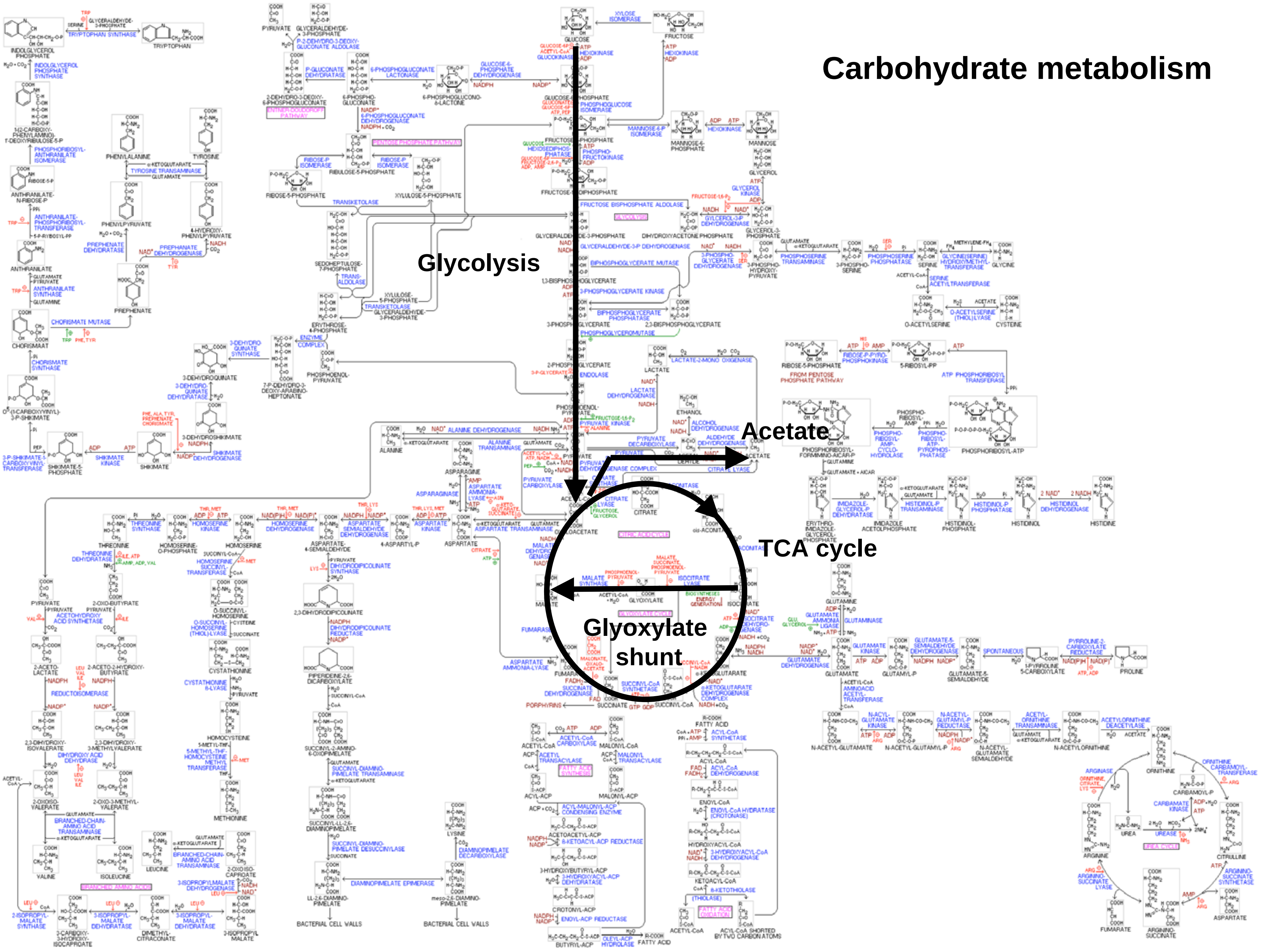
Switching lag in glu/ace (10:90)

