The role of frequency dependency in experimental microcosms

Jabus Tyerman
PhD Candidate
Dept. Zoology
UBC


H. Douglas Pratt
1977

Why is there (bio)diversity?
-Species
-Culture (language)

…and what happens if (when) we lose diversity?
-extinction
-globalization

Why is there (bio)diversity?

…and what happens if (when) we lose diversity?

Why is there (bio)diversity?

1. How is diversity maintained?

2. How does it arise?

…and what happens if (when) we lose diversity?

Why is there (bio)diversity?

1. How is diversity maintained?
    - Frequency-dependent fitness
    - Example 1: *Pseudomonas* bacteria (SM-WS-FS)
        - Tool: Invasion Experiment, ESSt.
    - Example 2a: *E. coli* bacteria (SS-FS)
    - Summary
2. How does it arise?
    - Adaptive landscapes – defining the problem
    - Adaptive Dynamics – solving the problem
    - Example 2b: Evolution to the branching point
    - Summary

…and what happens if (when) we lose diversity?

Why is there (bio)diversity?

1. How is diversity maintained?
    - How are populations (species) maintained in communities?
    - How is variation maintained within populations?

Why is there (bio)diversity?

1. How is diversity maintained?
    - How are populations (species) maintained in communities?
    - How is variation maintained within populations?
        - Frequency-dependent selection

Evolution 101

1. Variation
2. …heritable
3. Differential Performance

Evolution!
(by natural selection)

Evolution 101

1. Variation
2. …heritable
3. Differential Performance → "Fitness"

Evolution!
(by natural selection)

Frequency-dependent selection

Fitness: Relative measure of payoffs (reproductive success).

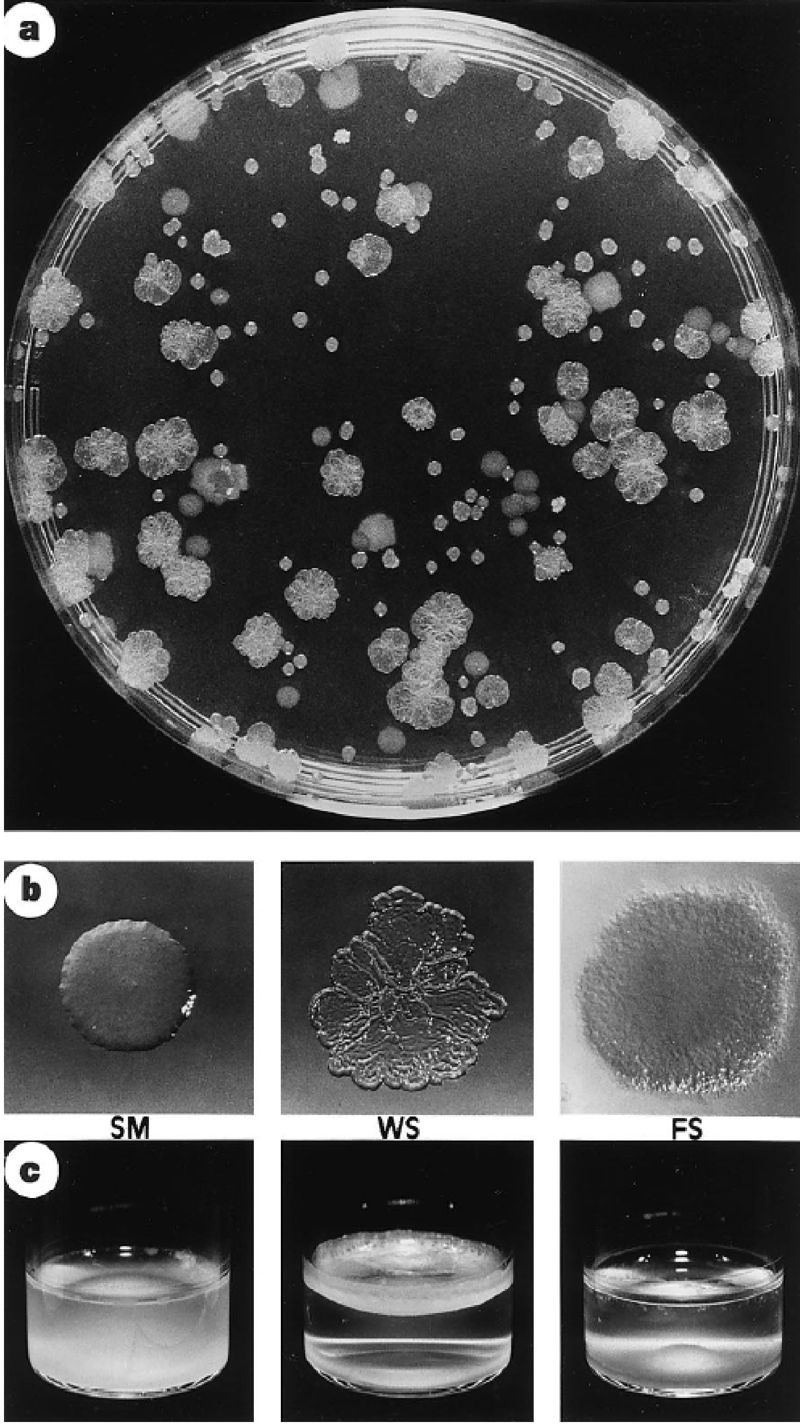
Frequency-dependent fitness: Payoff for phenotype ‘X’ depends on the freq(X) in a population.

Negative frequency-dependence:
-common phenotypes are penalized, rare phenotypes are rewarded

Example 1

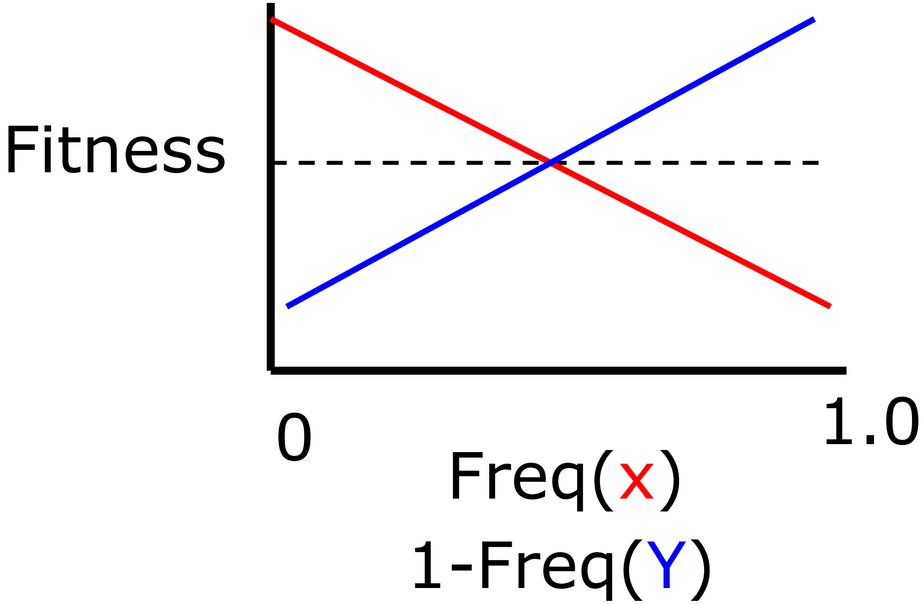
Reference

Rainey, P. & Travisano, M. 1998 Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69-72.



Invasion Experiment

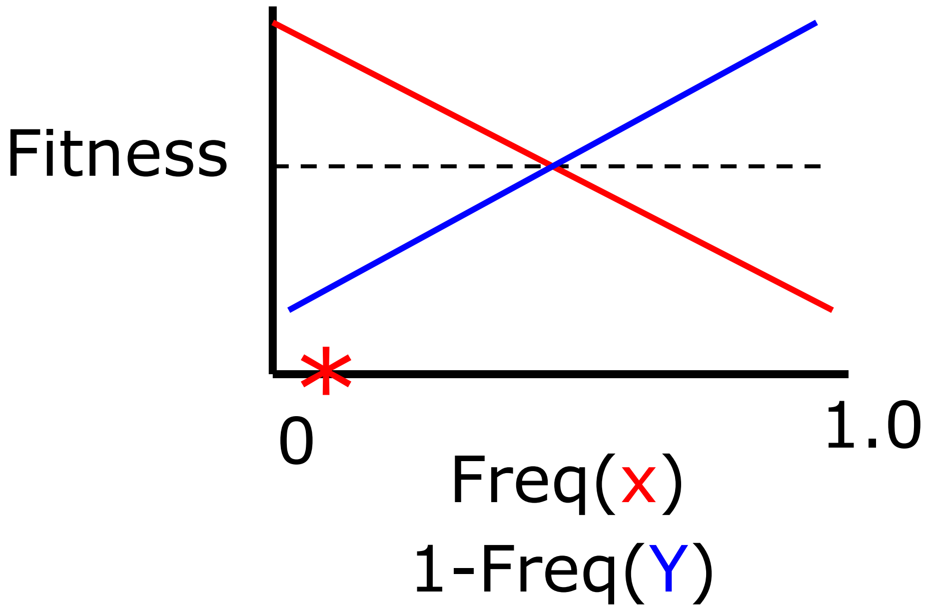
X,Y



$$\text{Fitness} = \frac{\ln(X'/X)}{\ln(Y'/Y)}$$

Invasion Experiment

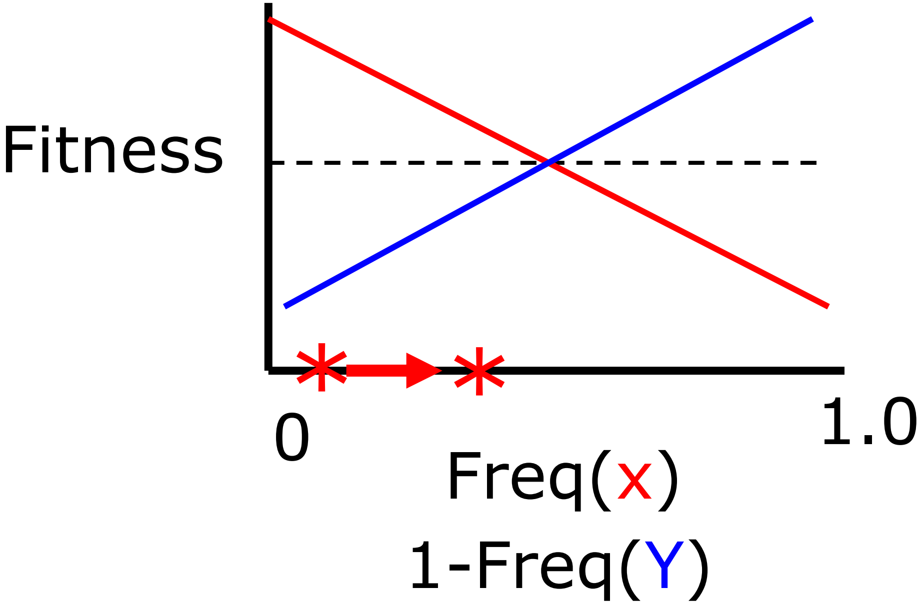
X,Y



$$\text{Fitness} = \frac{\ln (X'/X)}{\ln (Y'/Y)}$$

Invasion Experiment

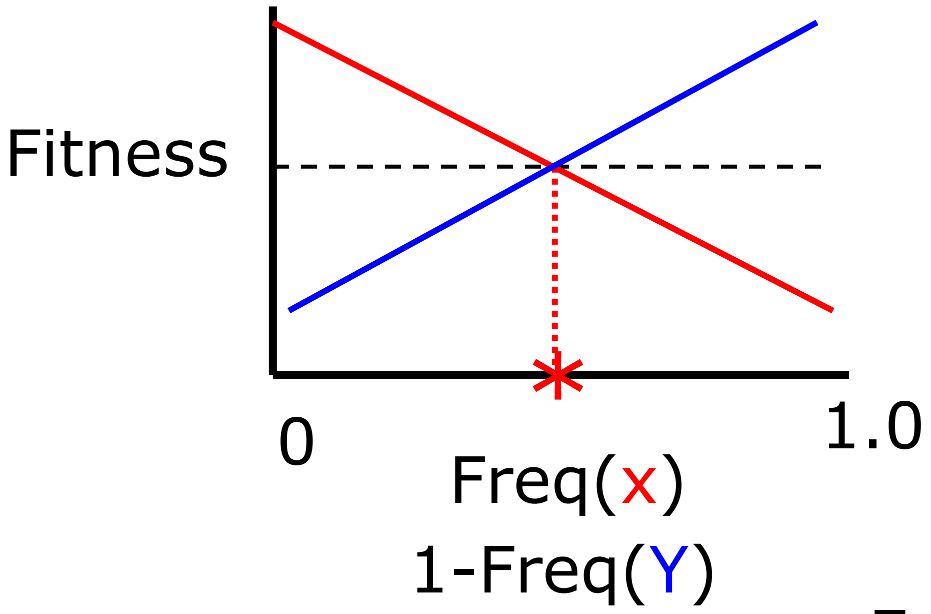
X,Y



$$\text{Fitness} = \frac{\ln (X'/X)}{\ln (Y'/Y)}$$

Invasion Experiment

X,Y



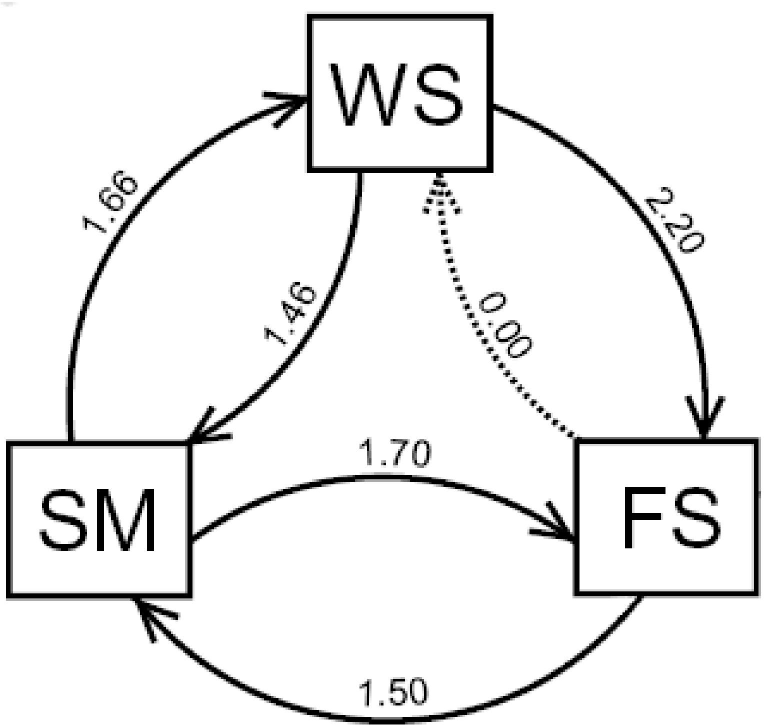
$$\text{Fitness} = \frac{\ln\ (X'/X)}{\ln\ (Y'/Y)}$$

