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## Eco-evolutionary dynamics, Part B

Sylvie Oddou-Muratorio

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# Contents

## ***Part 1 : Concepts related to eco-evolutionary dynamics***

*From Hendry, A. P. (2017). Eco-evolutionary Dynamics. Princeton University Press.*

*+ Course of David Claessen (Institut de Biologie de l'ENS )*

- Feedbacks between ecological and evolutionary processes
- Selection (types of selection, how to measure selection, selection in nature)
- Adaptation (response to selection, how to measure evolutionary change, adaptive landscapes)
- Population dynamics (relation between maladaptation and population decline)
- Genetics, genomics and plasticity

# *Eco-evolutionary feedbacks*

## *eco-to-evo*

Genetic change

Phenotypic change

Population dynamics

Community structure

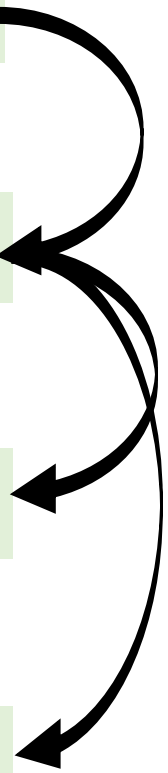
## *evo-to-eco*

Genetic change

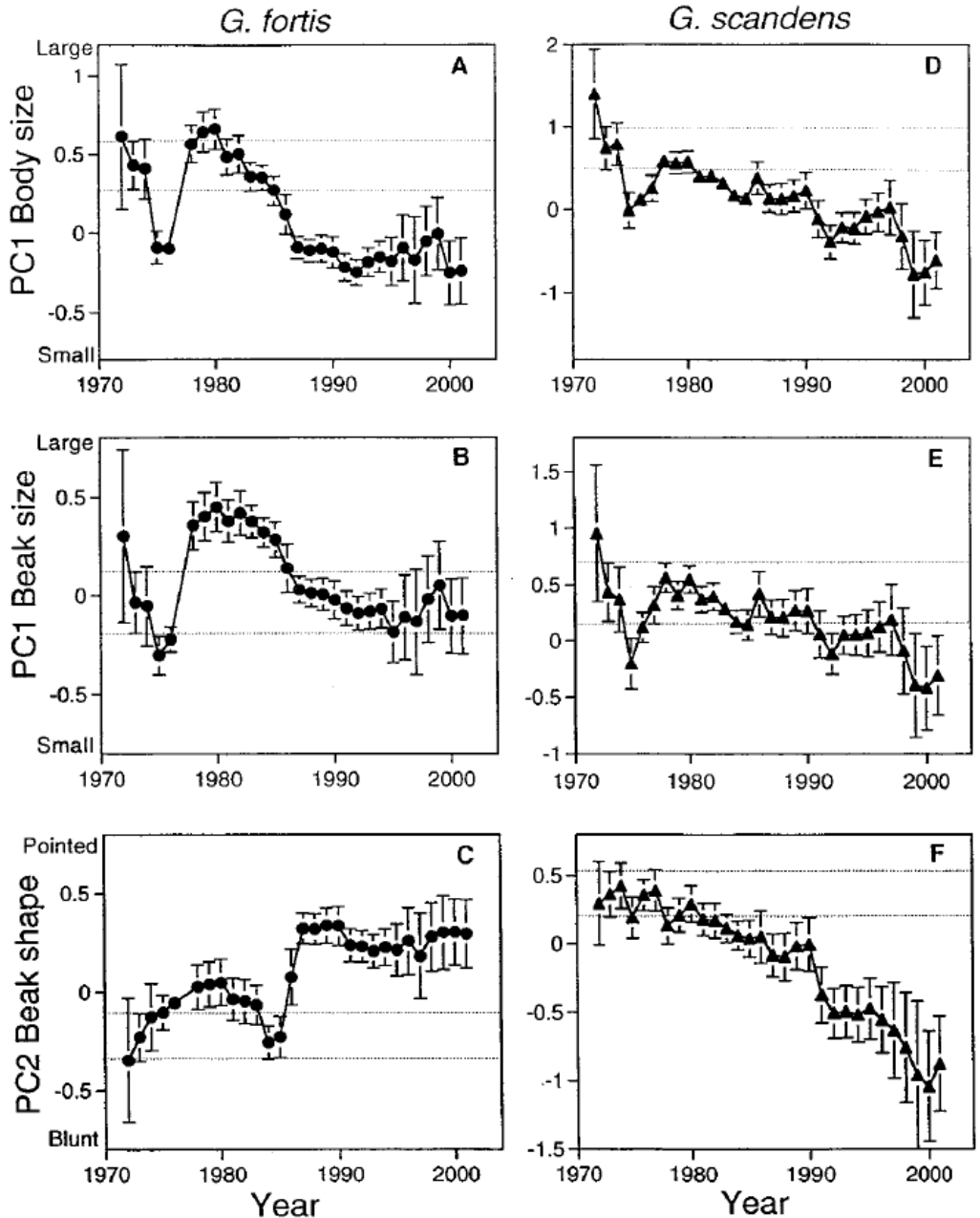
Phenotypic change

Population dynamics

Community structure



# Example: evolution of adaptive traits in finches



*Geospiza fortis* (medium ground finch)    *Geospiza scandens* (cactus finch)

- Study in medium ground finches during two drought periods on Galapagos
- Illustration of how an ecological change (seed size, drought) drives evolutionary change .

(Grant & Grant, 1995; Grant & Grant, 2002)

# Population dynamics

*evo-to-*

*eco*  
Genetic change

Phenotypic change

Population dynamics

Community structure

- When might evolution influence population dynamics? → the struggle for existence
- How to detect evolutionary effects on population dynamics?
- “Eco-evolutionary population dynamics in nature”

AN ESSAY  
ON THE  
**PRINCIPLE OF POPULATION;**  
OR,  
A VIEW OF ITS PAST AND PRESENT EFFECTS  
ON  
*HUMAN HAPPINESS;*  
WITH  
AN INQUIRY INTO OUR PROSPECTS RESPECTING THE FUTURE  
REMOVAL OR MITIGATION OF THE EVILS WHICH  
IT OCCASIONS.  
BY  
THE REV. T. R. MALTHUS, A. M. F. R. S.  
LATE FELLOW OF JESUS COLLEGE, CAMBRIDGE, AND PROFESSOR OF HISTORY AND POLITICAL  
ECONOMY IN THE EAST-INDIA COLLEGE, HERTFORDSHIRE.  
SIXTH EDITION.  
IN TWO VOLUMES.  
VOL. I.  
LONDON:  
JOHN MURRAY, ALBEMARLE STREET.  
MDCCCXXVI.

# *The struggle for existence*

*Thomas Malthus*  
1766-1834

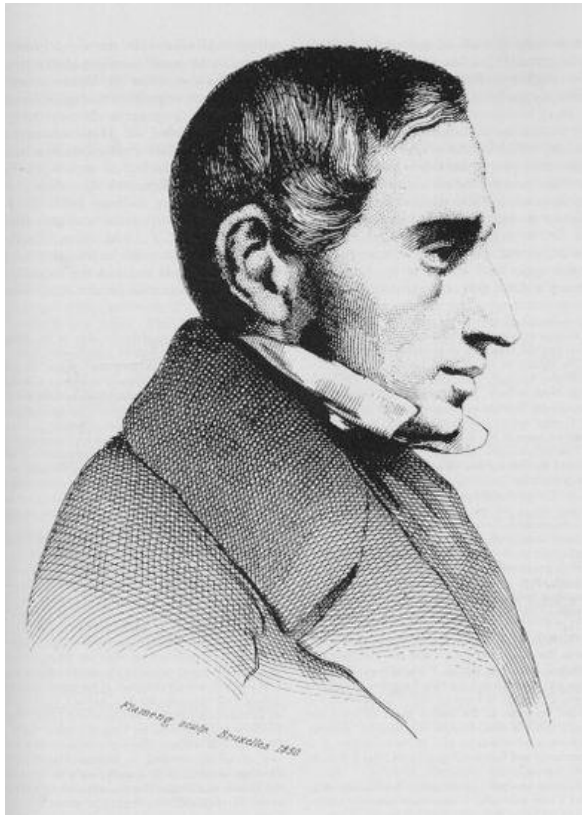


- The increase of population is necessarily limited by the means of subsistence
- The population does invariably increase when the means of subsistence increase
- The superior power of population is repressed, and the actual population kept equal to the means of subsistence, by misery and vice