● L type
● S type
┅ Ancestor



Connecting ecology to physiology and genetics…

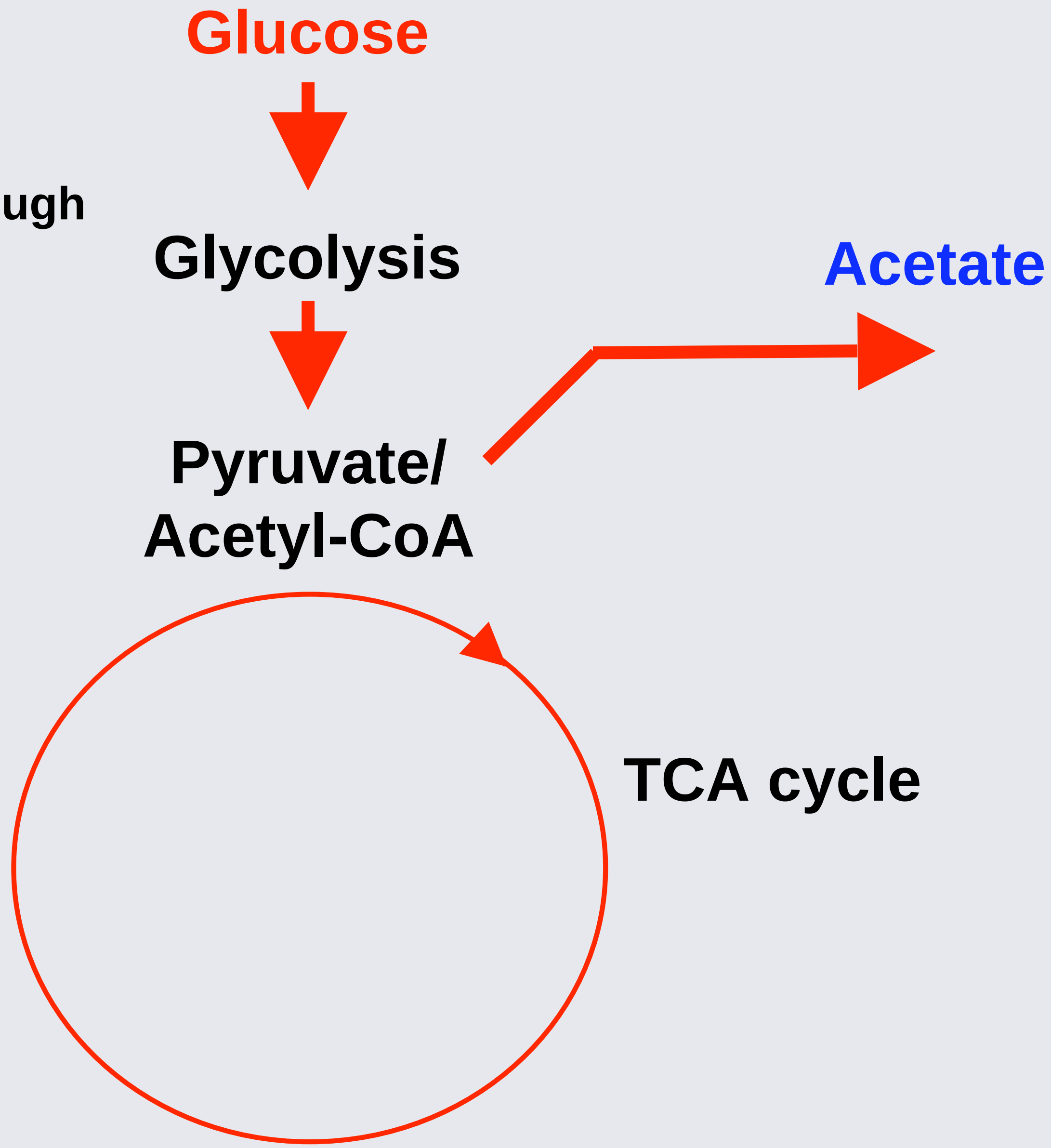
Carbohydrate metabolism



Basic glucose and acetate pathways:

"Fermenting":

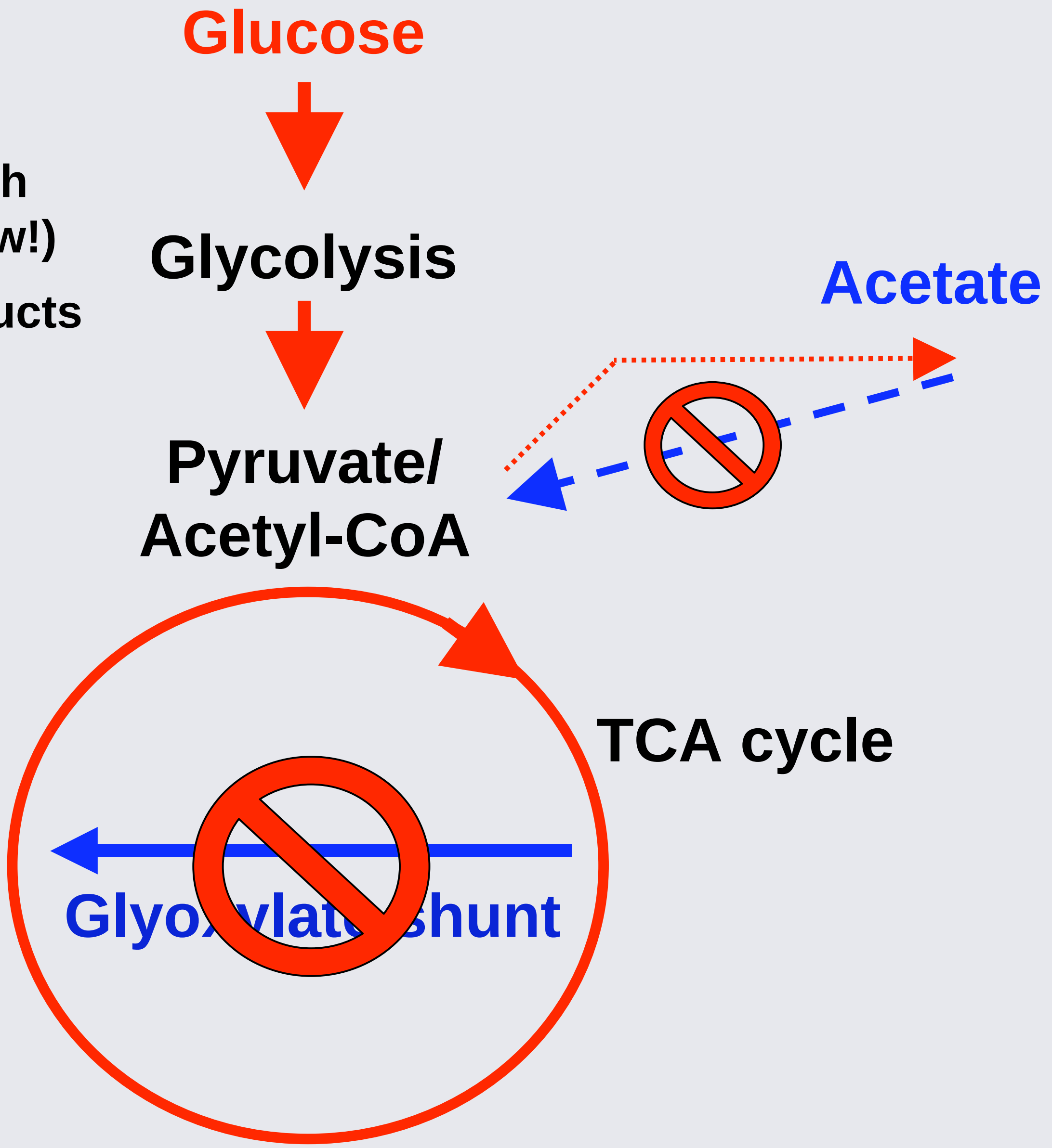
- Energy gain mainly through glycolysis (fast!);
- Secretes glycolysis byproducts (acetate)