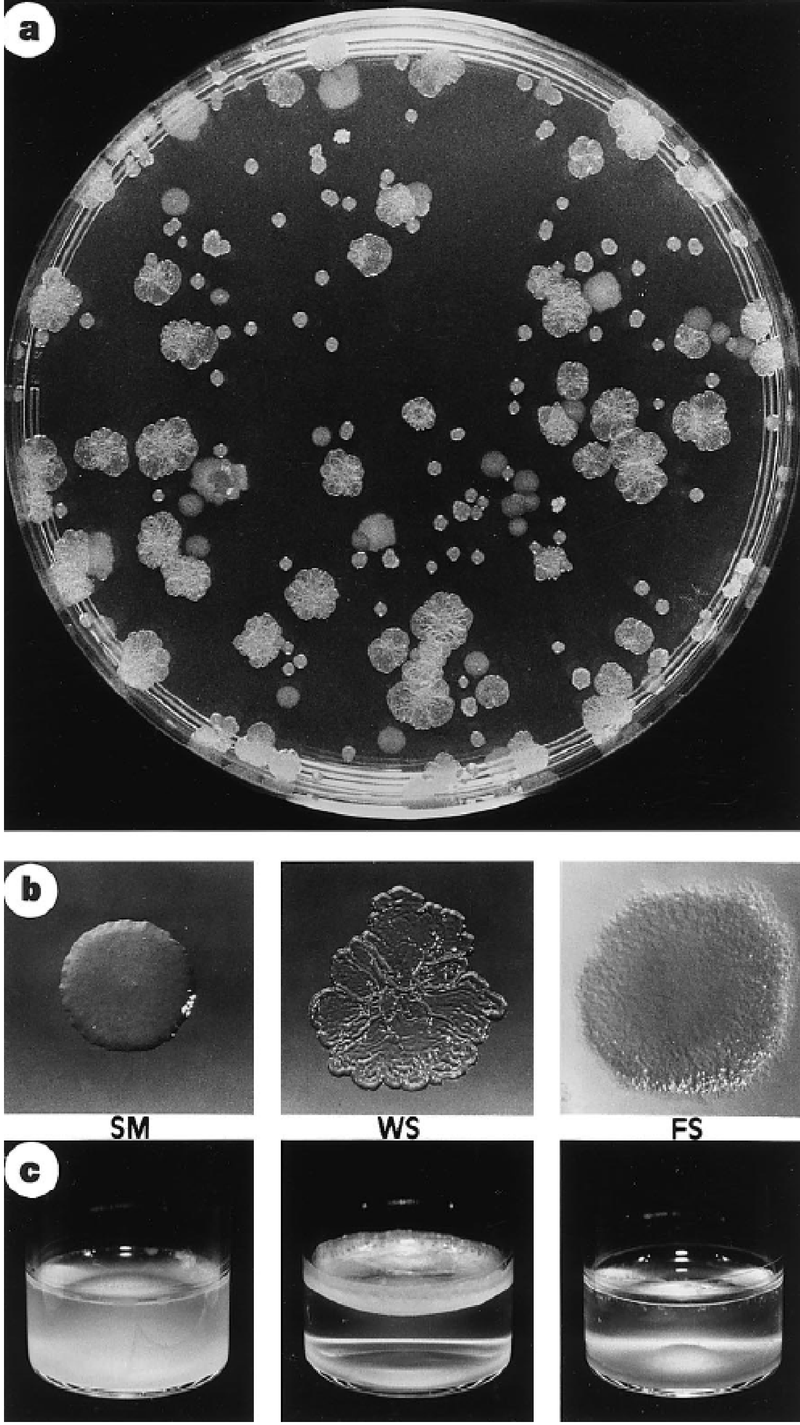
Evolutionary Stable State (ESSt)

[Evolutionary Stable Strategy (ESS) – J. Maynard Smith]

Example 1

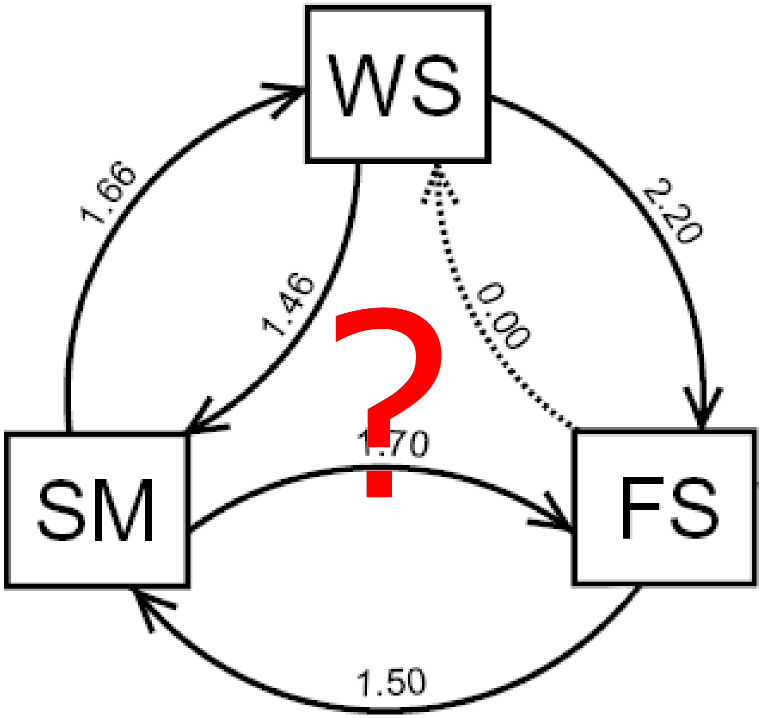
Rainey, P. & Travisano, M. 1998 Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69-72.

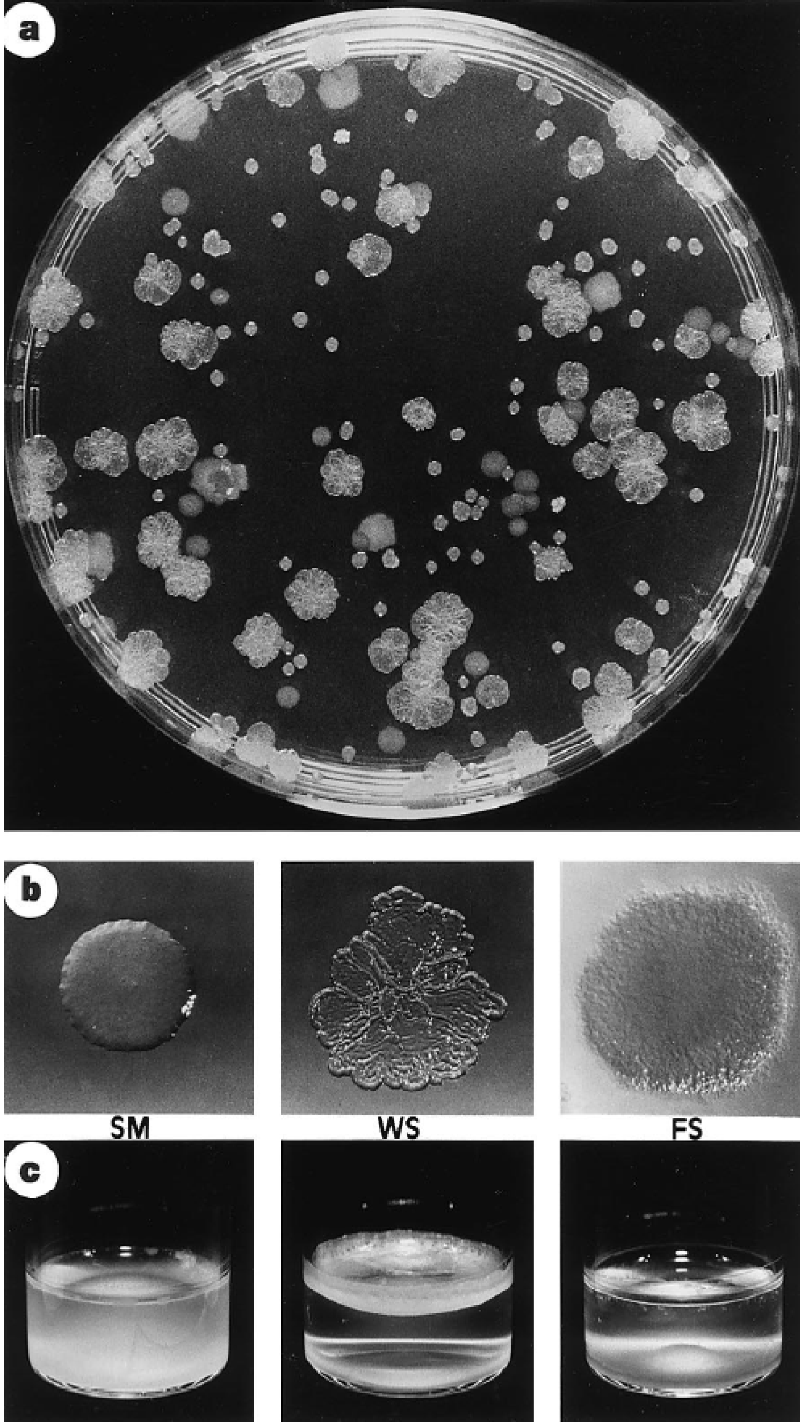




Example 1

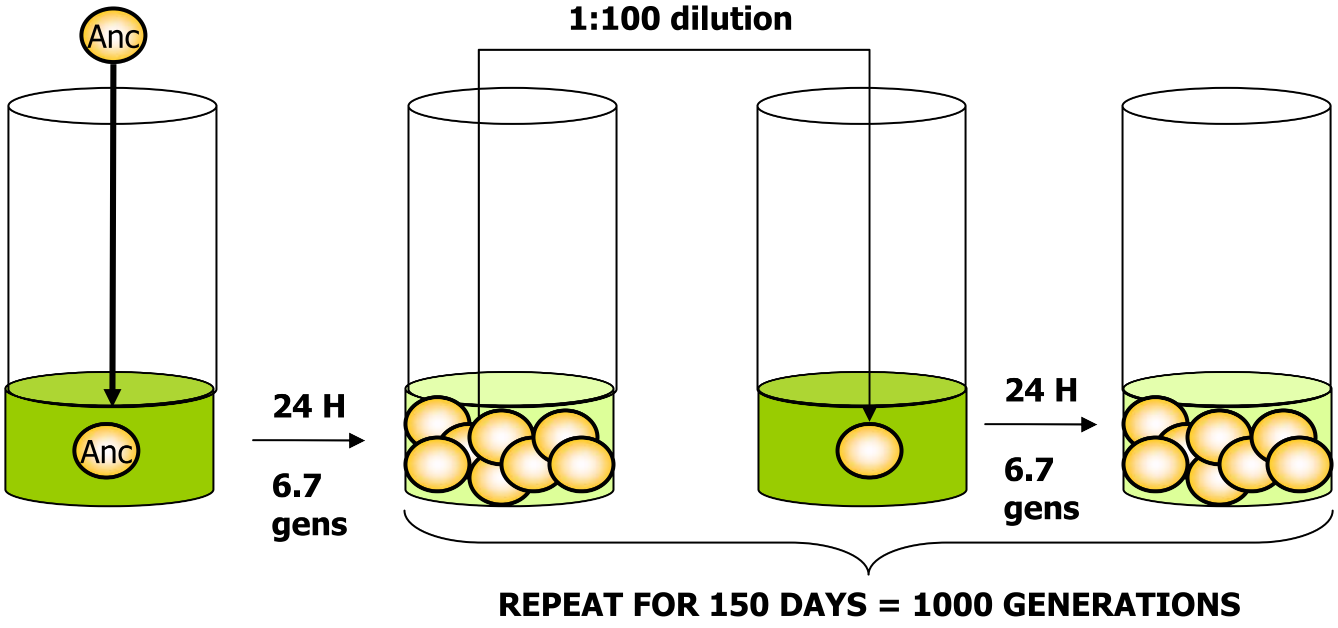
Rainey, P. & Travisano, M. 1998 Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69-72.





Example 2

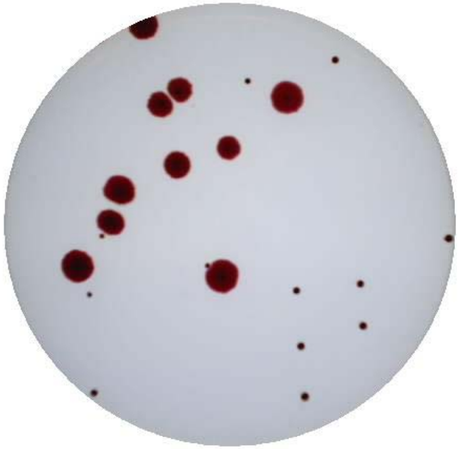
E. coli

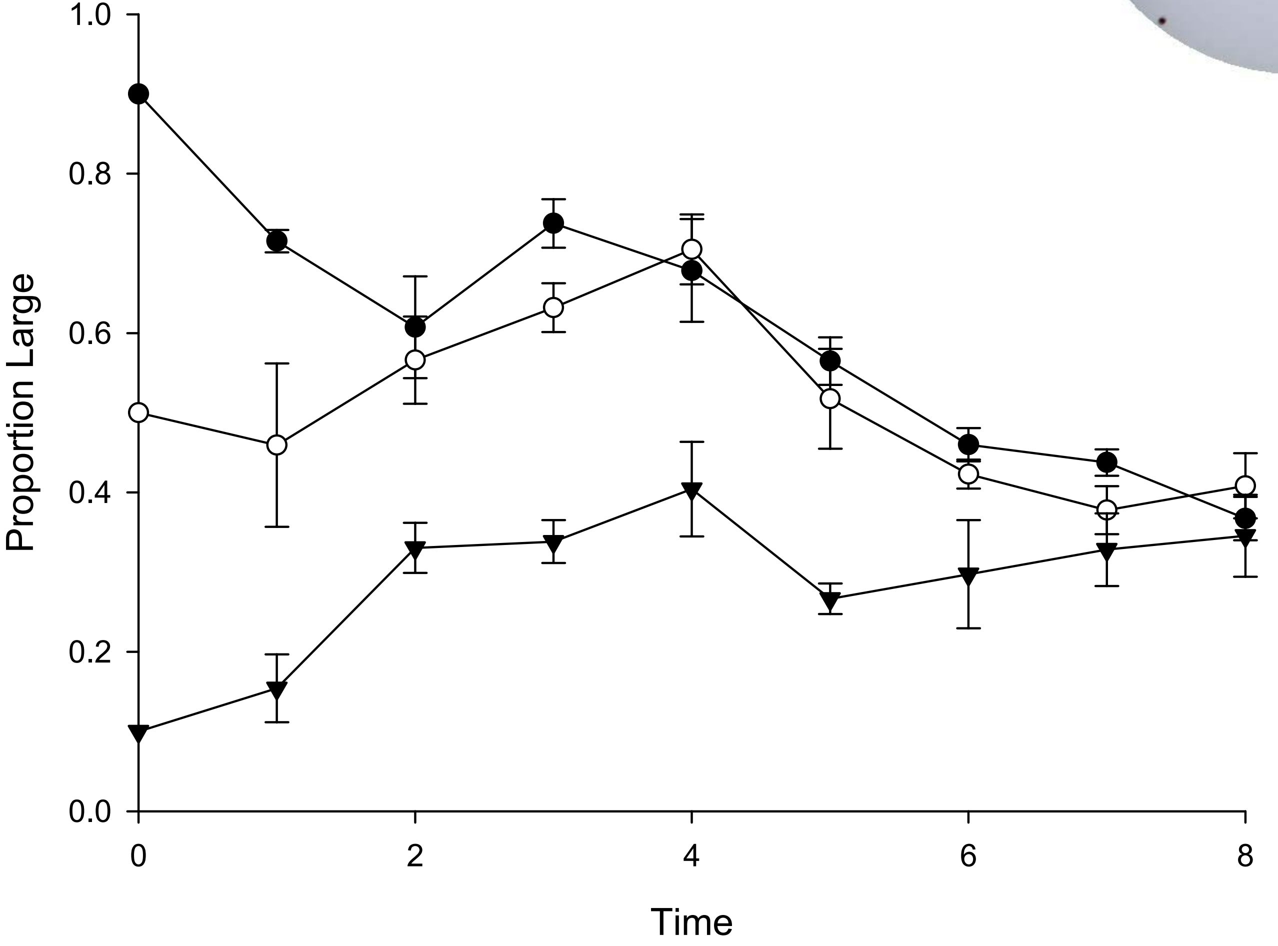


References:
Friesen, M. L., Saxer, G., Travisano, M. & Doebeli, M. 2004 Experimental evidence for sympatric ecological diversification due to frequency dependent competition in Escherichia coli. *Evolution* **58**, 245-60.
Tyerman, J. G., Havard, N., Saxer, G., Travisano, M. & Doebeli, M. 2005 Unparallel diversification in bacterial microcosms. *Proc R Soc Lond. B* **272**, 1393-8.
Spencer, C. C., Bertrand, M., Travisano, M. & Doebeli, M. (in press) Adaptive diversification in genes regulating resource use in Escherchicia coli. *PLoS Genetics*.