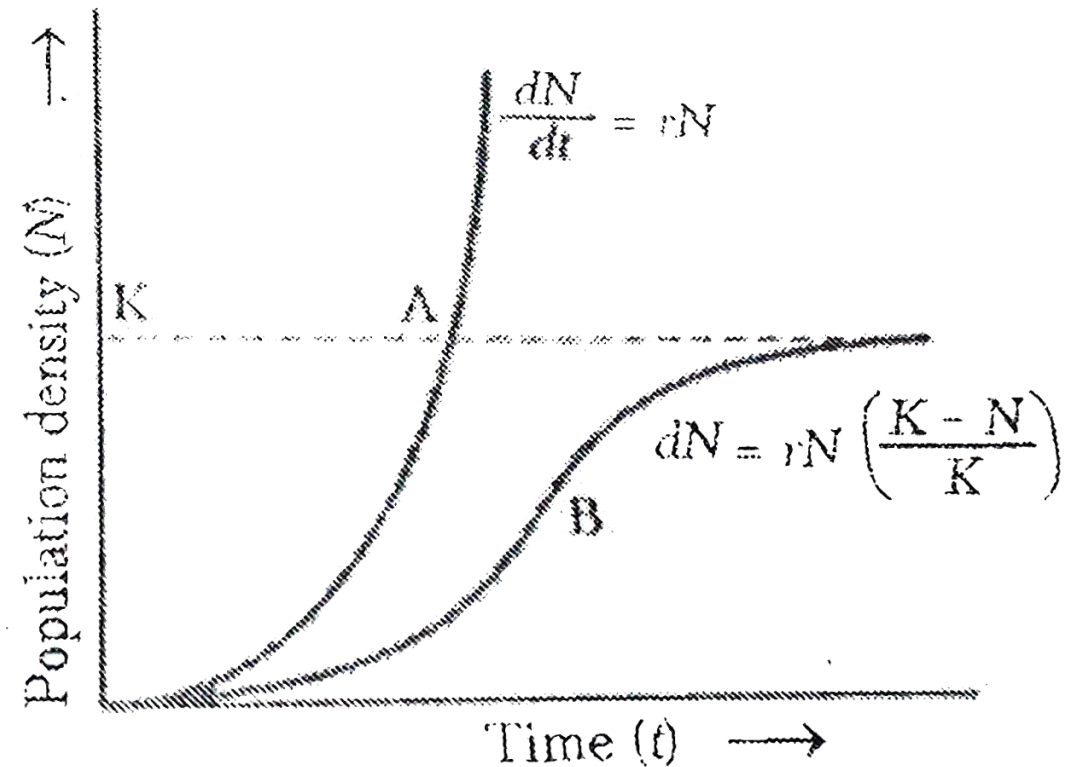
*Dia from David Claessen*

# The struggle for existence

A non-exponential model to describe the evolution of human and animal populations



Pierre-François  
Verhulst  
1804-1849



# *The struggle for existence*



*Charles Darwin*  
*1809-1882*

struggle for  
existence  
+  
heritable variation  
↓  
driving force of  
evolutionary change

## ON THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE  
PRESERVATION OF FAVOURED RACES IN THE STRUGGLE  
FOR LIFE.

By CHARLES DARWIN, M.A.,  
FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;  
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE  
ROUND THE WORLD.'

LONDON:  
JOHN MURRAY, ALBEMARLE STREET.  
1859.

*The right of Translation is reserved.*



### *Geometrical Ratio of Increase.*

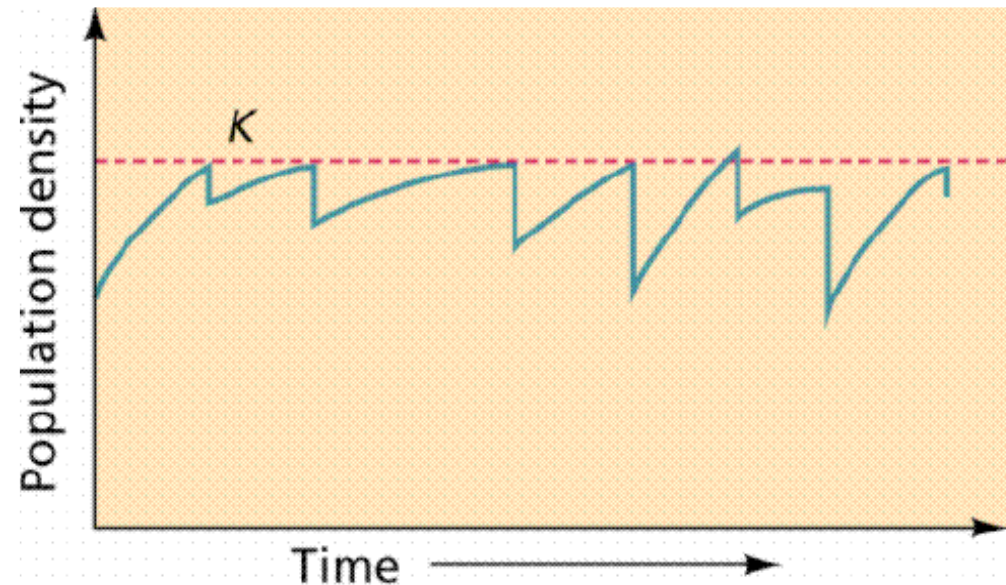
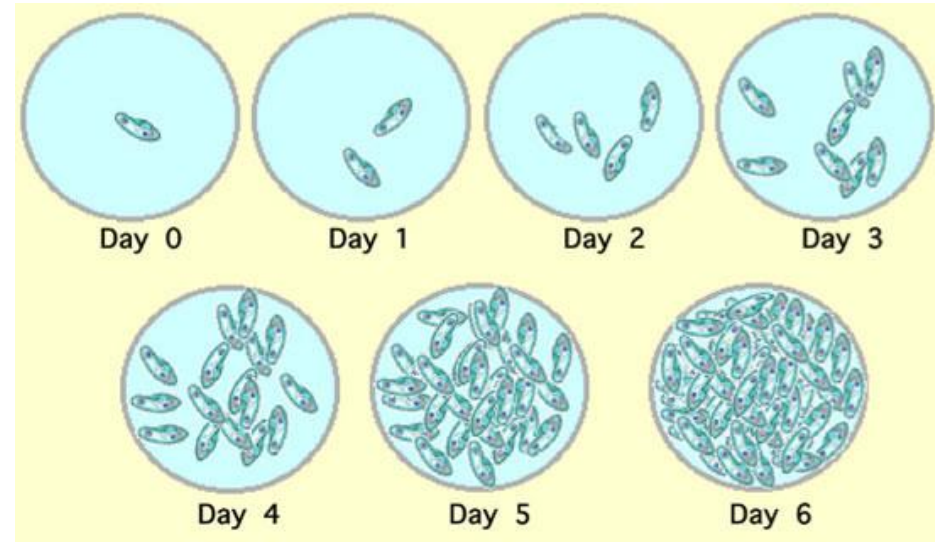
A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.