Basic glucose and acetate pathways:

“Respiring”:

- Energy gain also through glyoxylate pathway (slow!)
- Uses glycolysis byproducts in secondary pathways



Glucose

Glycolysis

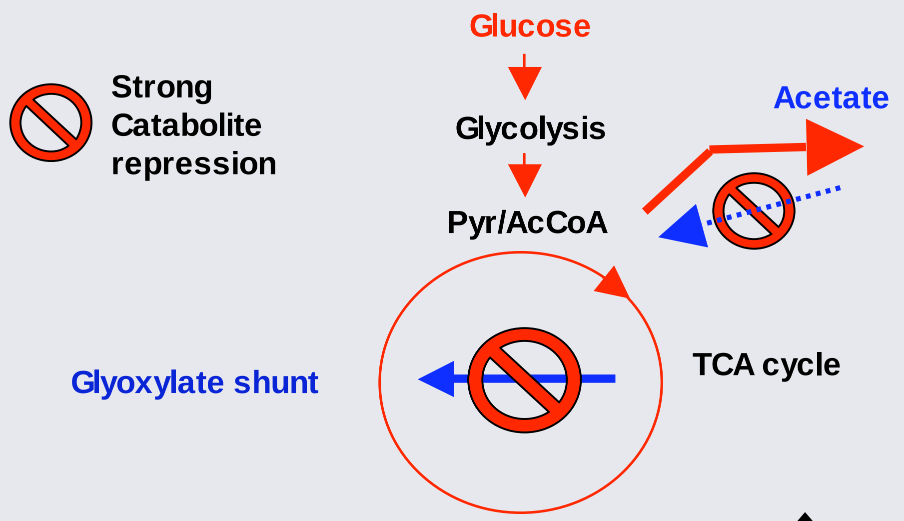
Pyruvate/
Acetyl-CoA

Acetate

TCA cycle

Glyoxylate shunt

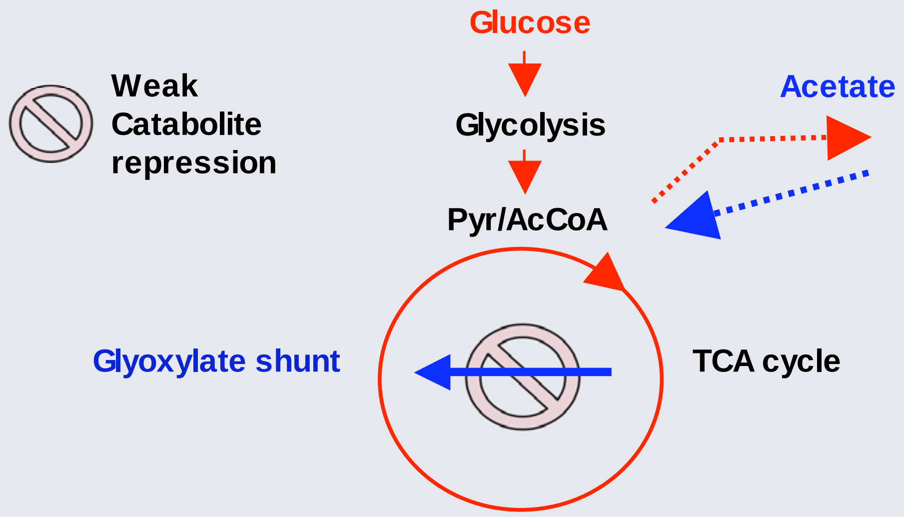
🚫 Catabolite repression during fermentation



Strong repression of acetate metabolism in glucose phase of diauxy (“*fermenter*”):