Example 2

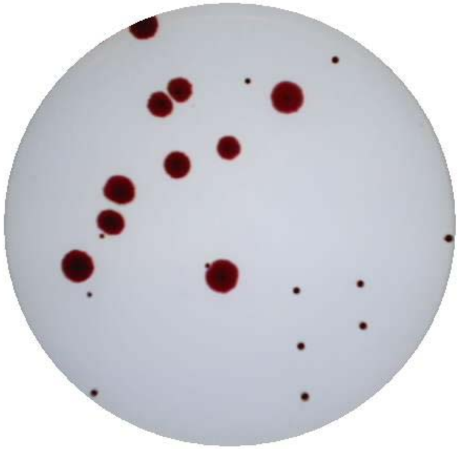
E. coli

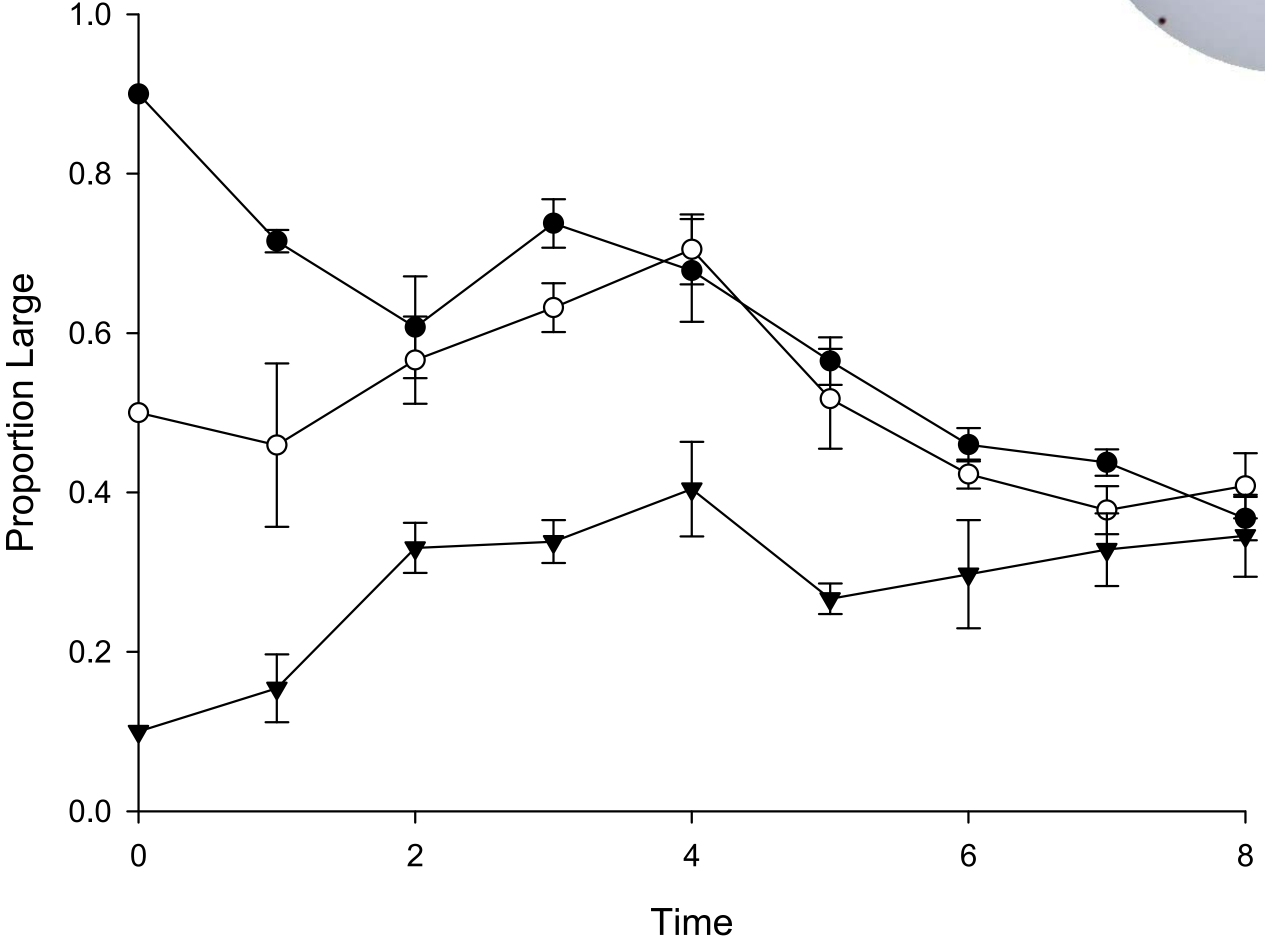


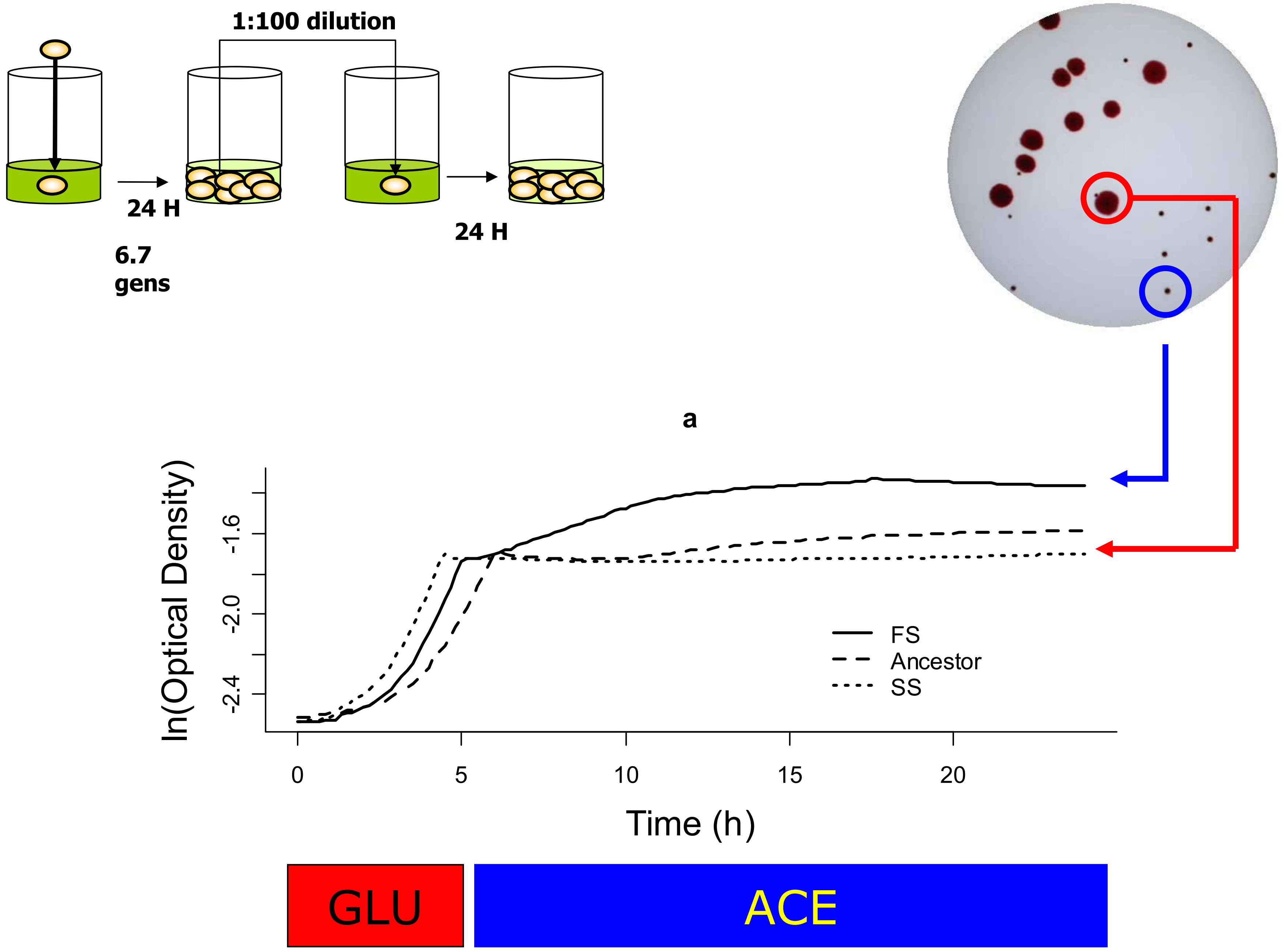


Example 2

E. coli






1:100 dilution
24 H
6.7
gens
24 H
a
ln(Optical Density)
-1.6
-2.0
-2.4
0
5
10
15
20
Time (h)
FS
Ancestor
SS
GLU
ACE

Frequency dependence maintains diversity in experimental systems.

Invasion experiment – Ability of a phenotype to increase in freq. when rare.

ESSt. - Evolutionary stable state (~mixed ESS).

Trade-offs are important:
-the ability to efficiently use one resource (GLU) comes at the expense of efficiently using the other (ACE).

Why is there (bio)diversity?

1. How is diversity maintained?
   - Frequency-dependent fitness
   - Example 1: *Pseudomonas* bacteria (SM-WS-FS)
     - Tool: Invasion Experiment, ESSt.
   - Example 2a: *E. coli* bacteria (SS-FS)
   - Summary
2. How does it arise?
   - Adaptive landscapes – defining the problem
   - Adaptive Dynamics – solving the problem
   - Example 2b: Evolution to the branching point
   - Summary

…and what happens if (when) we lose diversity?

Evolution

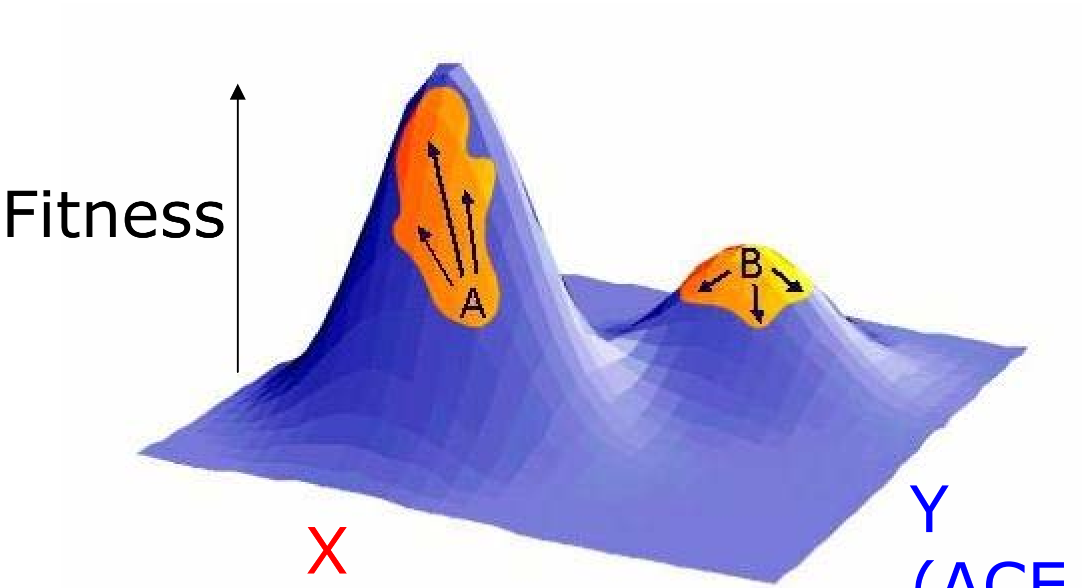
1. Variation
2. …heritable
3. Differential Performance

Evolution!
(by natural selection)

Evolution

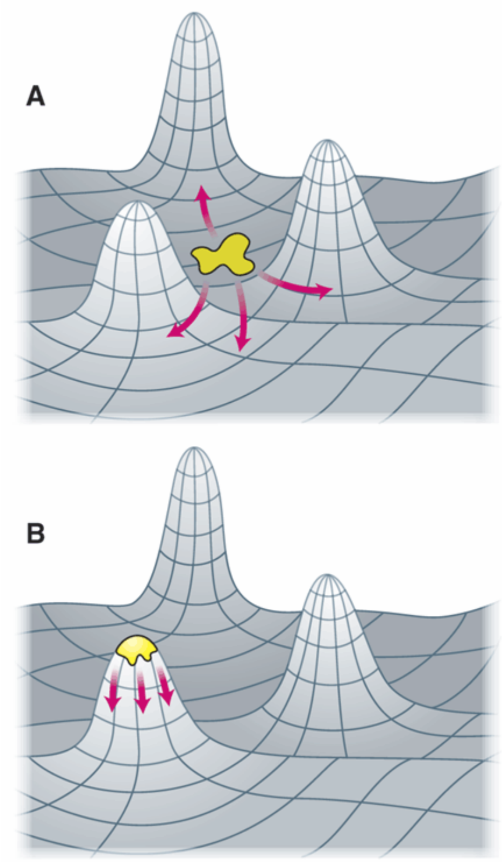
1. Populations change over time.

2. Lineages branch into new lineages.



X
(GLU efficiency)

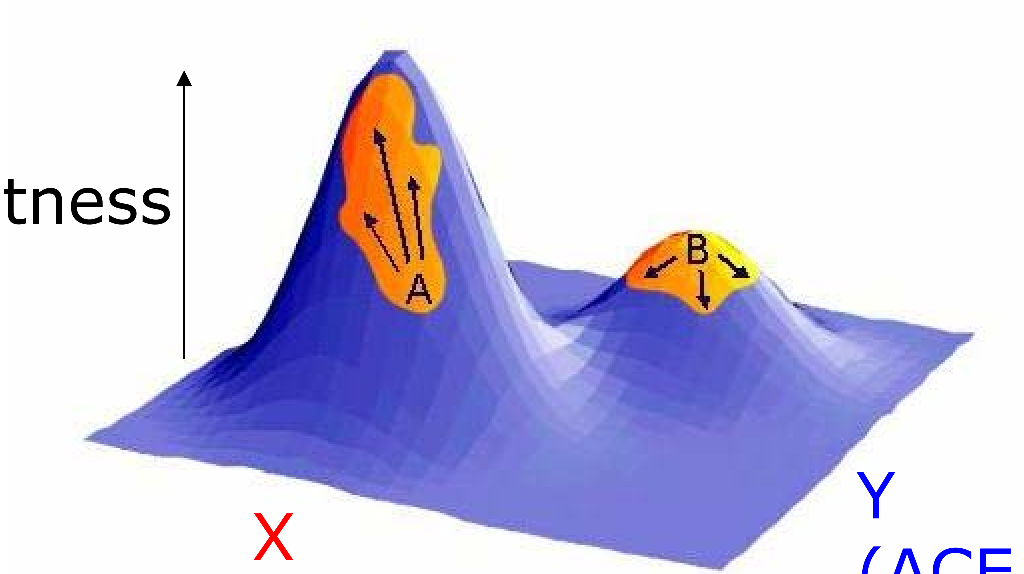
Y
(ACE efficiency)



Evolution

1. Populations change over time.
Adaptation (populations → environment.)

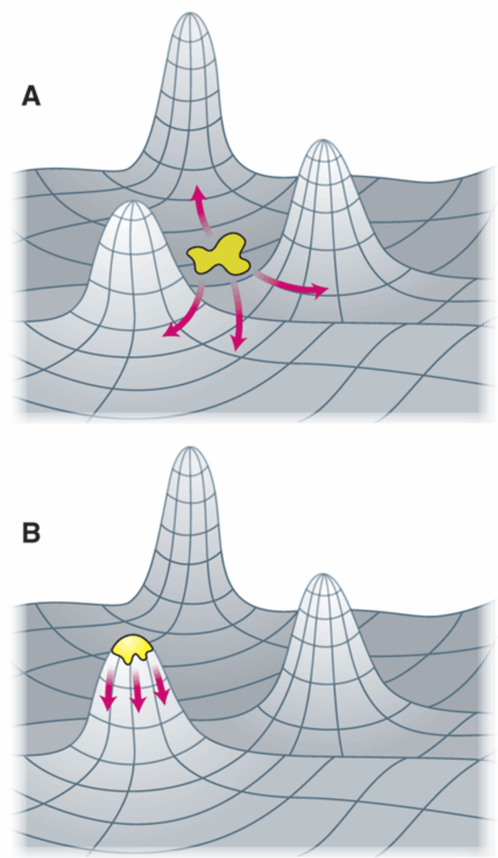
Adaptive landscape
– metaphor for evolution.