# The origin of this struggle

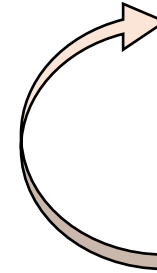
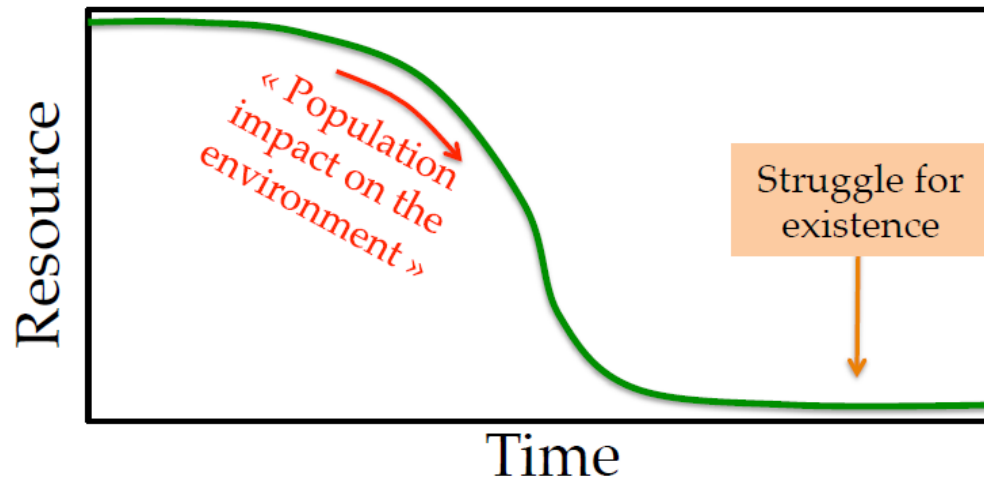
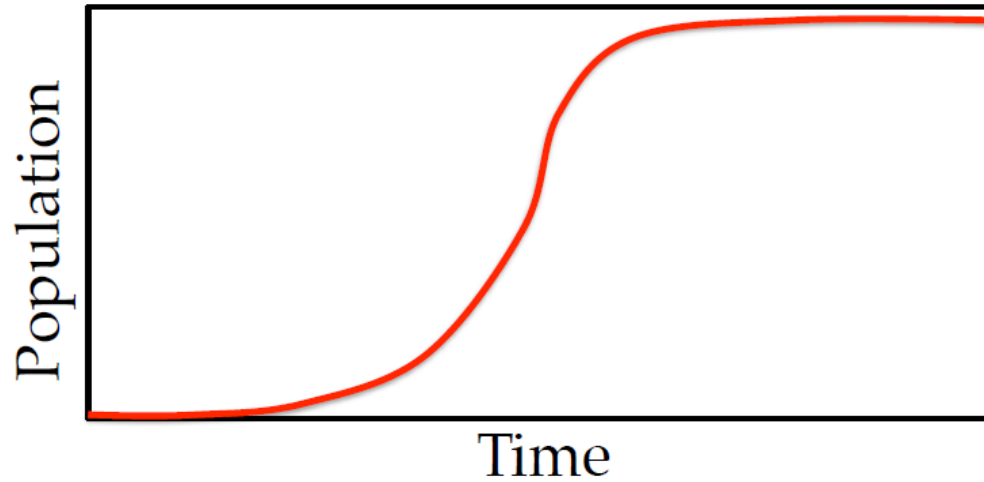
Two basic observations

1. All populations tend to grow exponentially

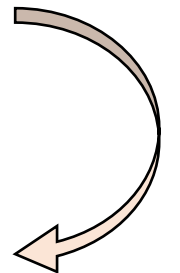
2. Exponentially growing populations are kept in check by regulatory mechanisms



# The origin of this struggle is a feedback loop



**Population  
size**



**Environnemental  
conditions**

# A very simple model example

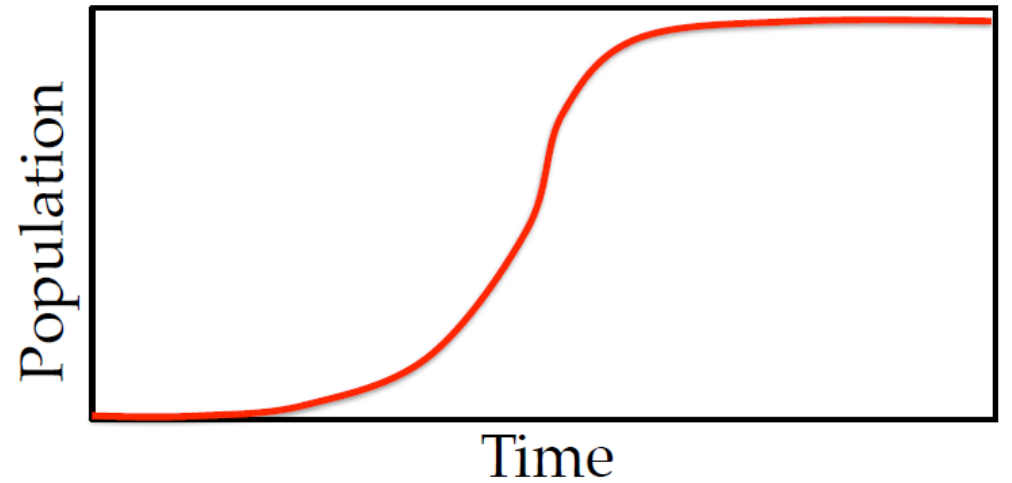
$$\frac{dN}{dt} = r(E)N \quad \text{Exponential growth}$$

with  $r(E) = \rho(E) - \mu(E)$

$$\mu(E) = \mu_0 \quad \text{Constant mortality}$$

$$\rho(E) = \rho_0 E \quad \text{Food dependent reproduction}$$

$$E = 1 - \frac{N}{\kappa} \quad \text{Population impact on the environment}$$



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

with  $r_{max} = \rho_0 - \mu_0$   
 $K = \kappa(1 - \mu_0/\rho_0)$

# *A simple mathematical model...*

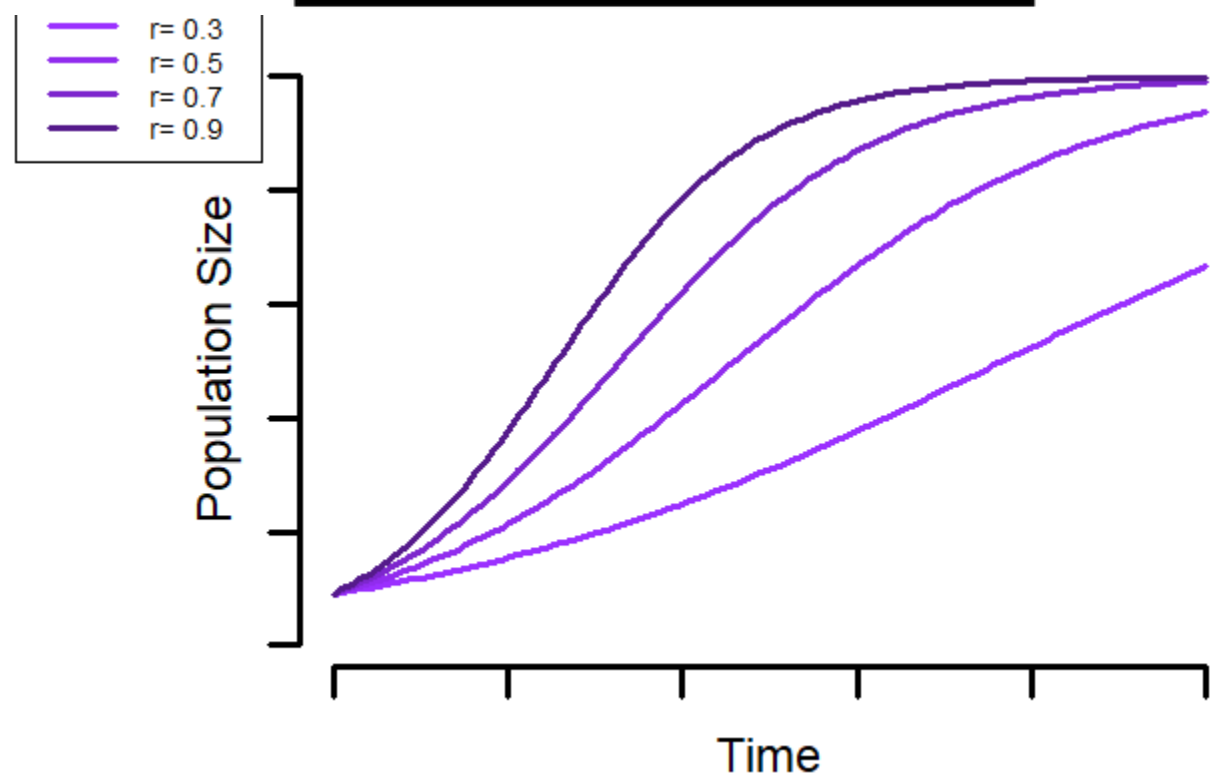
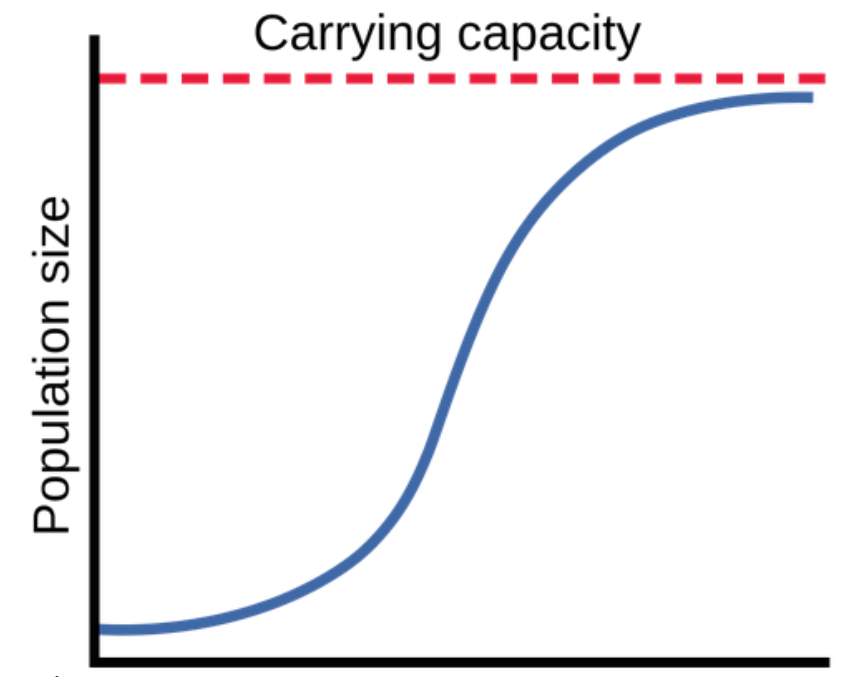
$$\frac{dN}{dt} = r_{max} N \left( 1 - \frac{N}{K} \right)$$