Rapid growth on glucose, but long switching lag to growth on acetate

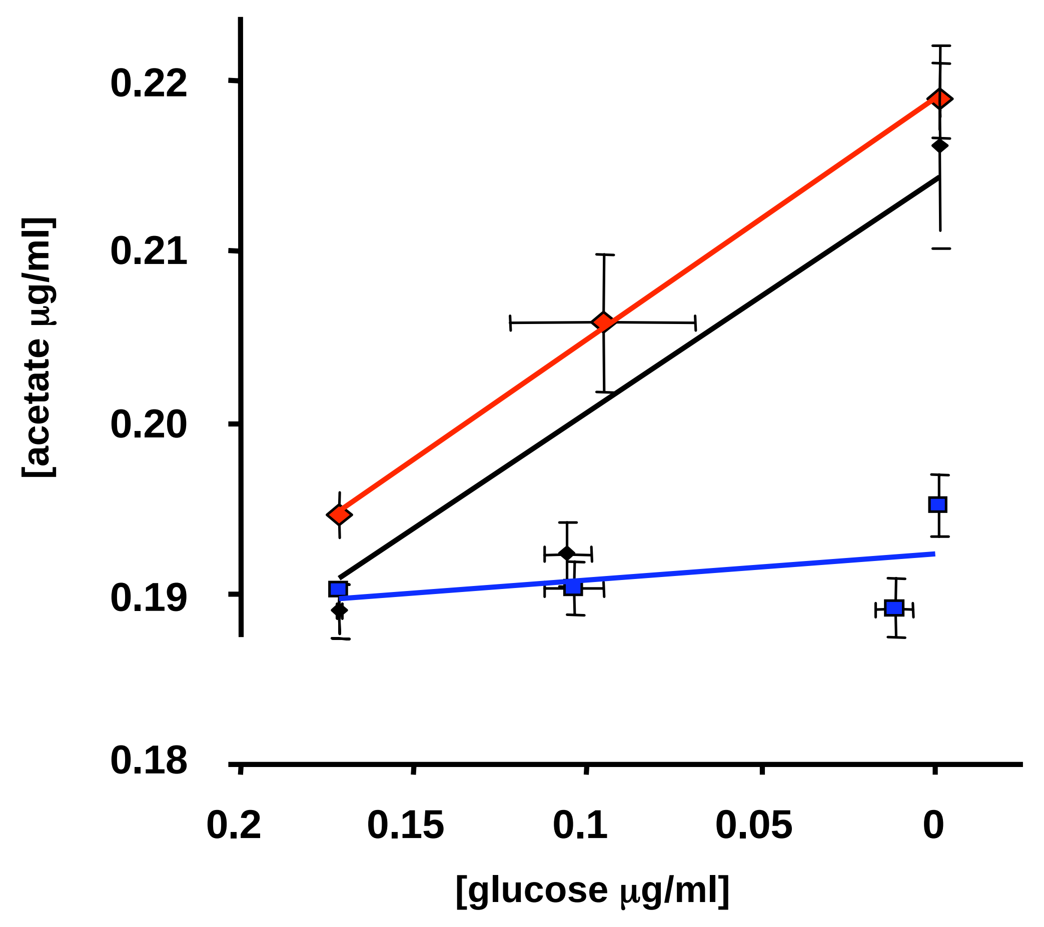
Tradeoff



Weak repression of acetate metabolism in glucose phase of diauxy (“*respirer*”):

Slower growth on glucose, but short switching lag to growth on acetate

Acetate production during glucose metabolism: Fermenters (Large) should secrete more acetate than respirers (Small)



◆ **Ancestor:** acetate is byproduct of glycolysis (**fermenter**)

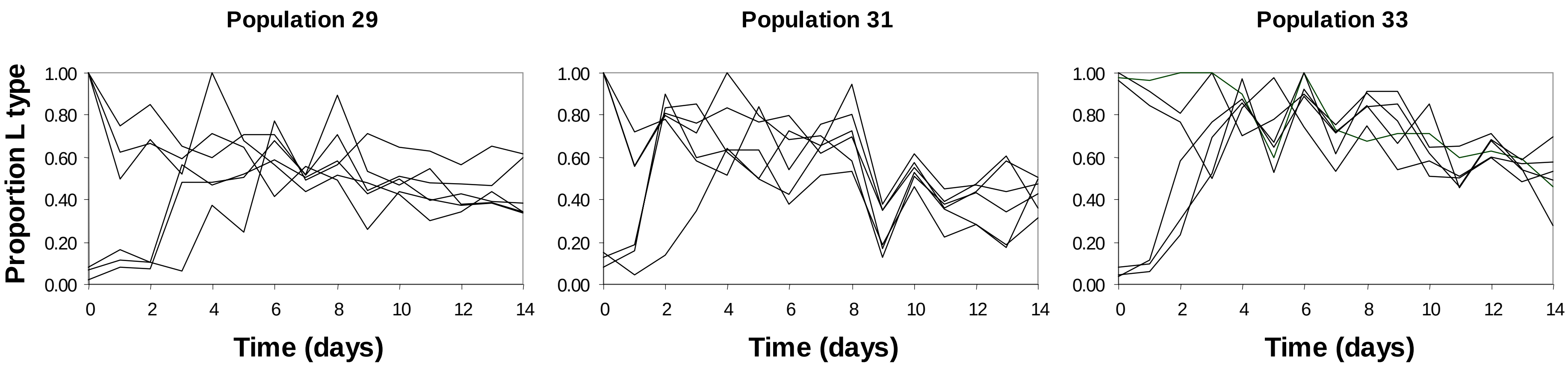
◆ **Large:** acetate is byproduct of glycolysis (**fermenter**)

■ **Small:** acetate concentration increases much less during glucose consumption (**respirer**)

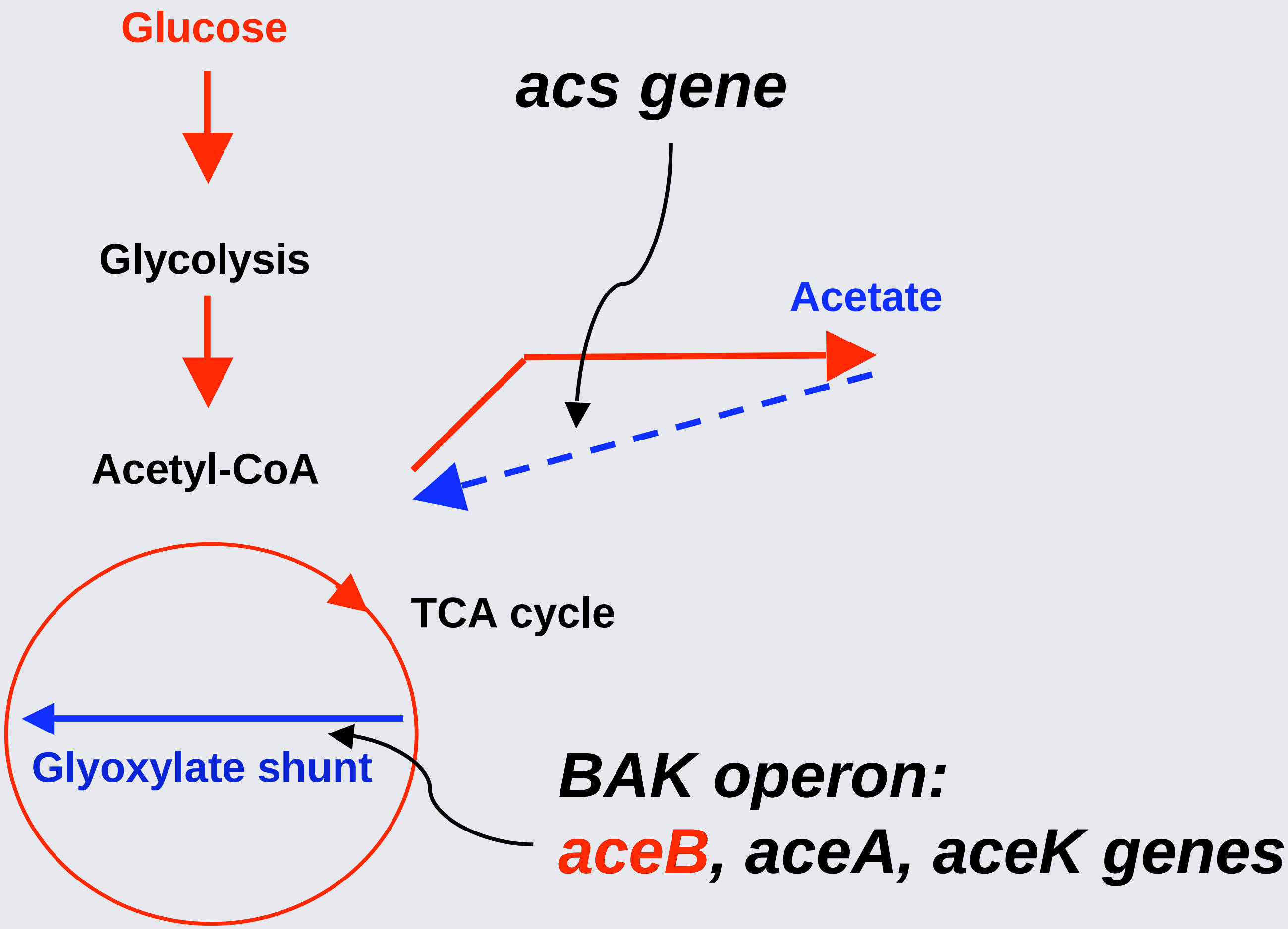
Frequency-dependent selection for position on tradeoff curve:

- **If everybody is a glucose specialist (fermenter), it pays to be a generalist (fast switcher, weak catabolite repressor)**
- **If everybody is a generalist (respirer), it pays to be a glucose specialist**

Invasion experiments reveal frequency dependence: Rare types can invade



Genetics of glucose and acetate metabolism:



Glucose

Glycolysis

Acetyl-CoA

TCA cycle

Glyoxylate shunt

Acetate

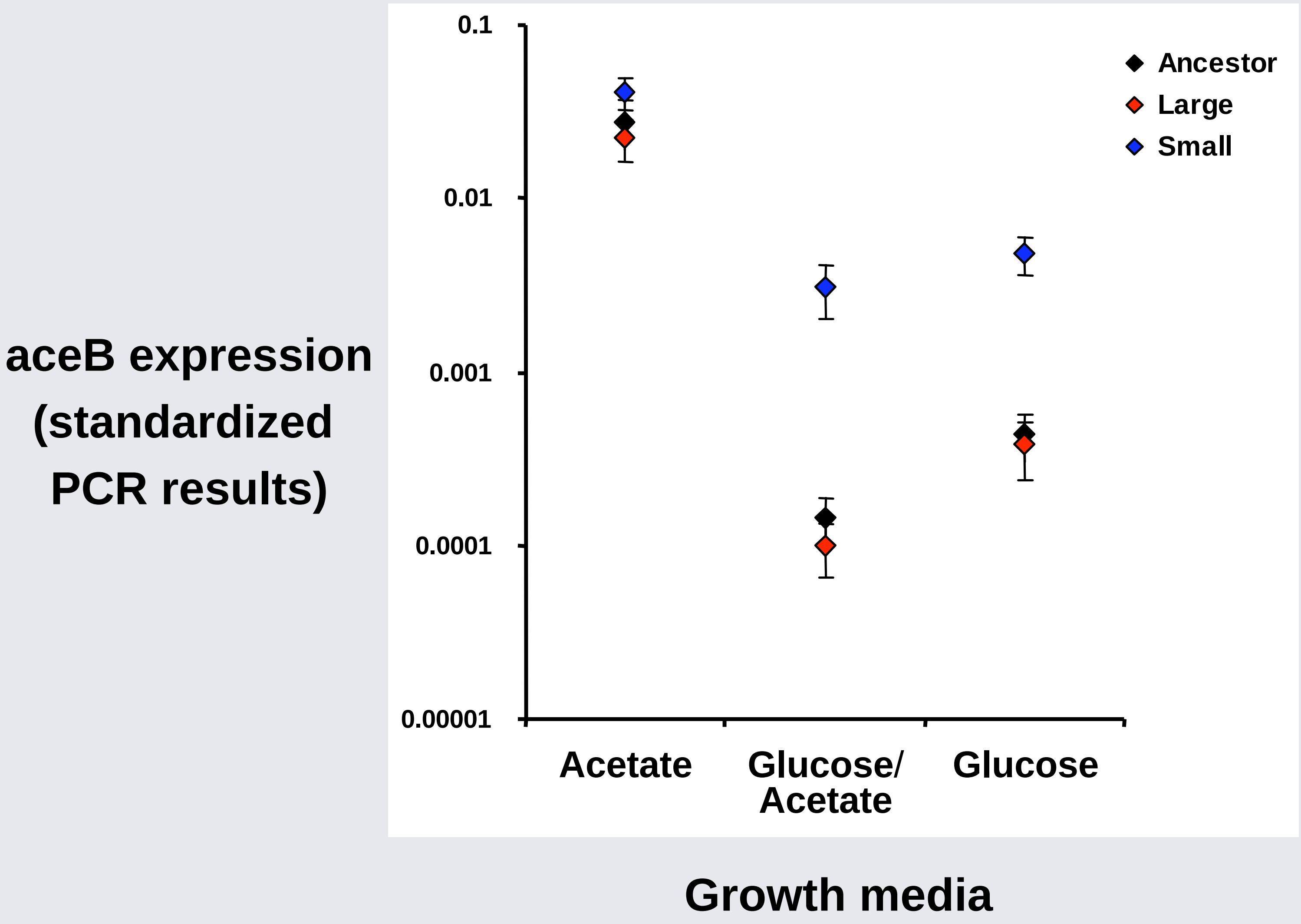
acs gene

BAK operon:

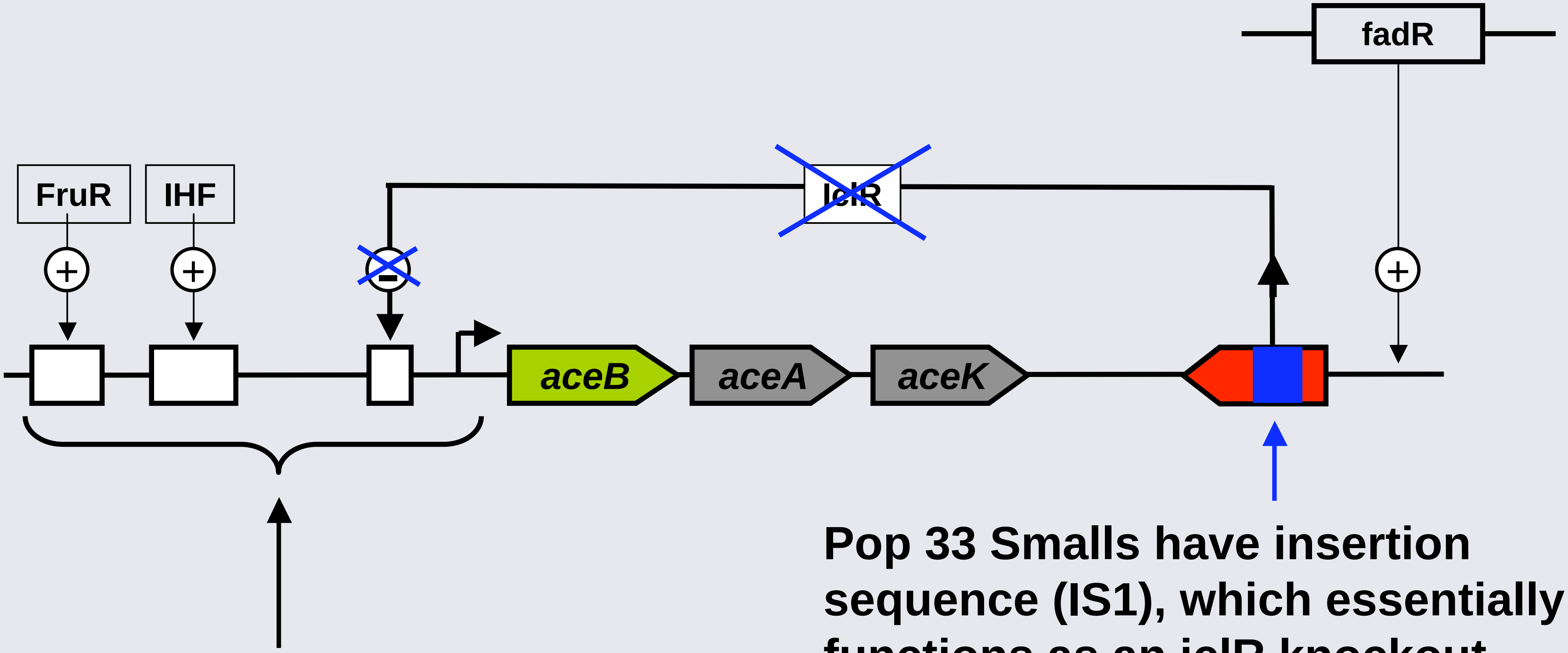
aceB, aceA, aceK genes

Expectation: when growing on glucose, aceB is expressed more in Small (respirer) than in Large (fermenter)

When growing on glucose, Smalls express the aceB gene (glyoxylate pathway is active)



Regulation of aceB:



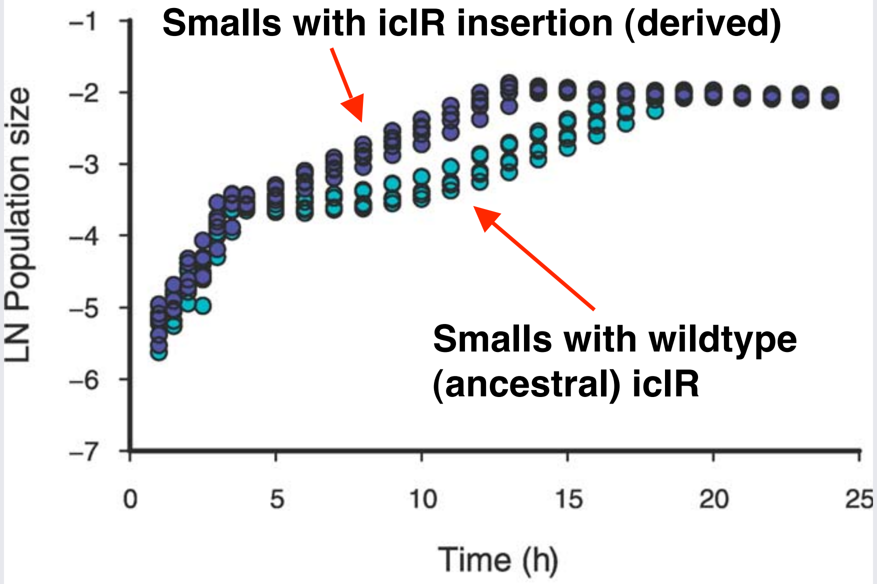
Pop 33 Smalls have insertion sequence (IS1), which essentially functions as an iclR knockout

Regulatory sequence is the same in ancestor, Large, Small types

(But: Smalls from other populations don’t have the IS1 element!)