Fitness

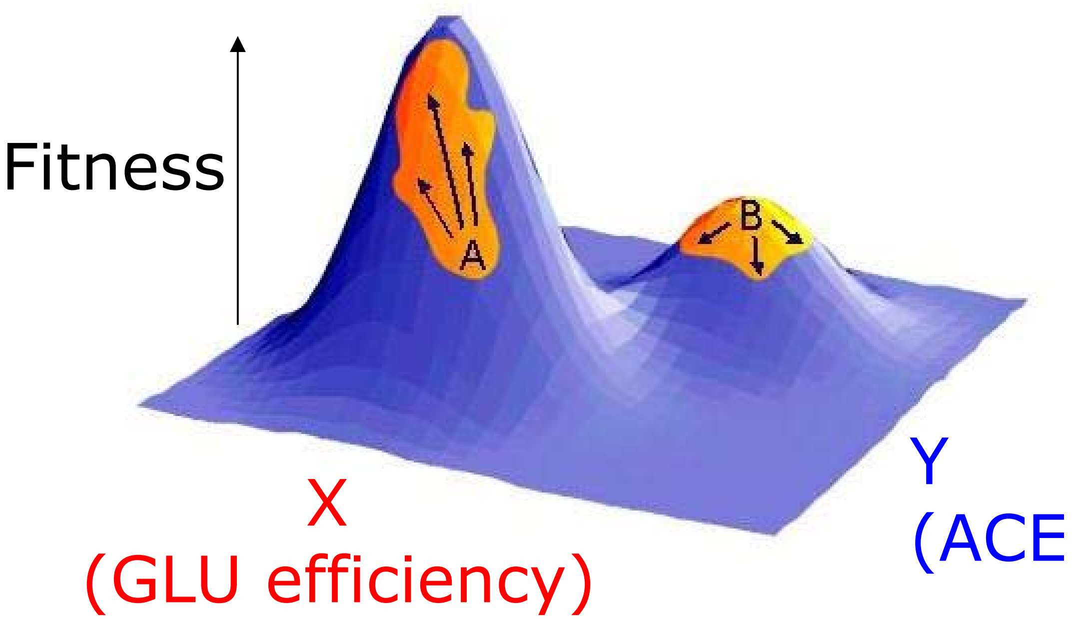
X
(GLU efficiency)

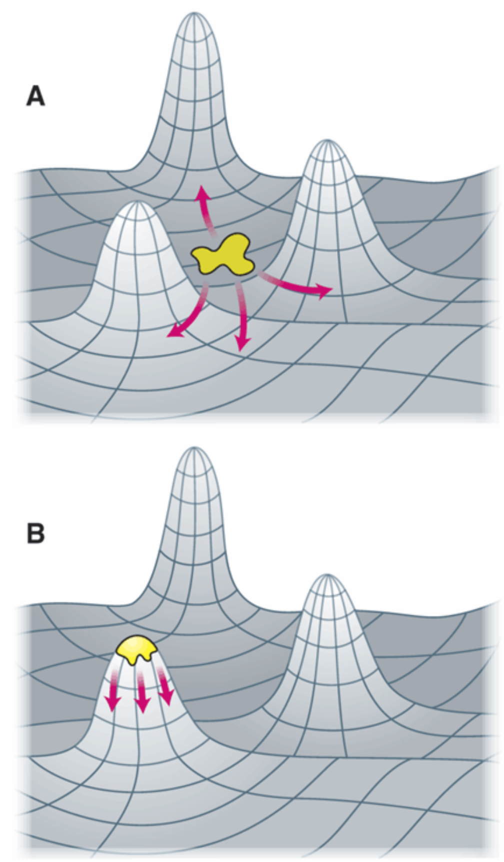
Y
(ACE efficiency)



Evolution – Adaptive Landscape

1. Populations change over time.
Adaptation (populations → environment.)
"Hill climbing"

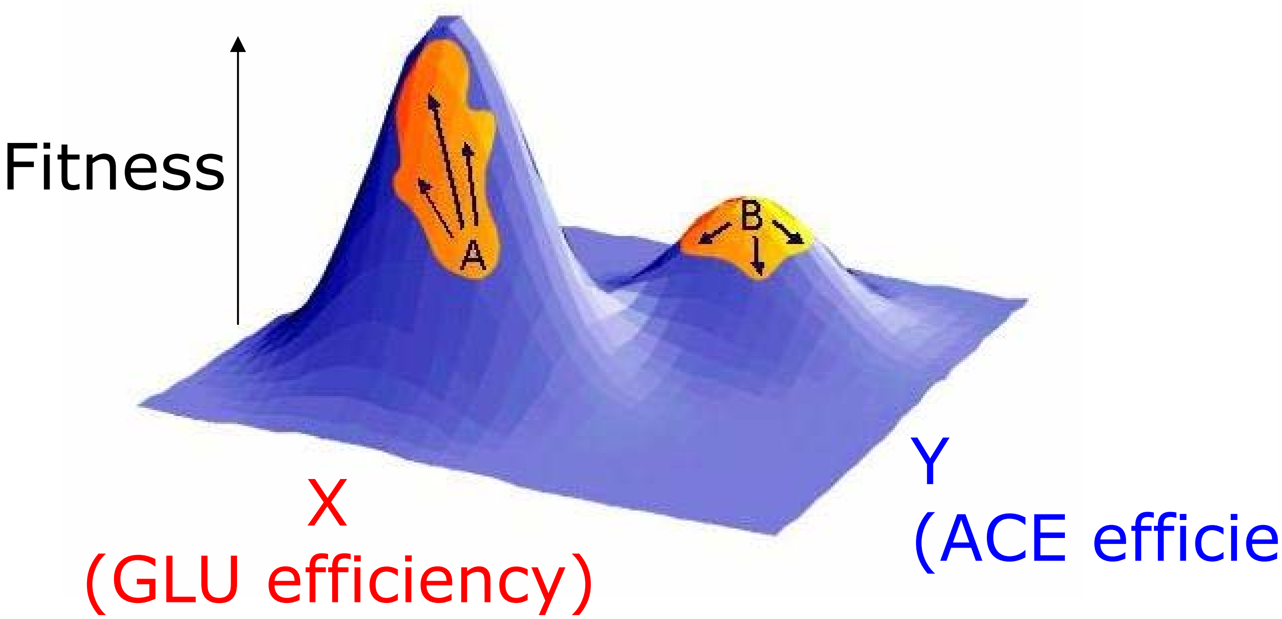


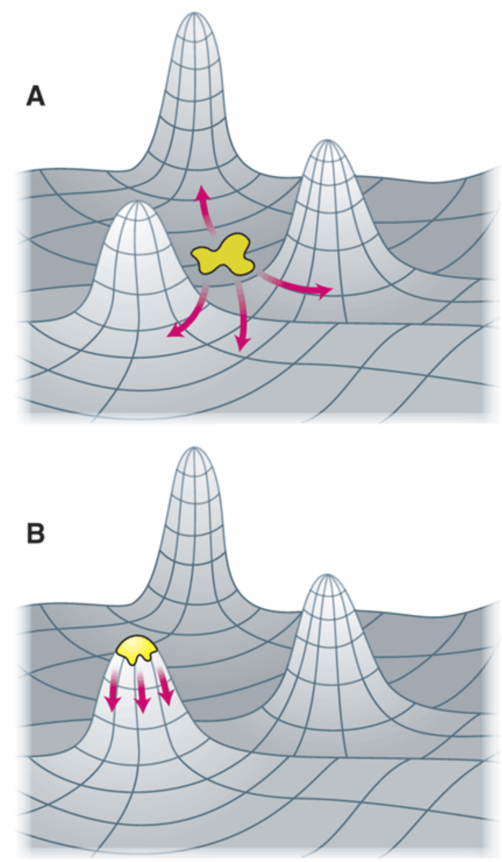


Evolution – Adaptive Landscape

1. Populations change over time.
Adaptation (populations → environment.)
"Hill climbing"

2. Populations splitting to create new populations (speciation)
"Valley crossing"

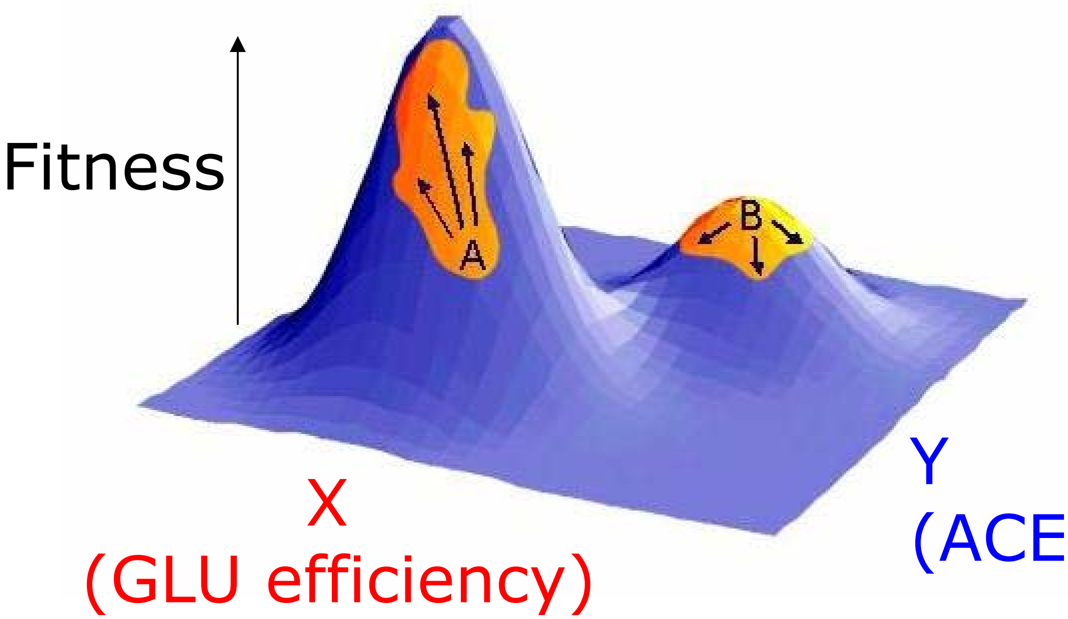


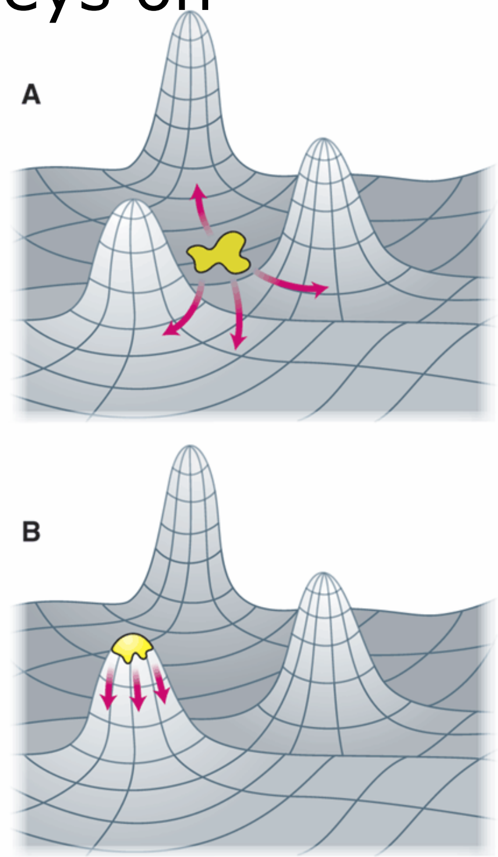


Evolution – Adaptive Landscape

How does diversity arise? (speciation?)

i.e., How do sub-populations cross valleys on the adaptive landscape?





Evolution

Assumption: adaptive landscapes are static.

What if they're not?

…and what mechanisms generate dynamic adaptive landscapes?

Frequency dependence

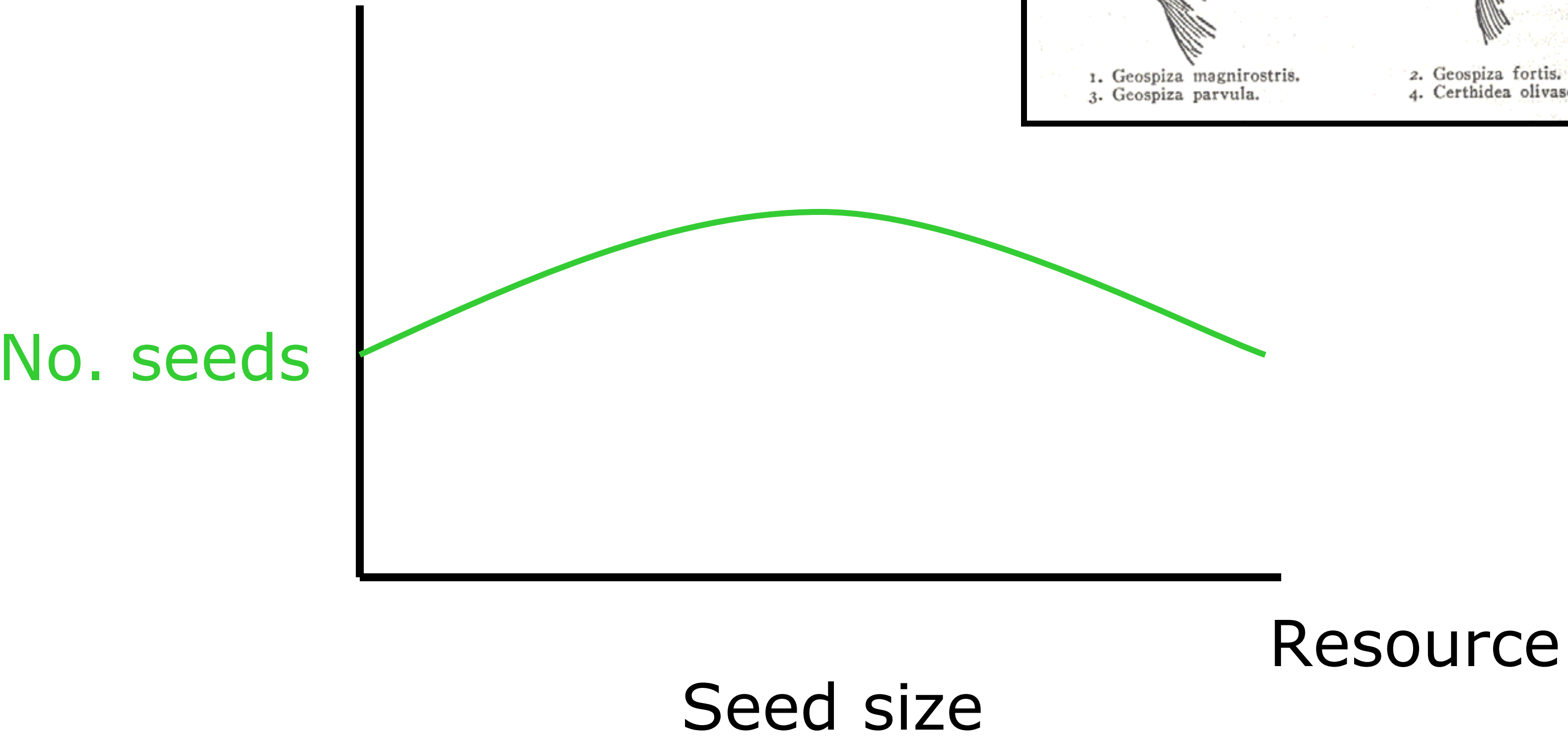
“Adaptive dynamics”

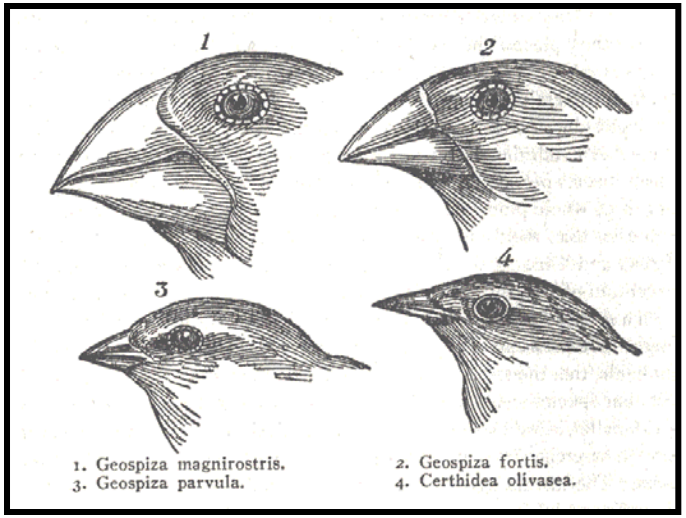
Evolution (speciation) across a dynamic landscape