Rate of change in population size

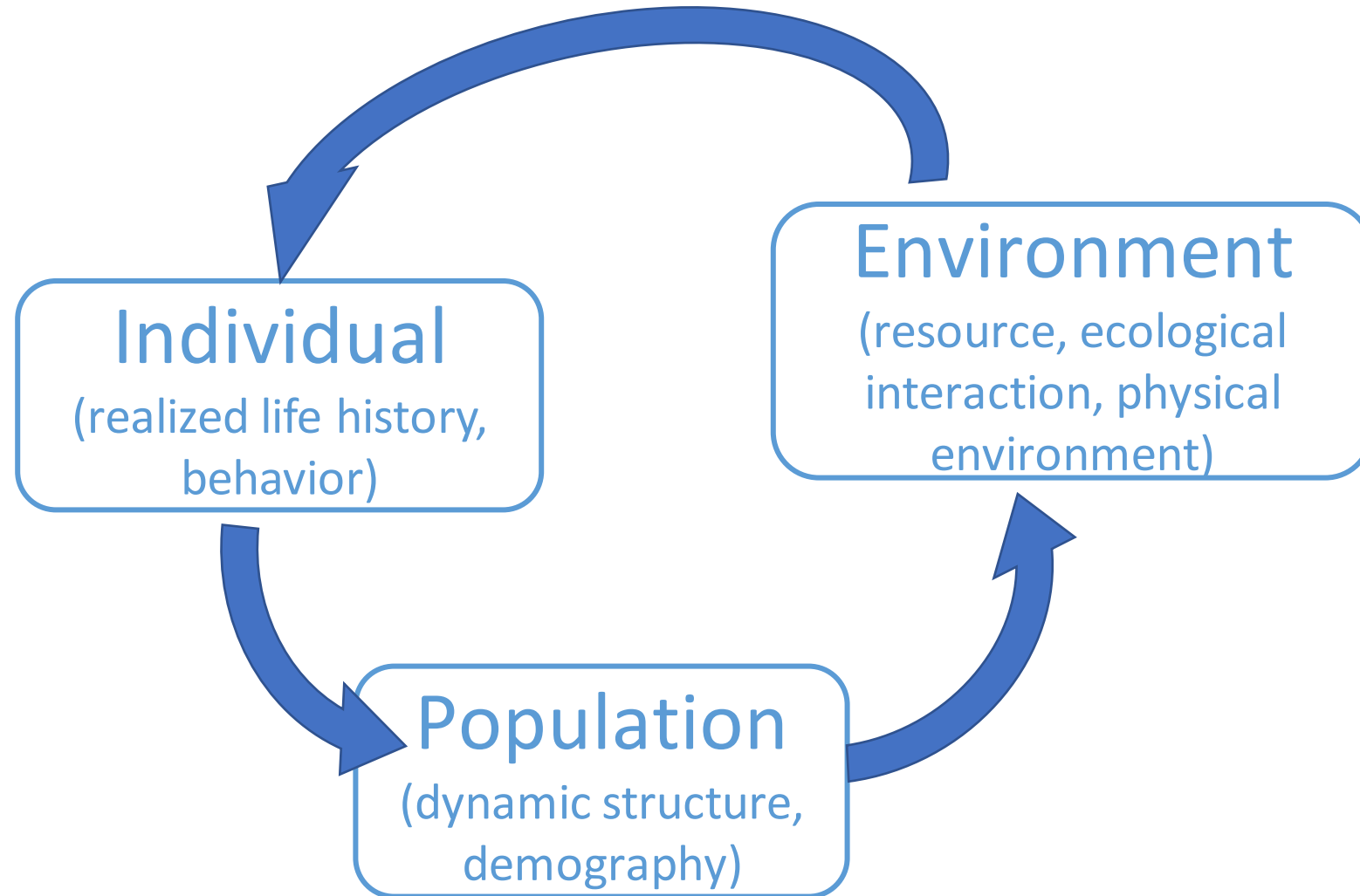
Current population size

Maximum per capita population growth rate

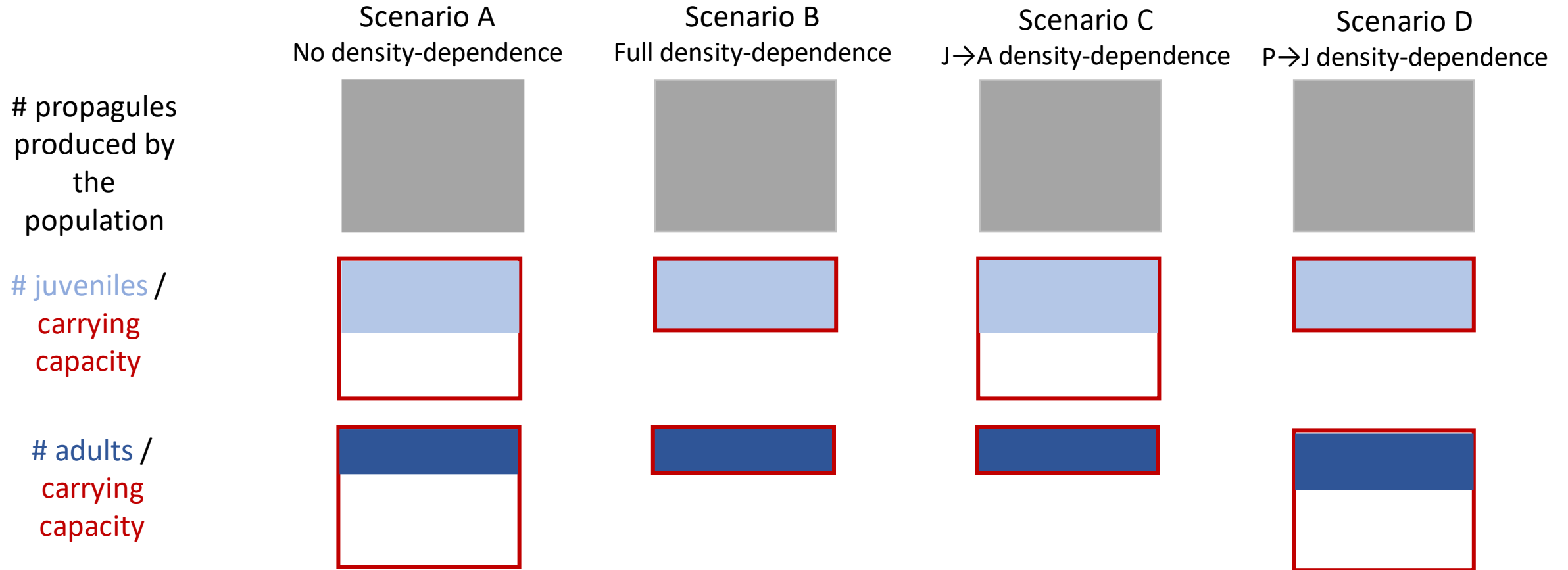
Carrying capacity



*...to study when might evolution influence population dynamics*



# Density-dependence drives the influence of evolution on $r_{max}$ and $K$



$r_{max}$  ↑

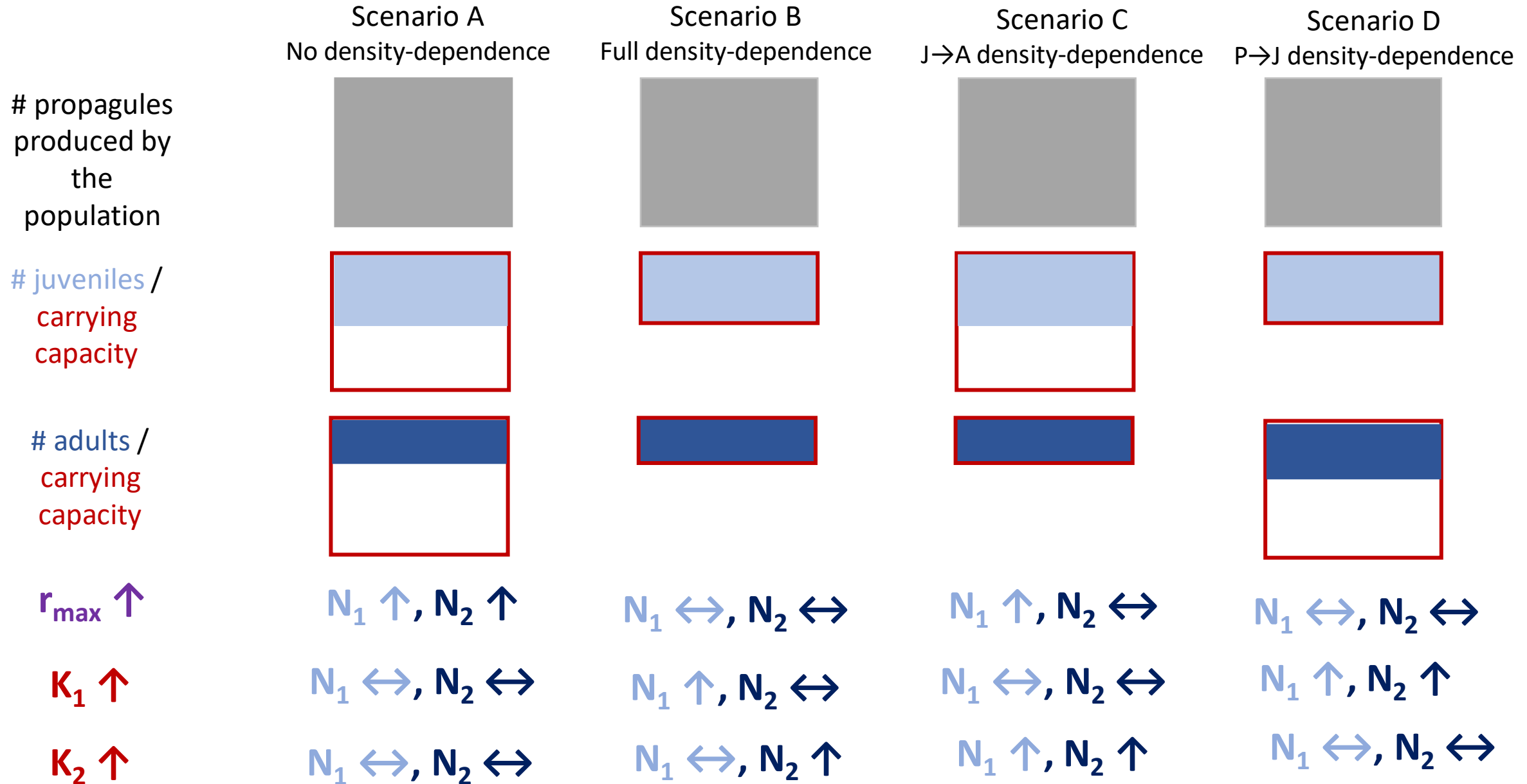
$K_1$  ↑

$K_2$  ↑

Impacts on :  
N1 = the number of propagules  
N2 = the number of adults



# Density-dependence drives the influence of evolution on $r_{max}$ and $K$





# *The relationships between individual traits and population growth*

## Traits that influence $r_{\max}$

**Reproduction** : fecundity, reproductive rate

**Survival** : Juvenile survival rate, early life development (maturation)

**Resource acquisition**, e.g., physiological efficiency (metabolic rate), resource acquisition efficiency

## Traits that influence **K**

**Resource use efficiency**: Foraging efficiency, energy efficiency

**Competition and territoriality**: Aggressive behaviors, social structure vs cooperative behaviors.