What makes a Small?
Transform ancestral iclR gene to Smalls using plasmids and conjugation

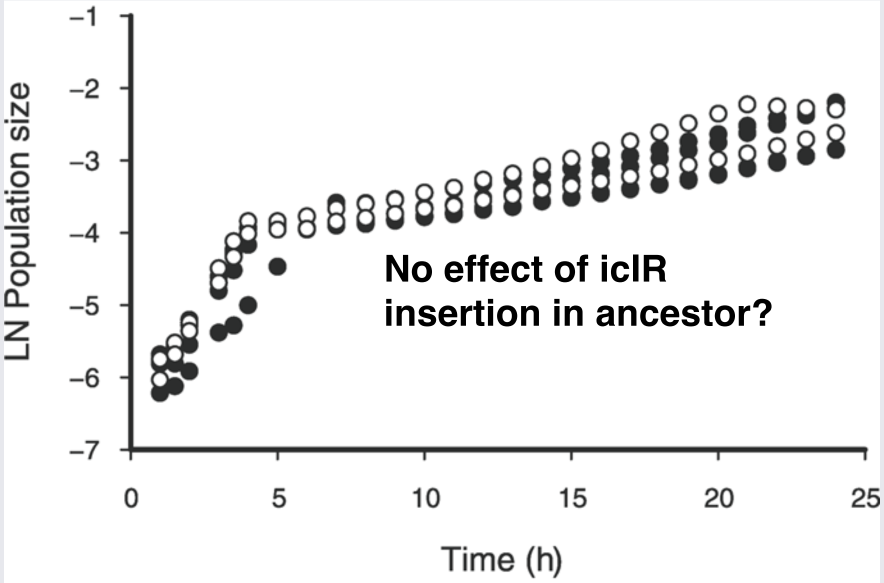
Swapping genes in the derived strain



Smalls with iclR insertion (derived)

Smalls with wildtype (ancestral) iclR

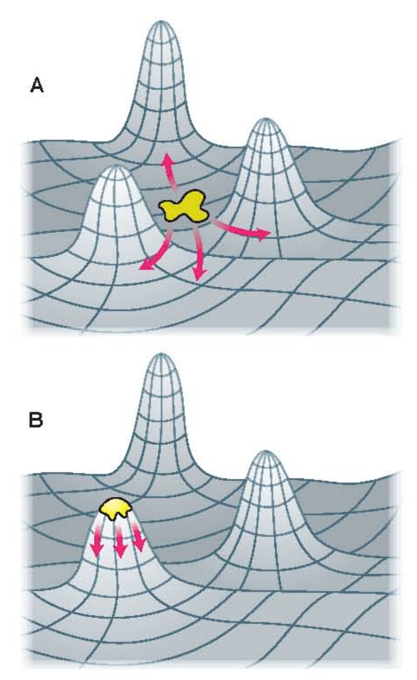
Swapping genes in the ancestral strain



No effect of iclR insertion in ancestor?

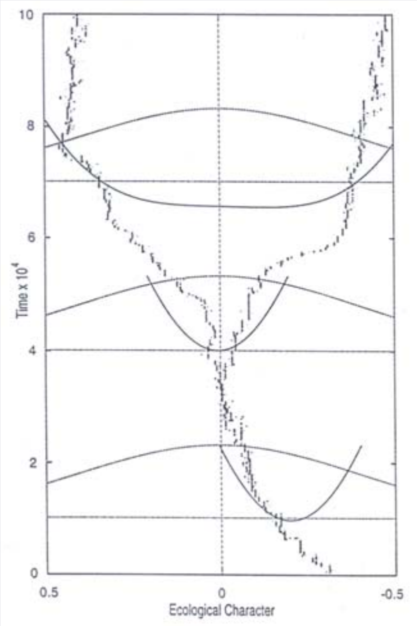
Swapping genes affects the derived strain, but not the ancestral strain:

- **Effect of iclR depends on genetic background (epistatic effects)**
- **More than one genetic change is necessary to produce derived strains**



Traditional view: static fitness landscapes

- Diversification originates in adaptive valleys
- As populations climb adaptive peaks, the likelihood of diversification *decreases*

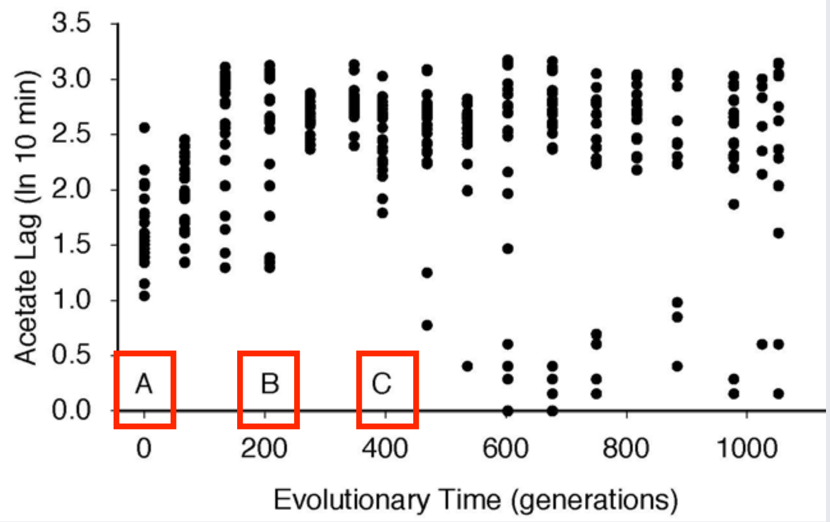


Evolutionary branching: dynamic fitness landscapes

- Diversification occurs *after* convergence to the branching point
- The likelihood of diversification *increases* over time

Evidence for Evolutionary Branching:
The likelihood of diversification increases over time

Evolutionary branching in switching lag:

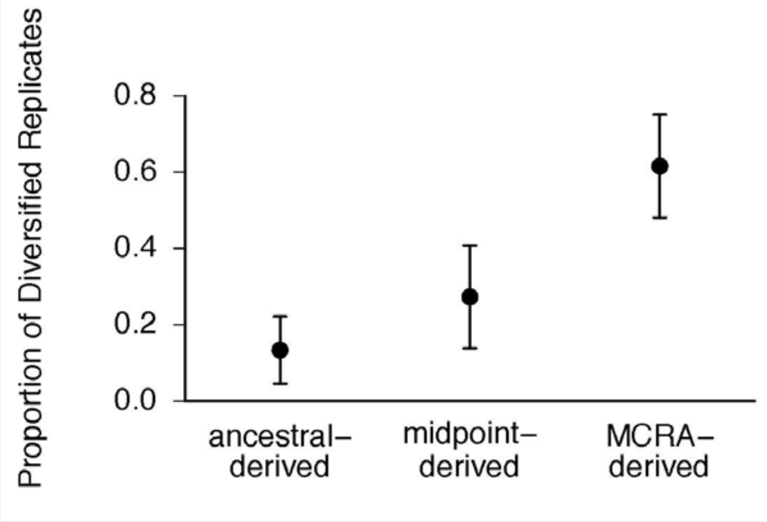


A: ancestral strain

B: midpoint

C: Most recent common ancestor (MRCA)