Reference

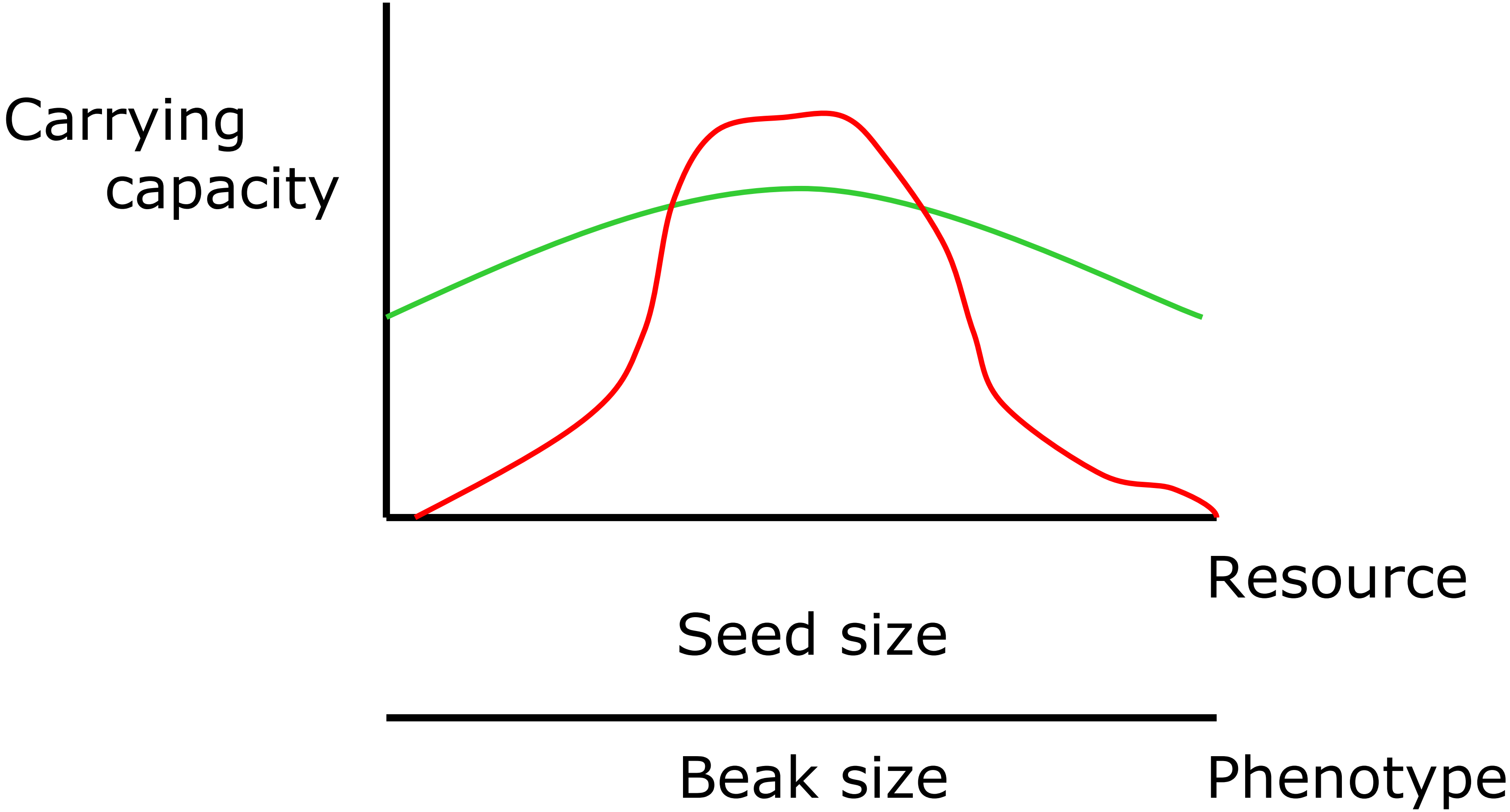
Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354-7.

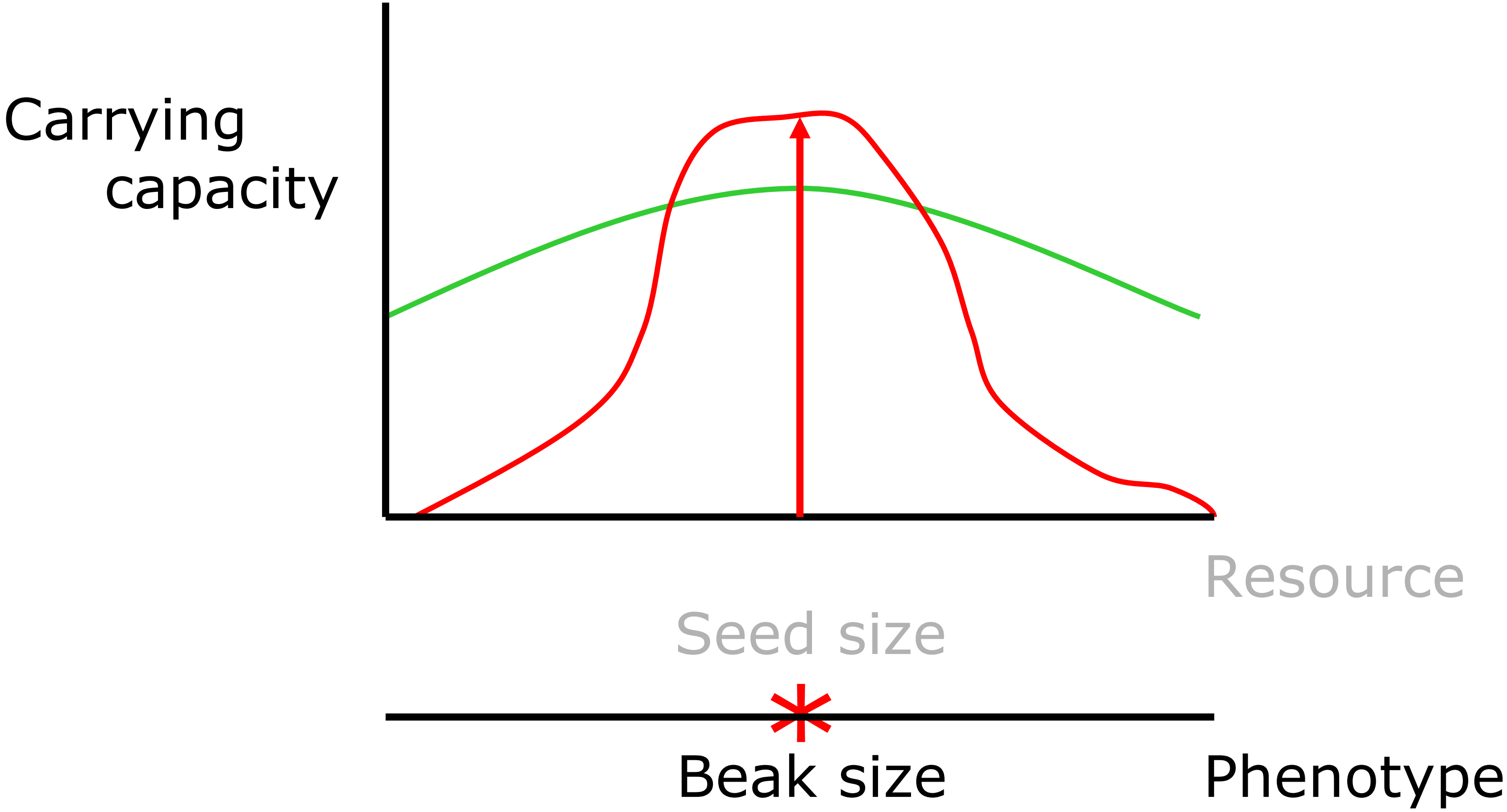
$$N(X_0, \sigma_K)$$



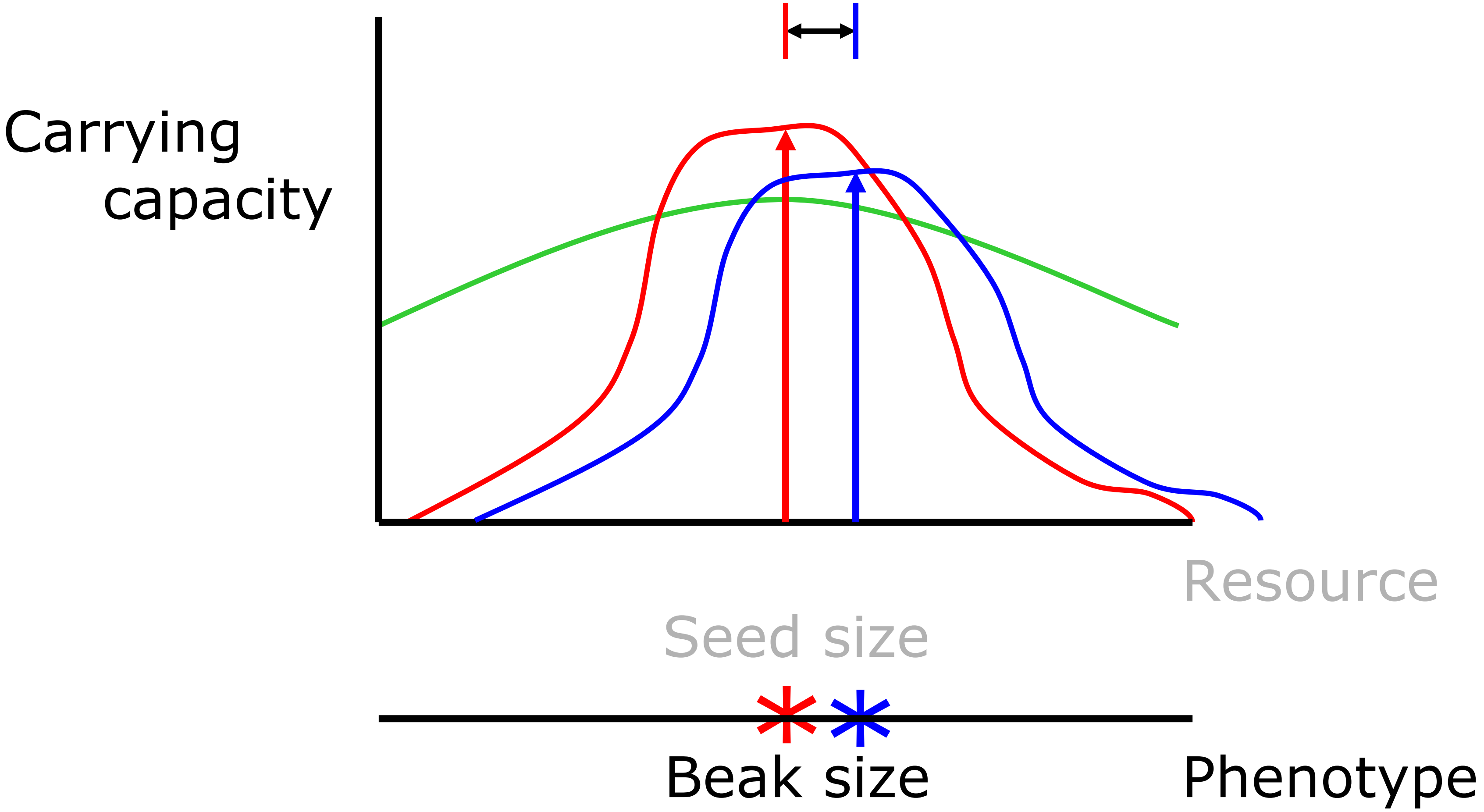


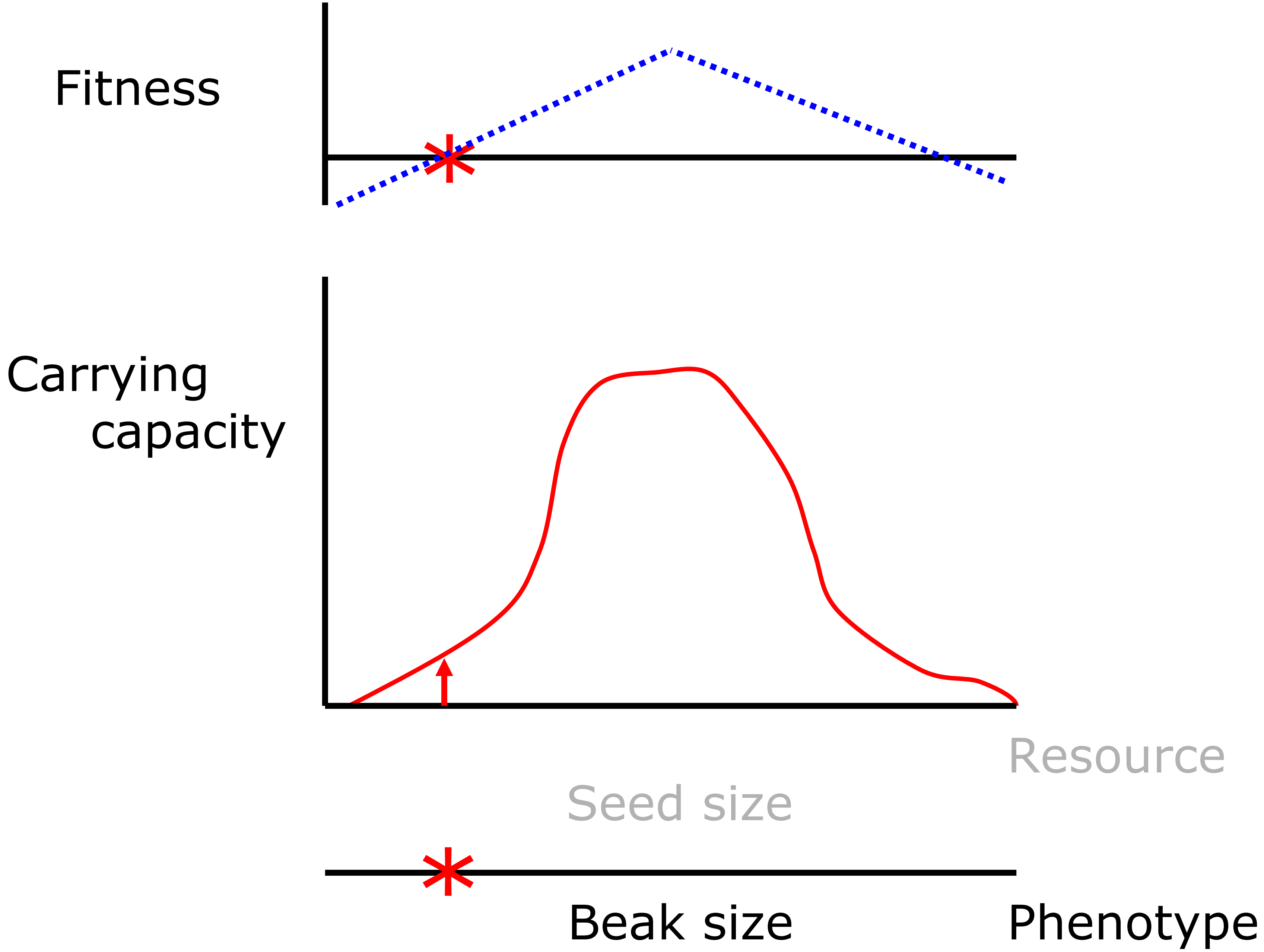
1. Geospiza magnirostris.
2. Geospiza fortis.
3. Geospiza parvula.
4. Certhidea olivasea.