**Tolerance to environmental variation**:  
Adaptation to stress: Generalist vs. specialist:

## Metabolic theories in ecology :

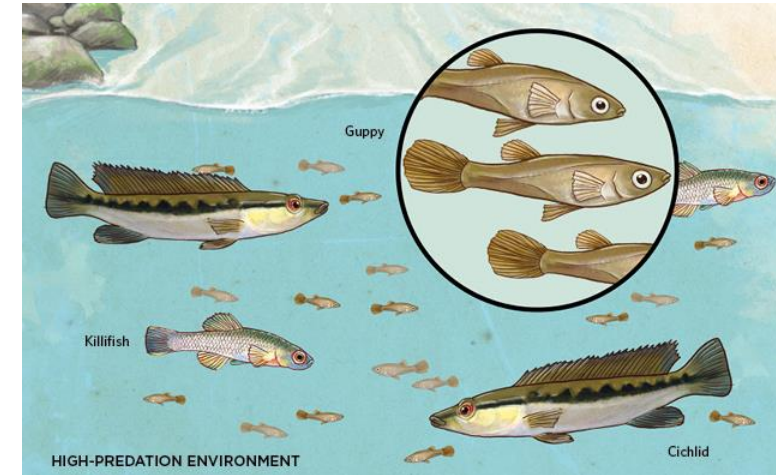
**Metabolism** = process by which individuals acquire energy/materials from their environment, and use them for maintenance, growth, reproduction

### **Two main theories:**

- Kooijman's dynamic energy budget (DEB) theory
- West, Brown, and Enquist (WBE) theory

*Complexity: (1) traits influencing  $r_{max}$  and  $K$  have generally themselves evolved under density-dependent/independent conditions*

- Populations facing high density-independent mortality often evolve traits that increase  $r_{max}$ ,
- Populations facing density-dependent mortality often evolve traits that increase competitive ability,



Predation

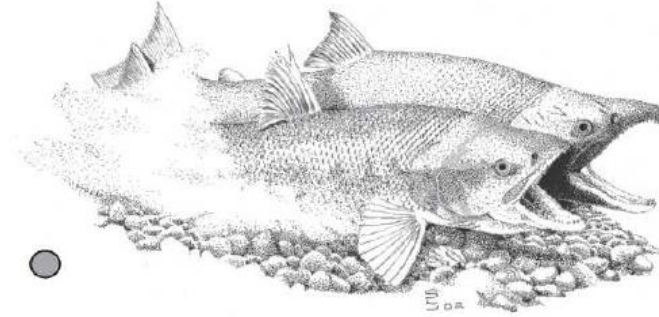
Resource

- r-type life histories
  - Early reproduction
  - High reproductive effort
  - Many small offspring