Rediversification experiment:
Evolution from different time points in the "fossil record"



Populations evolved from single strains taken at later points in the fossil record have higher probability of being diverse after 140 generations

Conclusions from experimental microcosms

Diversity evolved in E. coli populations growing on a mixture of glucose and acetate due to frequency-dependent selection on traits governing resource use (evolutionary branching)

Evolution experiments integrate processes on different levels of biological organization:

- **Evolution of bacterial diversity**
- **Ecological coexistence between competing strains**
- **Physiological differentiation in carbon metabolism**
- **Genetic differentiation in genes regulating metabolic pathways**

Summary

- **Adaptive speciation, i.e., evolutionary branching as an adaptive response to frequency-dependent ecological interactions, is a theoretically plausible evolutionary process**
- **Ecology is as important as population genetics for understanding speciation processes**
- **In spatially structured populations, adaptive speciation can generate “allopatric” patterns of species abundance**
- **Evolutionary experiments with microorganisms are a promising tool to understand processes of adaptive diversification on different levels (genetics, physiology, ecology, evolution)**

Thanks:

Ulf Dieckmann, IIASA, Vienna

Maren Friesen, UC Davis

Melanie Bertrand, UBC

Gerda Saxer, University of Houston

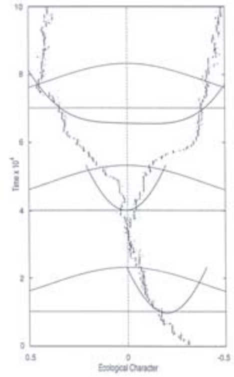
Michael Travisano, University of Houston

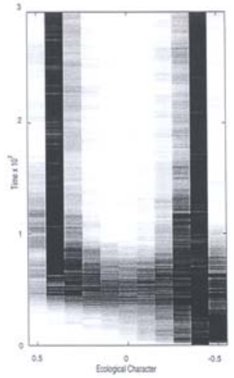
Chrissy Spencer, Jabus Tyerman, UBC

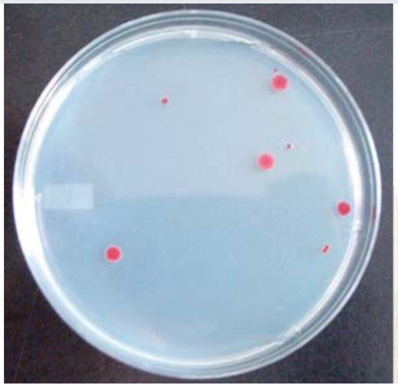
Rosie Redfield, Sally Otto, UBC

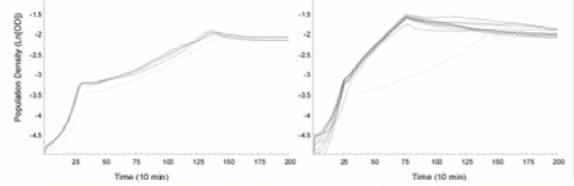
James S. McDonnell Foundation

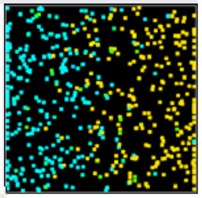
NSERC Canada











Adaptive dynamics model of catabolite repression:

Population dynamics with catabolite repression (Michaelis – Menten kinetics for bacterial growth on two resources):

***E. coli* dynamics:**

$$\frac{dN}{dt} = \frac{r_g CN}{k_g + C} \cdot \boxed{cr} + \frac{r_a AN}{k_a + A} \cdot [(1 - \boxed{cr}) + \underline{S(cr)}]$$

$$0 \leq \boxed{cr} \leq 1$$

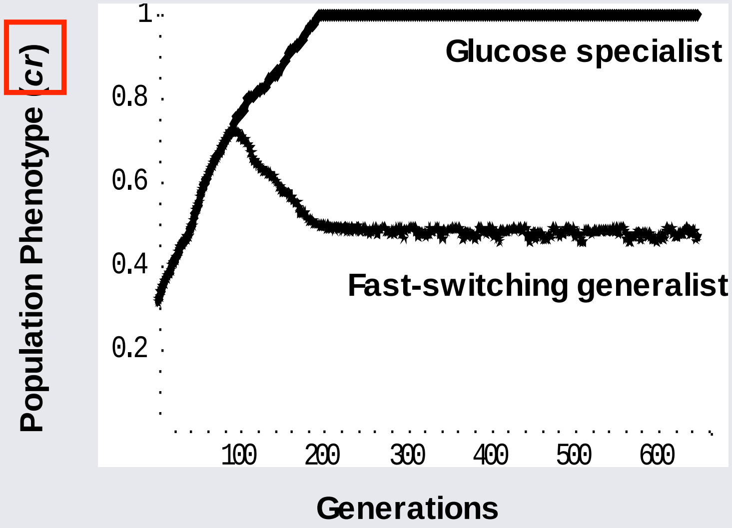
Evolving Phenotype (catabolite repression)

Switching function (tradeoff):
high *cr* induces slow switch
low *cr* induces fast switch

Glucose dynamics: $$\frac{dC}{dt} = -\frac{1}{y_g} \frac{r_g CN}{k_g + C} \cdot cr$$

Acetate dynamics: $$\frac{dA}{dt} = -\frac{1}{y_a} \frac{r_a AN}{k_a + A} \cdot [(1 - cr) + S(cr)]$$

Adaptive dynamics:



If tradeoff is strong enough:

Evolutionary branching into glucose specialist (strong catabolite repression) and fast-switching generalist (weak repression)