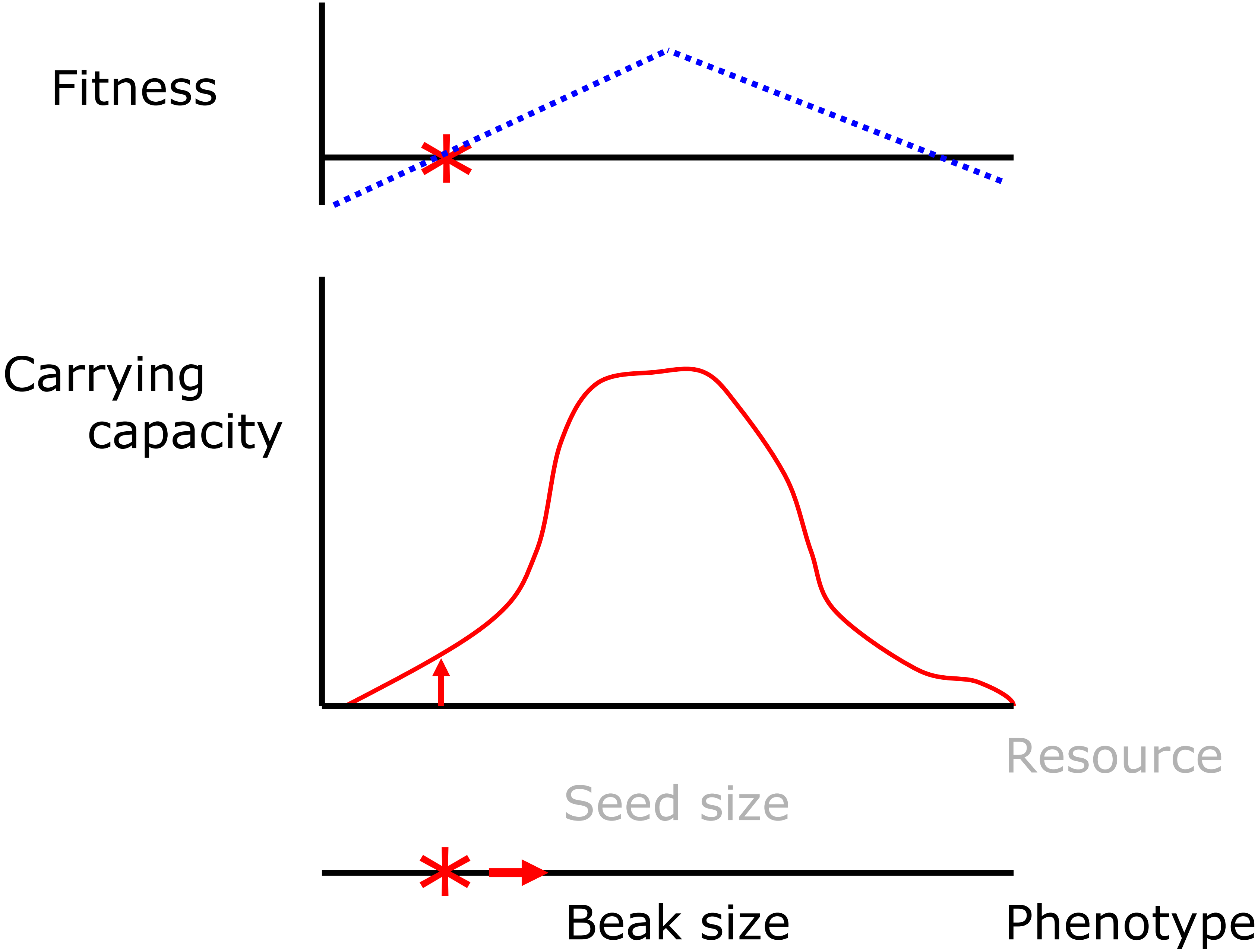

Carrying capacity
Resource
Seed size
Beak size
Phenotype

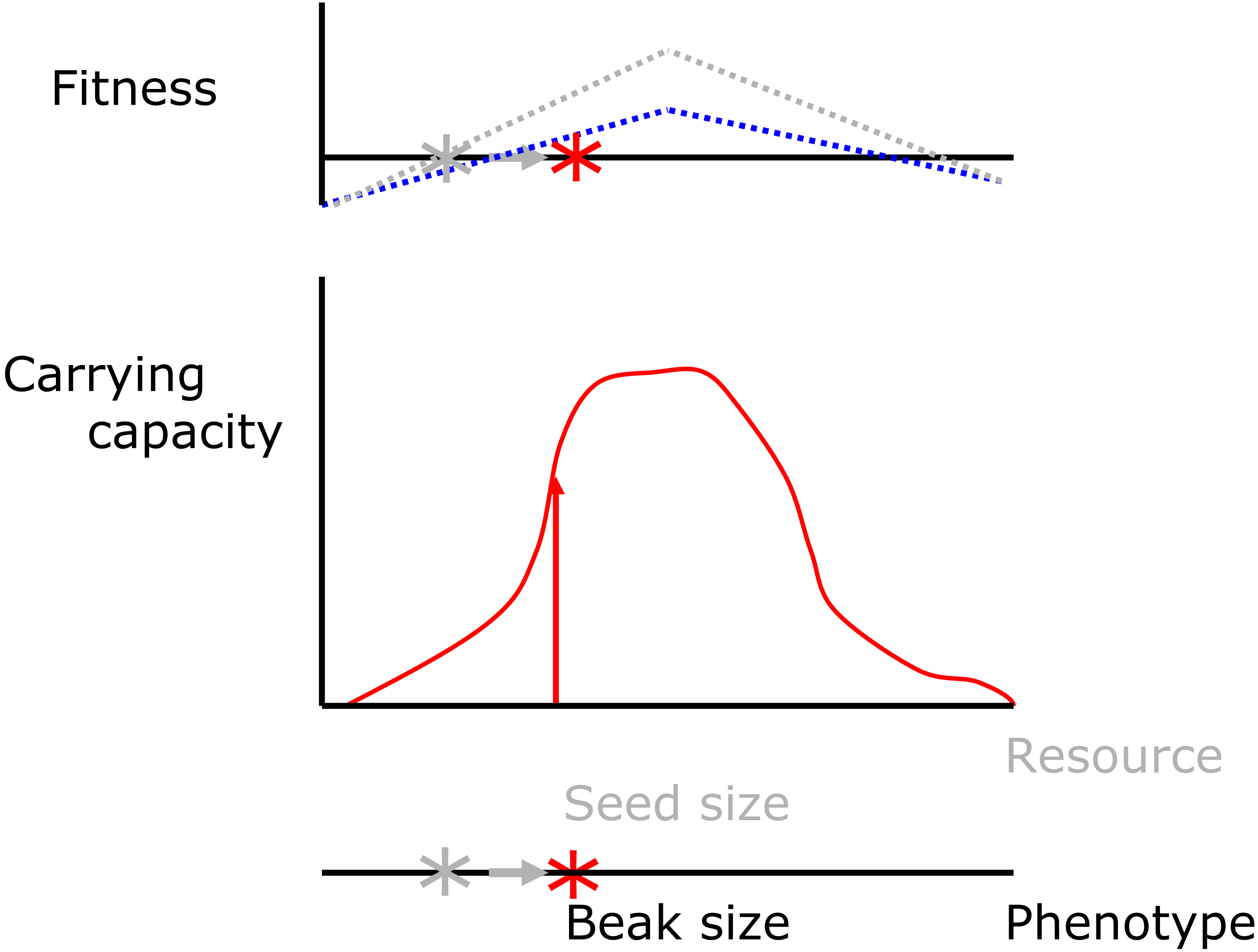

Carrying
capacity
Resource
Seed size
Beak size
Phenotype

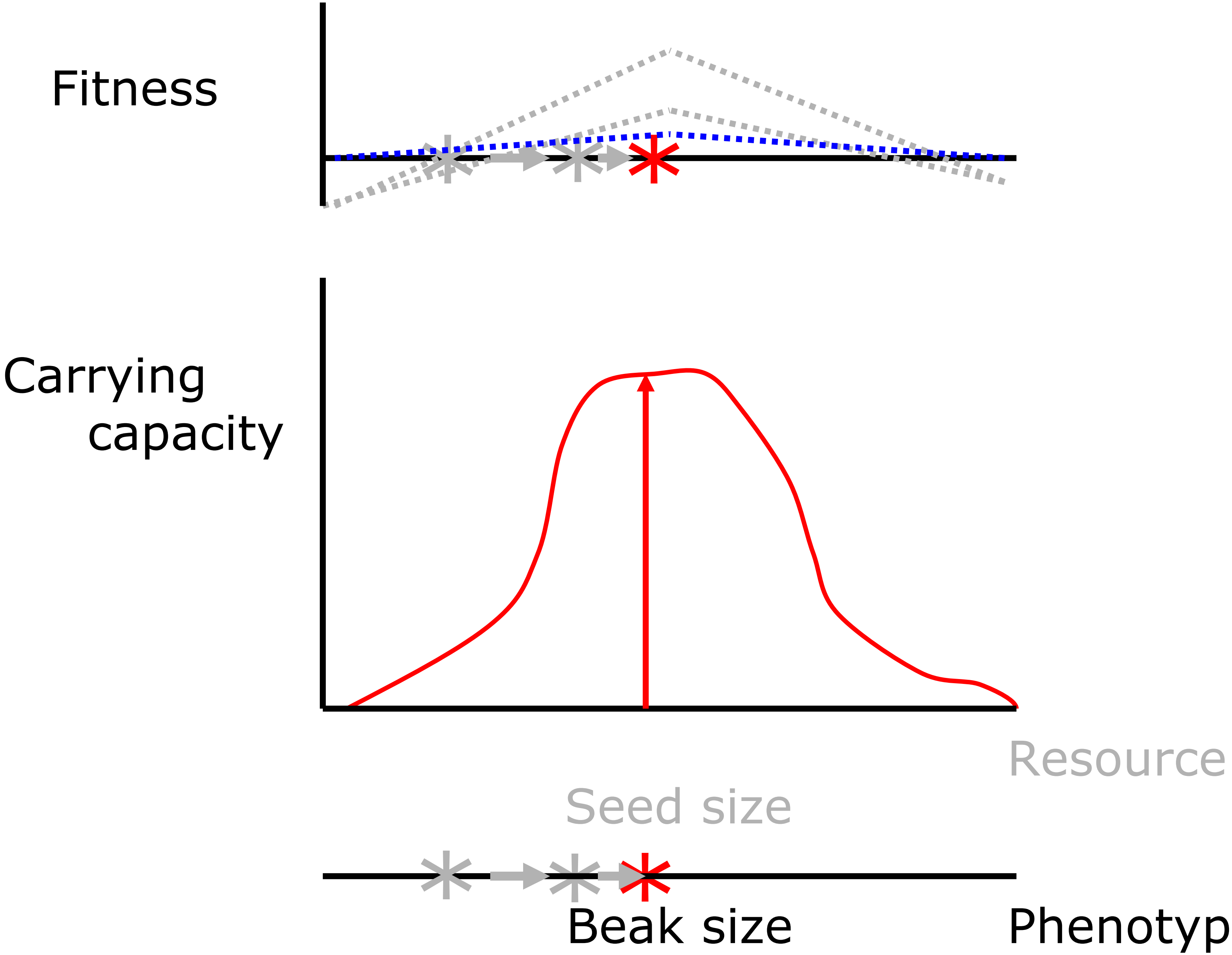
$N(0, \sigma_C)$

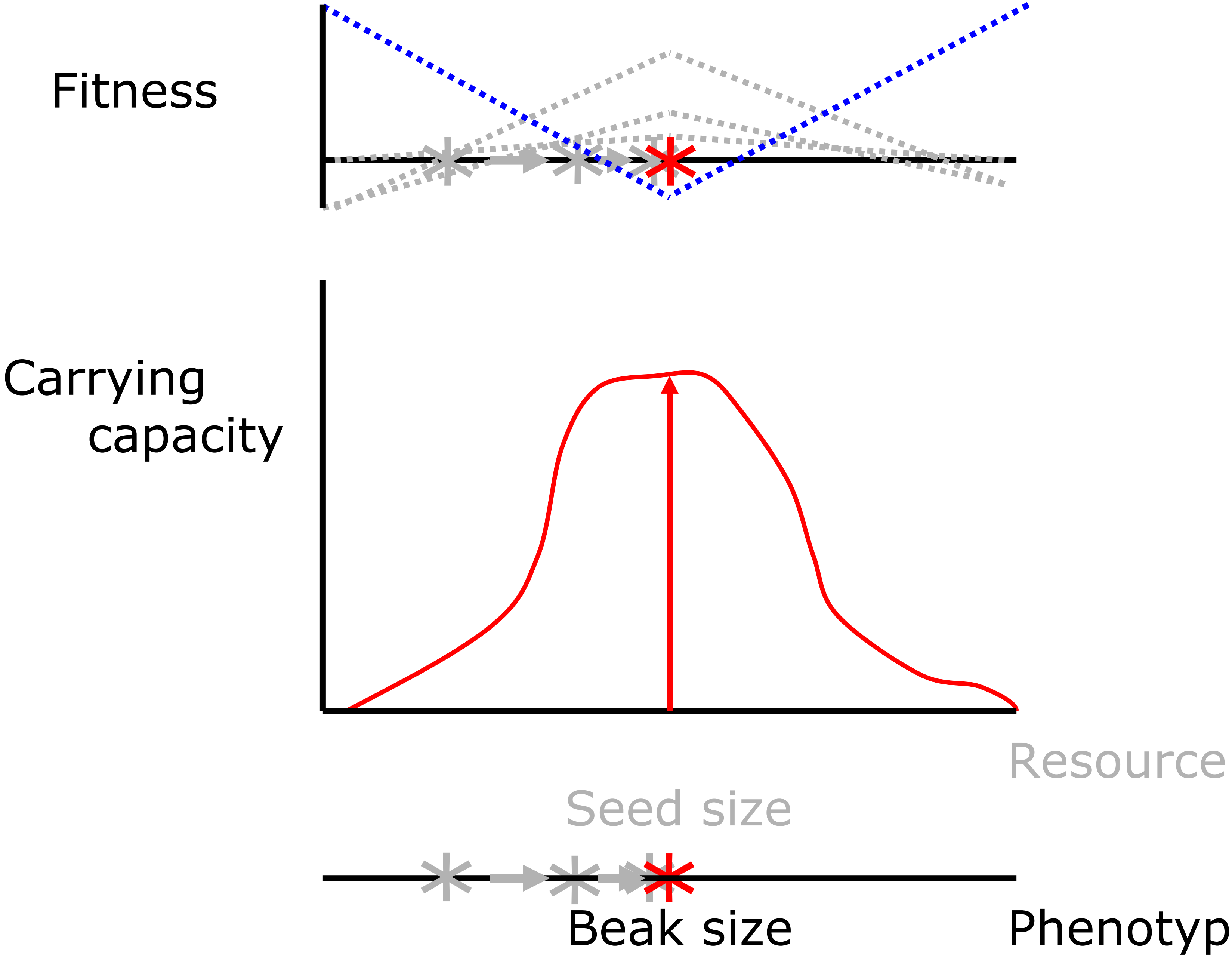


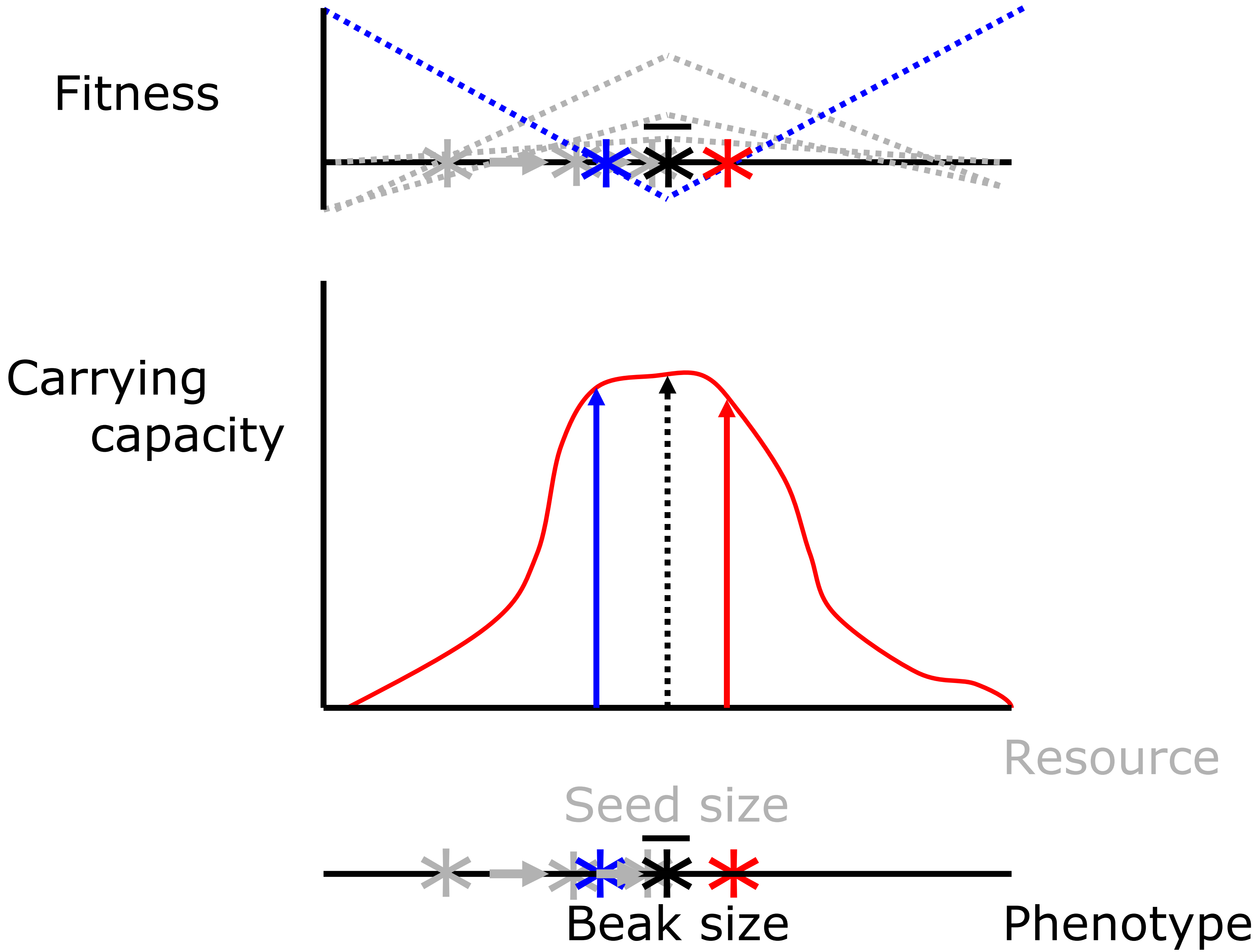

Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype

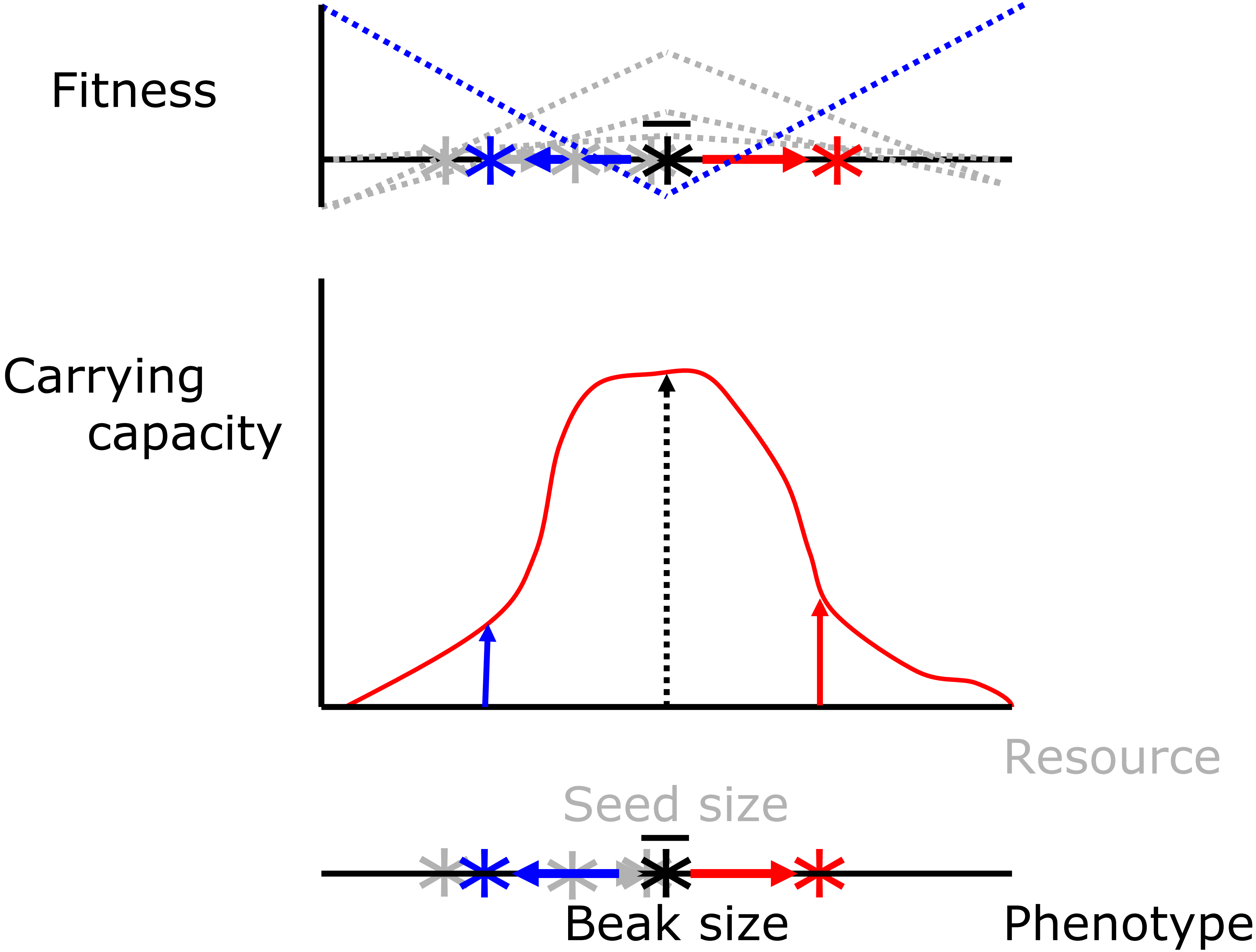

Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype

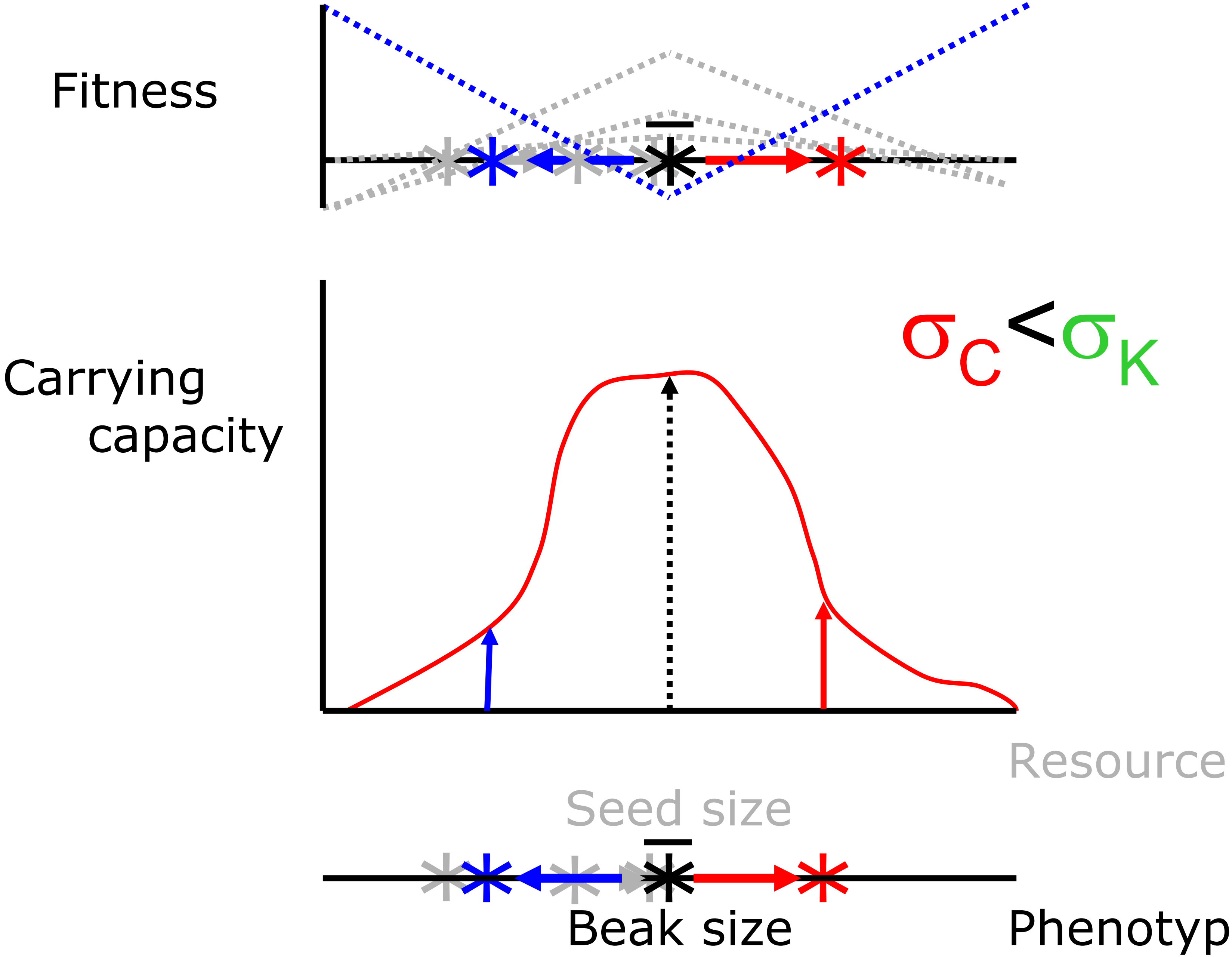

Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype


Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype


Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype


Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype

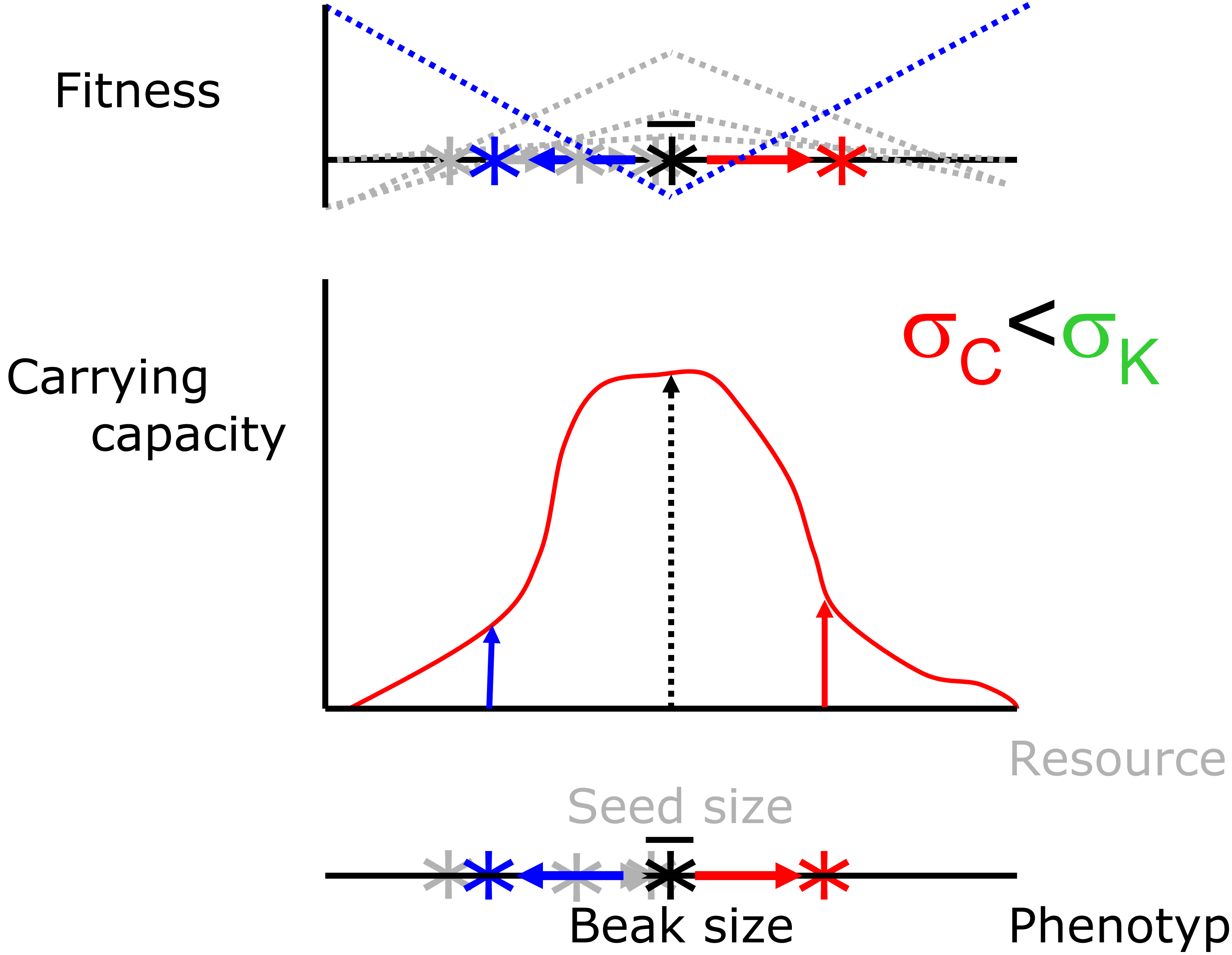

Fitness
Carrying capacity
Resource
Seed size
Beak size
Phenotype

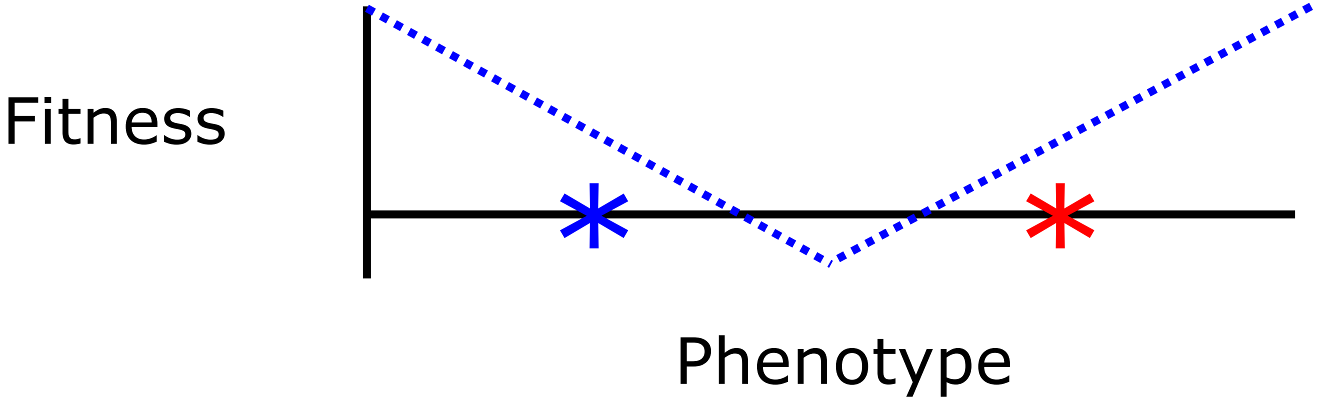

Fitness
Carrying capacity
$\sigma_C < \sigma_K$
Resource
Seed size
Beak size
Phenotype

Summary

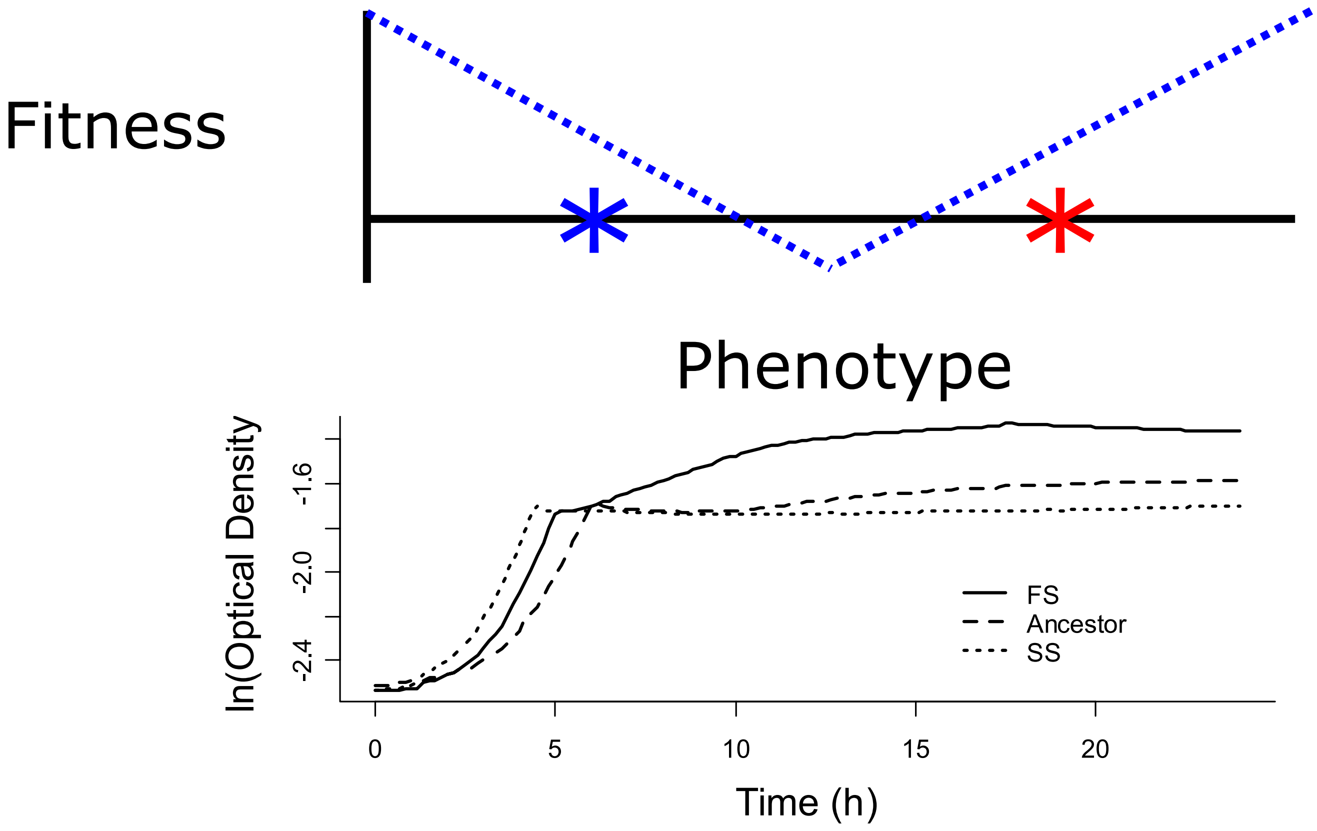
1. Directional selection (under-utilized resources)
2. Disruptive selection (strong competition)
3. Note that the “adaptive landscape” is dynamic – fitness depends on the population composition.
4. At the “evolutionary branching point,” the population splits into two ($\sigma_C < \sigma_K$)

Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354-7.