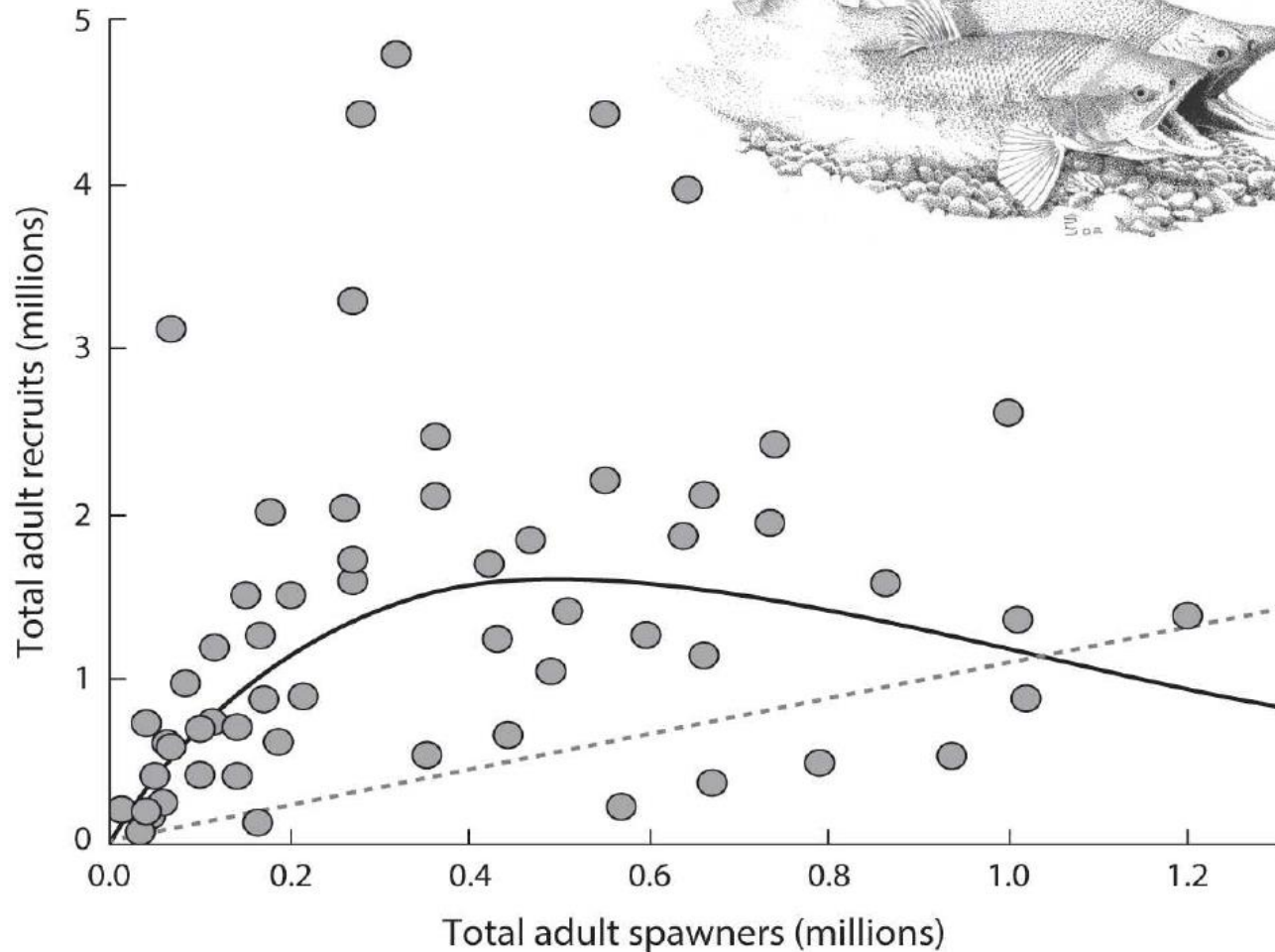
- K-type life histories
  - Late reproduction
  - Small reproductive effort
  - Few large offspring

# Complexity (2) Evolution in $r_{max}$ can affect population size under density-dependence

- high  $r_{max}$  can cause an **overshoot** of  $K$ , which can then lead to a sharp decrease in per capita reproductive success and, hence, a decrease in population size at subsequent stages.



the “Ricker Curve” of stock recruitment

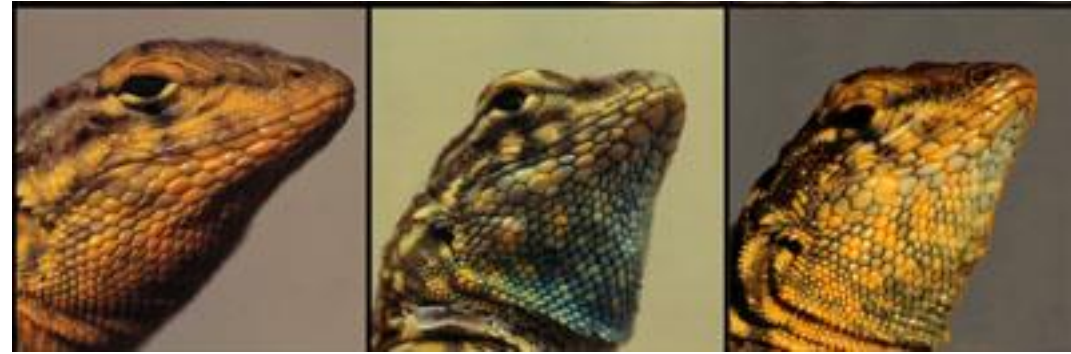


In Hendry 2017

# Complexity (3) Feedback in life-histories evolutions

- Population density and life history evolution can influence each other, a situation that can lead to eco-evolutionary feedbacks

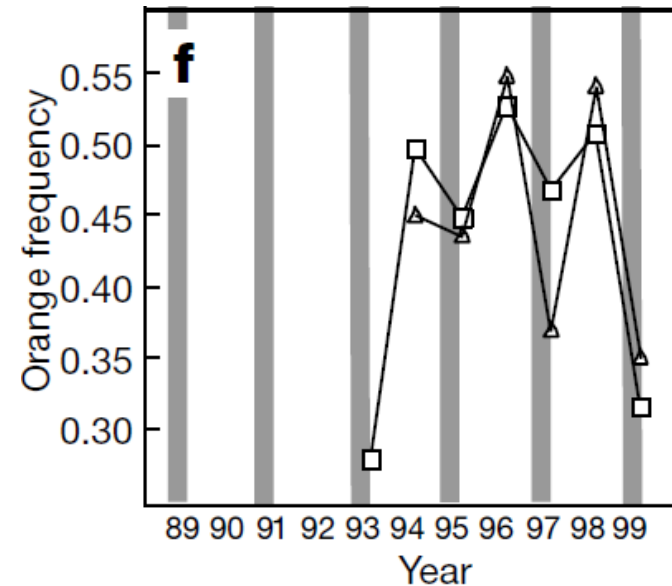
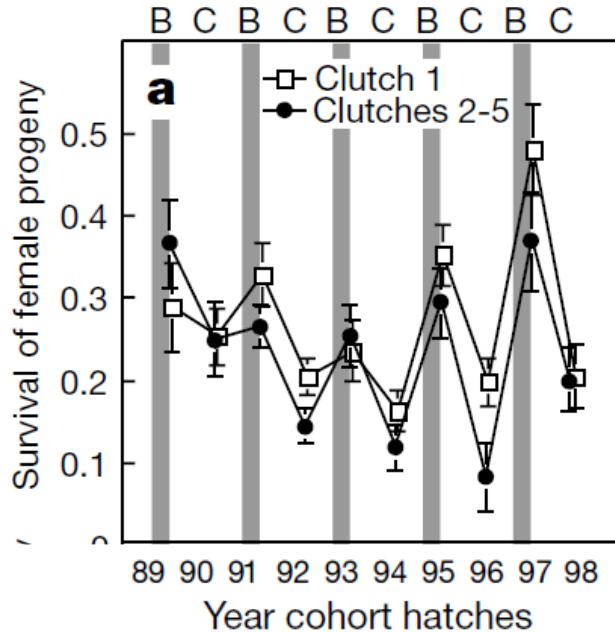
## Side-blotched lizards



Orange-throated females have few large offspring (K-type life histories)

Yellow-throated females have many small offspring (r-type life histories)

Favored in years of high-density  
→ decrease population growth



Favored in years of low-density  
→ increase population growth

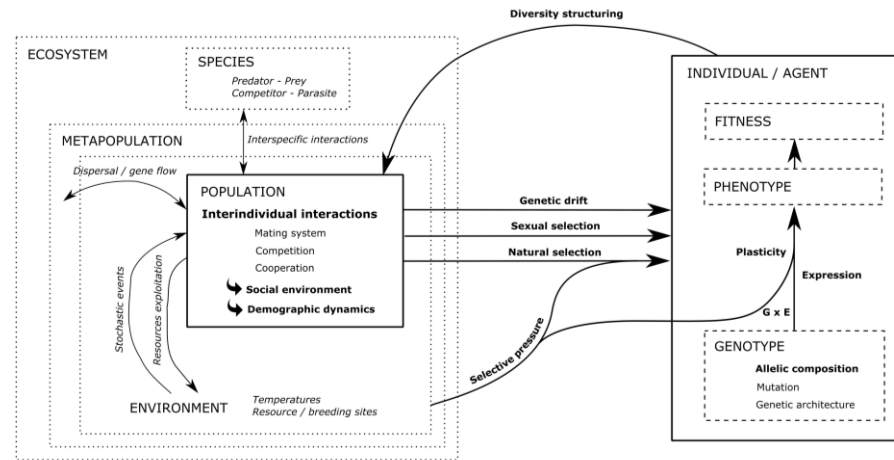
Sinervo, Svensson, & Comendant, 2000

# How to detect evolutionary effects on population dynamics ?

- **Experimental manipulations:** manipulate phenotypic/genotypic distributions and monitor the resulting population dynamics: in controlled conditions (mesocosm) or in situ (reciprocal transplant experiments) (Farkas et al. 2013; Zamorano et al. 2023)
- **“Empirical” modeling:** mechanistic simulation model integrating empirical knowledge on eco-evolutionary dynamics → detailed after
- **Observational studies :** monitors the dynamics of natural populations and statistically relates year-to-year (“real time”) changes in population dynamic parameters to year-specific phenotypic trait values or allele frequencies (Hanski and Saccheri 2006)



*Timema cristinae*

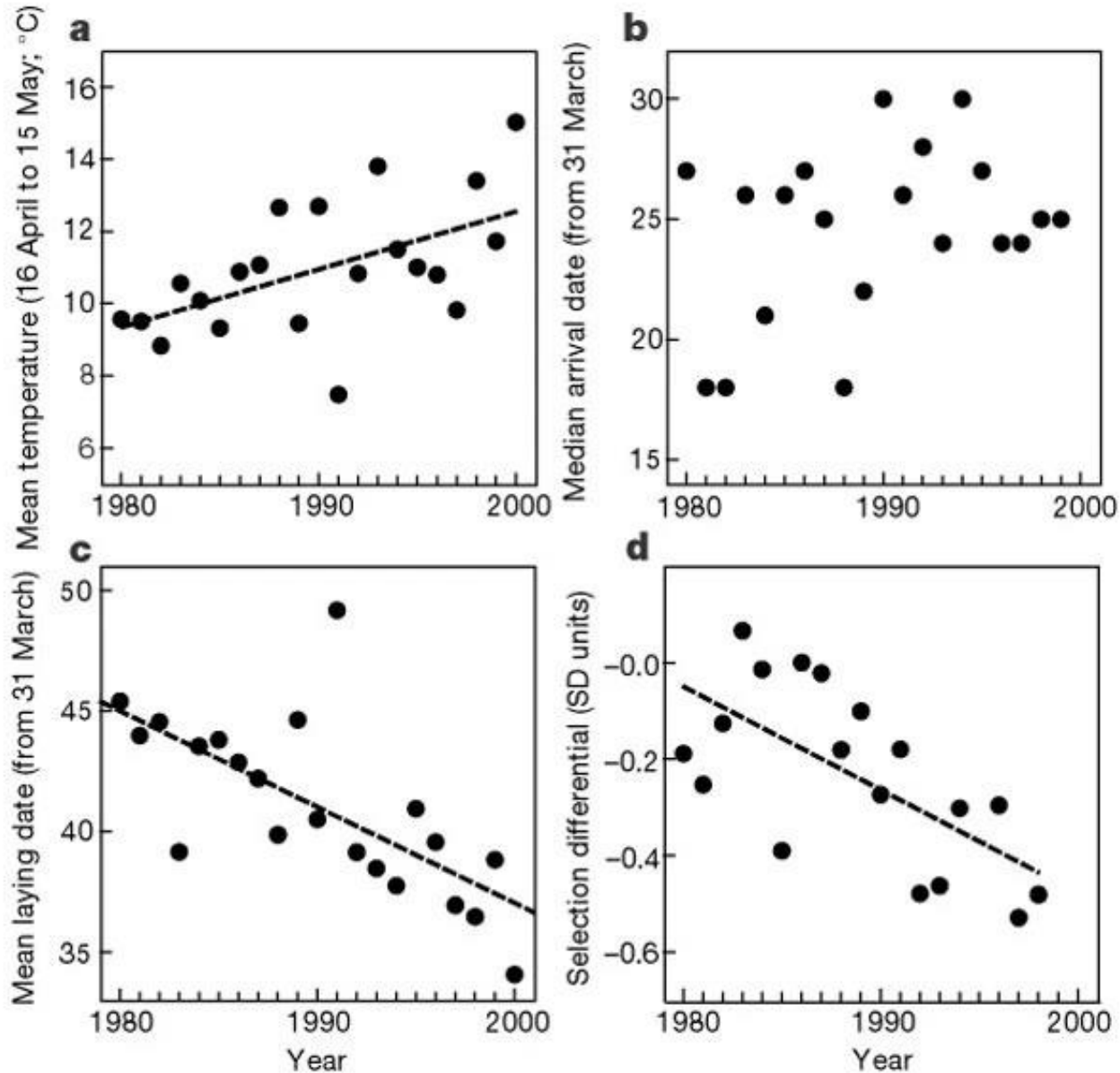


*Melitaea cinxia*

# *"Eco-evolutionary population dynamics in nature"*

- Q1. To what extent does maladaptation cause population declines?
- Q2. To what extent, and how rapidly, does adaptation increase individual fitness?
- Q3. To what extent does adaptation influence population growth ?
- Q4. Does adaptation allow evolutionary rescue?
- Q5. Does adaptation aid range expansion ?
- Q6. Does intraspecific diversity influence population dynamics ?

# Q1. To what extent does maladaptation cause population declines?



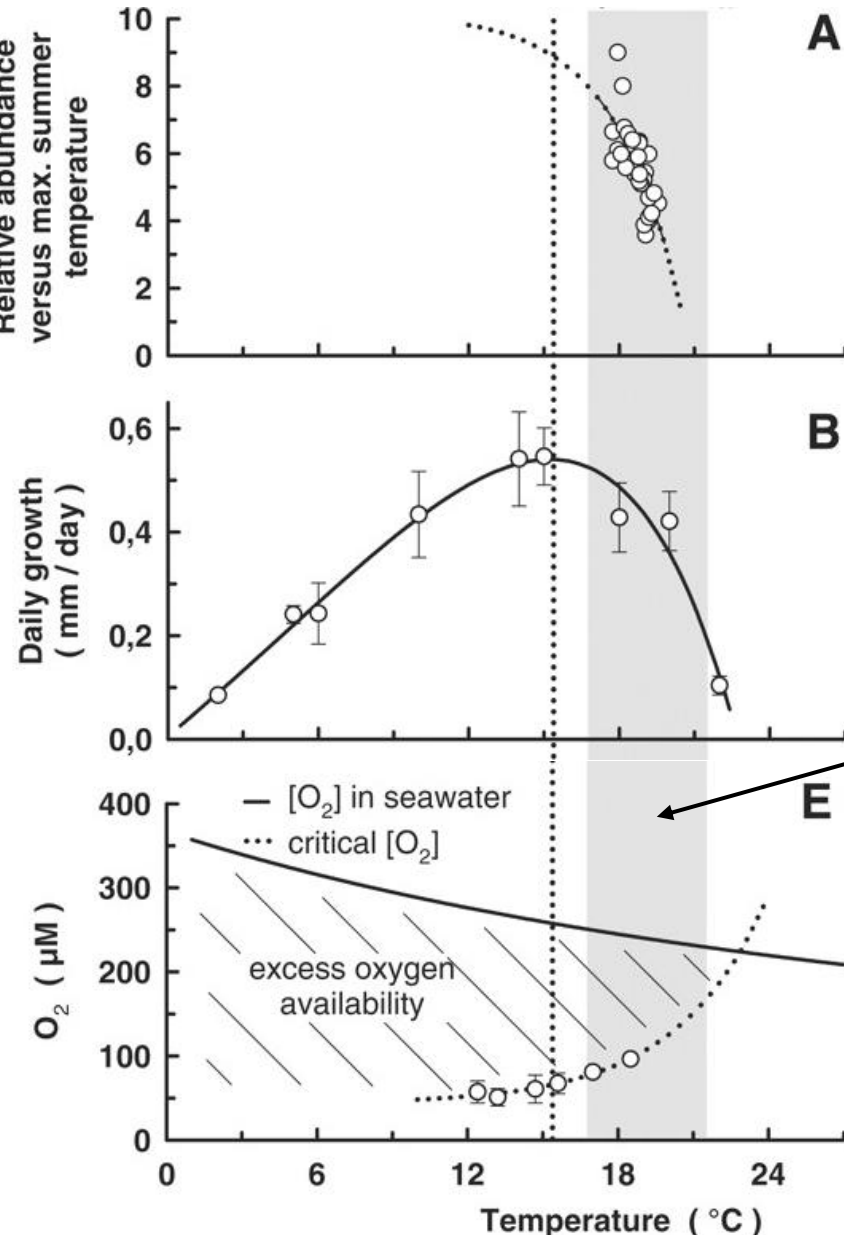
Spring temperature, breeding and spring arrival date of a pied flycatcher population in the Netherlands from 1980 to 2000