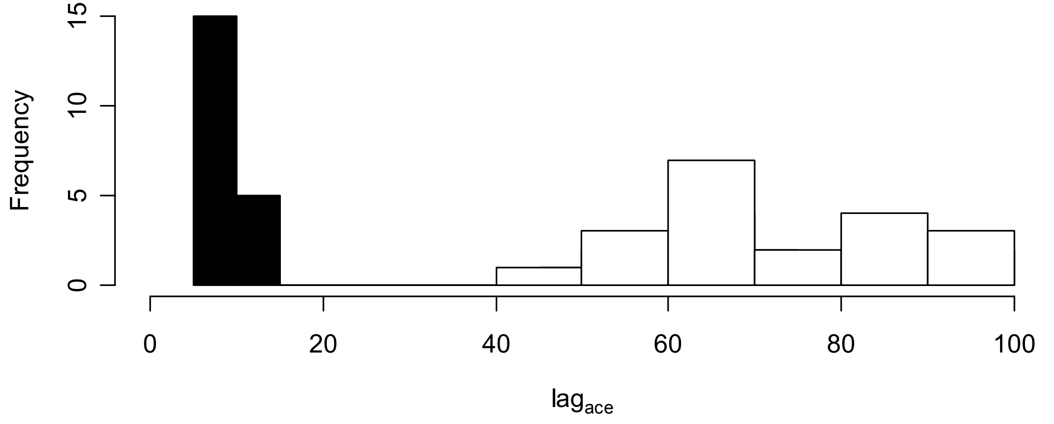

Fitness
Carrying capacity
$\sigma_C < \sigma_K$
Resource
Seed size
Beak size
Phenotype

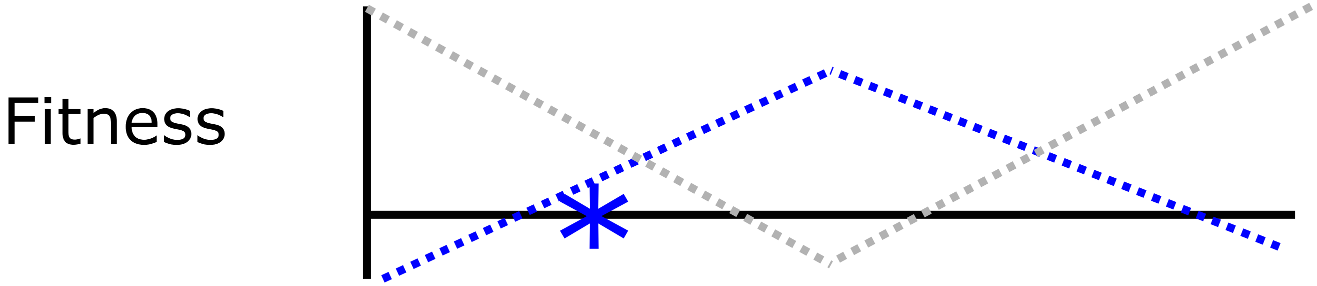

Fitness
*
*
Phenotype

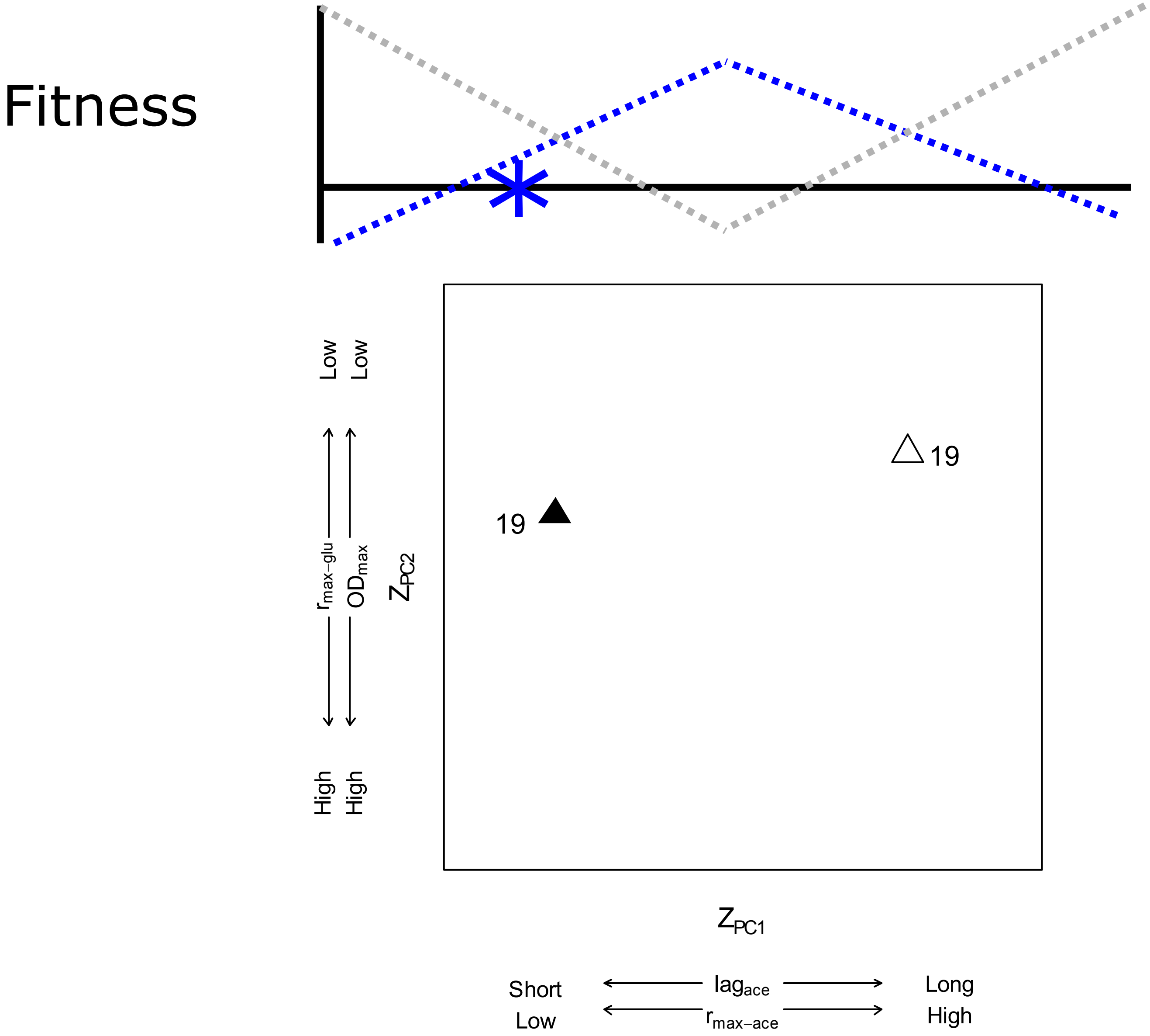
?

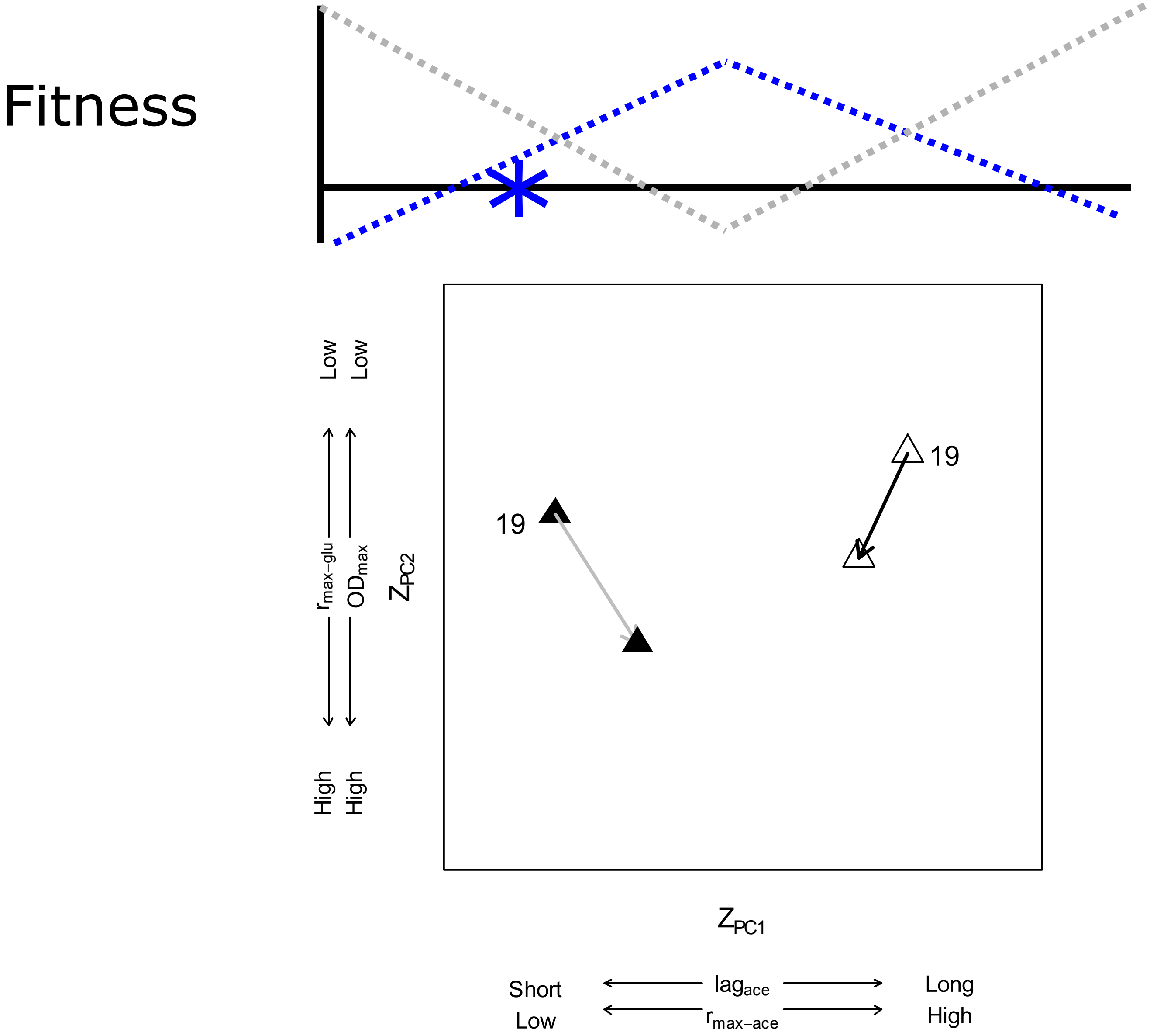

Fitness
Phenotype
ln(Optical Density)
-1.6
-2.0
-2.4
0
5
10
15
20
Time (h)
FS
Ancestor
SS

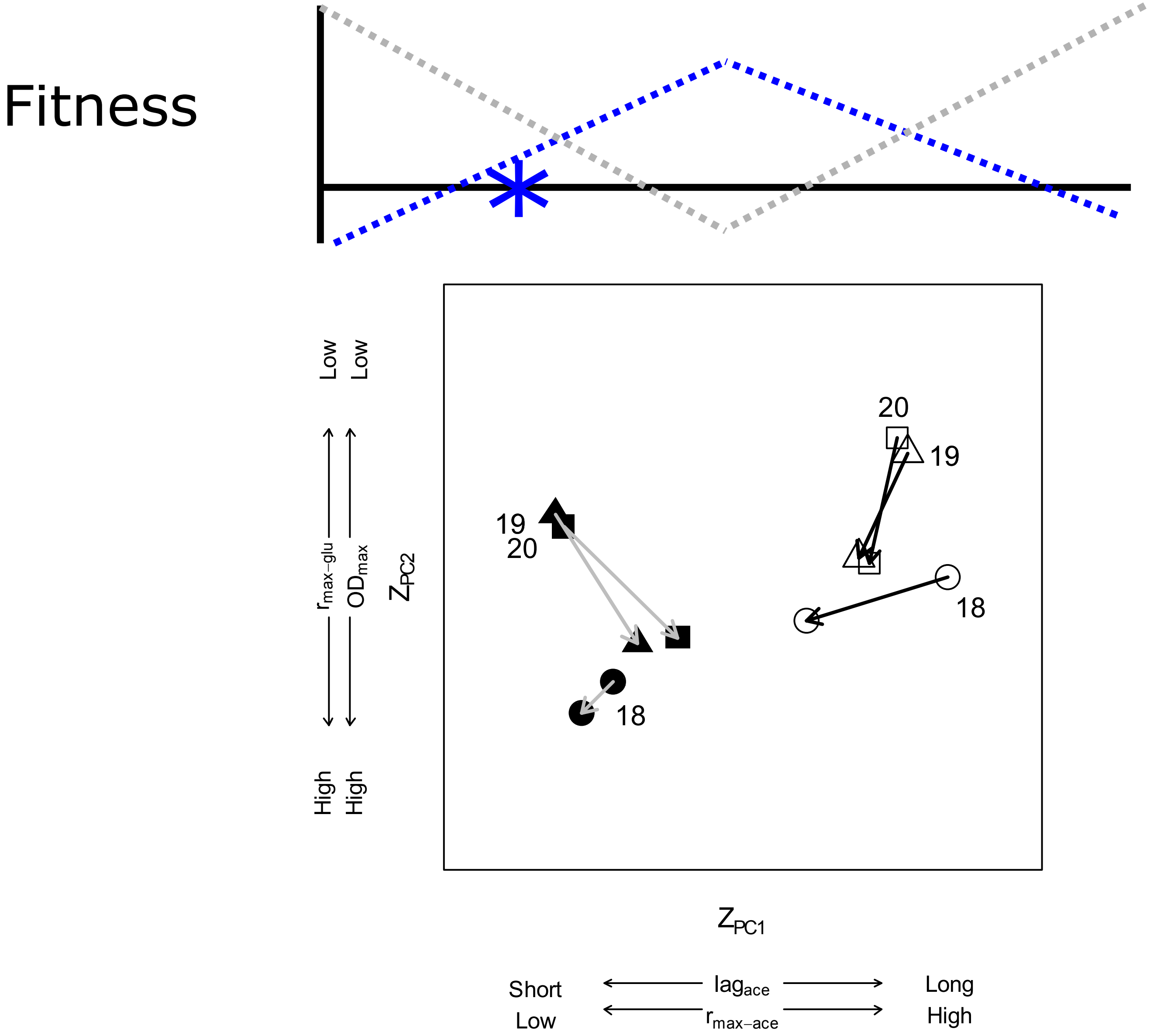
b


Frequency
0
5
10
15
0
20
40
60
80
100
lag$_{ace}$


Fitness
*


Fitness
Low
Low
$r_{max-glu}$
OD_{max}
Z_{PC2}
High
High
19
19
Z_{PC1}
Short
Low
lag_{ace}
$r_{max-ace}$
Long
High


Fitness
19
19
Low
Low
r max–glu
OD max
Z PC2
High
High
Z PC1
Short
Low
lag ace
r max–ace
Long
High


Fitness
Low
Low
r_max−glu
OD_max
High
High
Z_PC2
20
19
19
20
18
18
Z_PC1
Short
lag_ace
Long
Low
r_max−ace
High

Summary

Evolution to the branching point – support for Adaptive Dynamics (frequency dependence drives diversification).

Re-branching? Yes, from one type but not the other.

Why is there (bio)diversity?

1. How is diversity maintained?
    - Frequency-dependent fitness
    - Example 1: *Pseudomonas* bacteria (SM-WS-FS)
        - Tool: Invasion Experiment, ESSt.
    - Example 2a: *E. coli* bacteria (SS-FS)
    - Summary
2. How does it arise?
    - Adaptive landscapes – defining the problem
    - Adaptive Dynamics – solving the problem
    - Example 2b: Evolution to the branching point
    - Summary

…and what happens if (when) we lose diversity?

Take home messages

Processes that maintain and generate divesity in nature can be informed by study of microcosms in the lab.

The importance frequency dependence in maintaining and generating diversity.

Effective management of diversity in the natural world requires an appreciation for frequency dependence.

Fini!

Jabus Tyerman
PhD Candidate
Dept. Zoology
UBC

Michael Doebeli (Supervisor)
Christine Spencer (Post Doc)
Melanie Bertrand (Lab Tech)

Doebeli lab: http://www.zoology.ubc.ca/~tyerman/DoebeliLab/ExperimentalGroup.htm

Finches pic
http://www.oeb.harvard.edu/faculty/donohue/Finches.html