*Pied Flycatcher - Ficedula hypoleuca*

Both & Visser, 2001

# Q1. To what extent does maladaptation cause population declines?



- Thermal limitation in Eelpout, illustrated by
- The negative correlation between summer water temperatures and relative abundance
  - An overshoot of daily growth for high summer temperature
  - The underlying mechanism= mismatch between the demand for oxygen and the capacity of oxygen supply to tissues

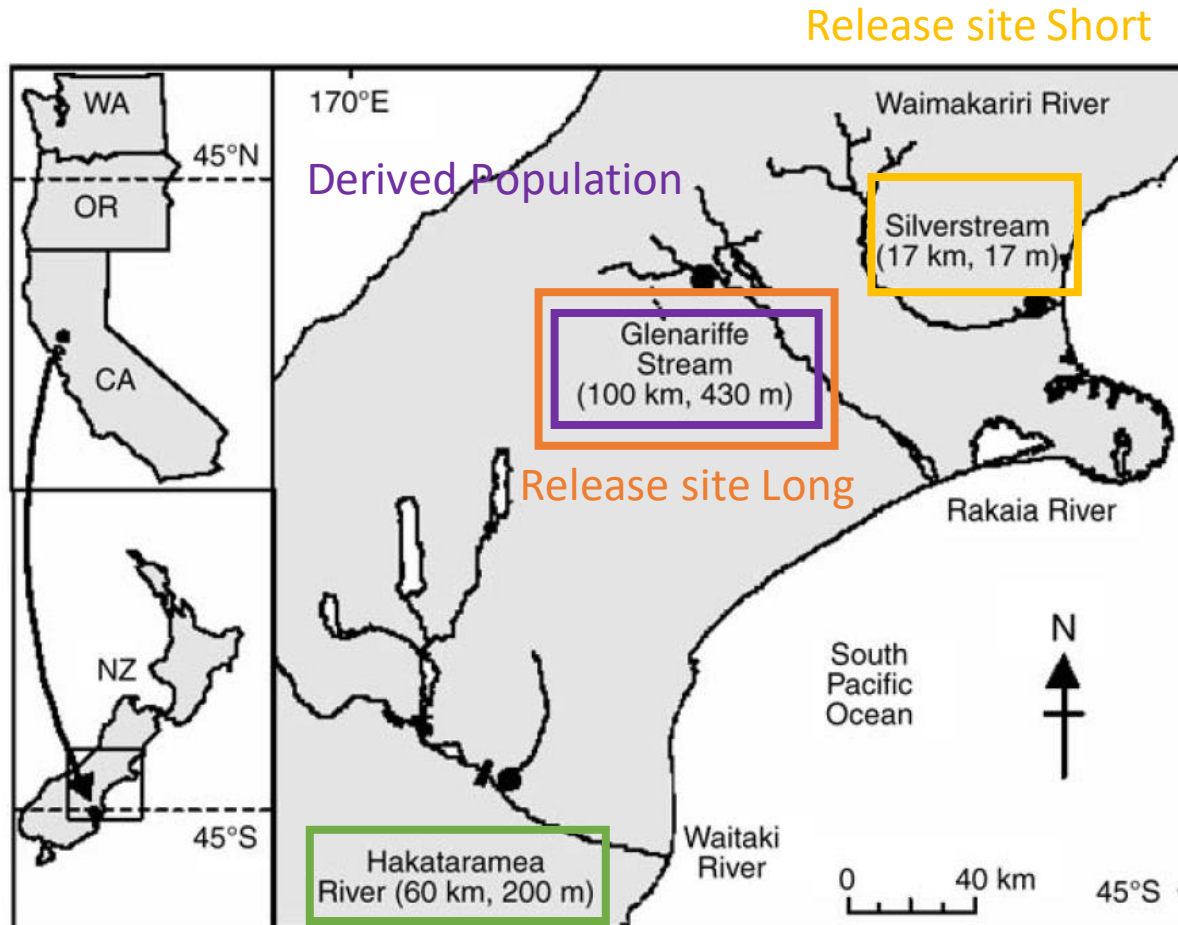
Critical temperature range where an organism's ability to perform aerobically begins to decline





# Q2. To what extent/ how rapidly, does adaptation increase individual fitness?

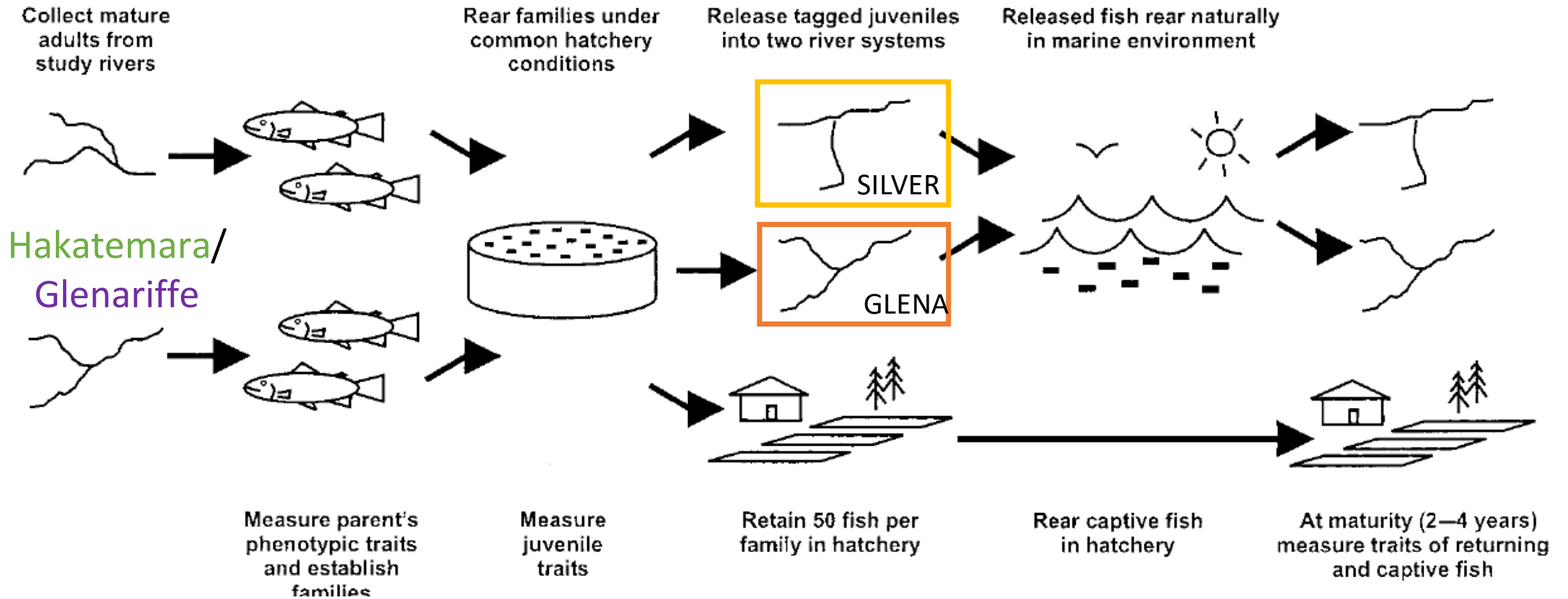
The contribution of adaptive trait changes to improvements in fitness is not well understood



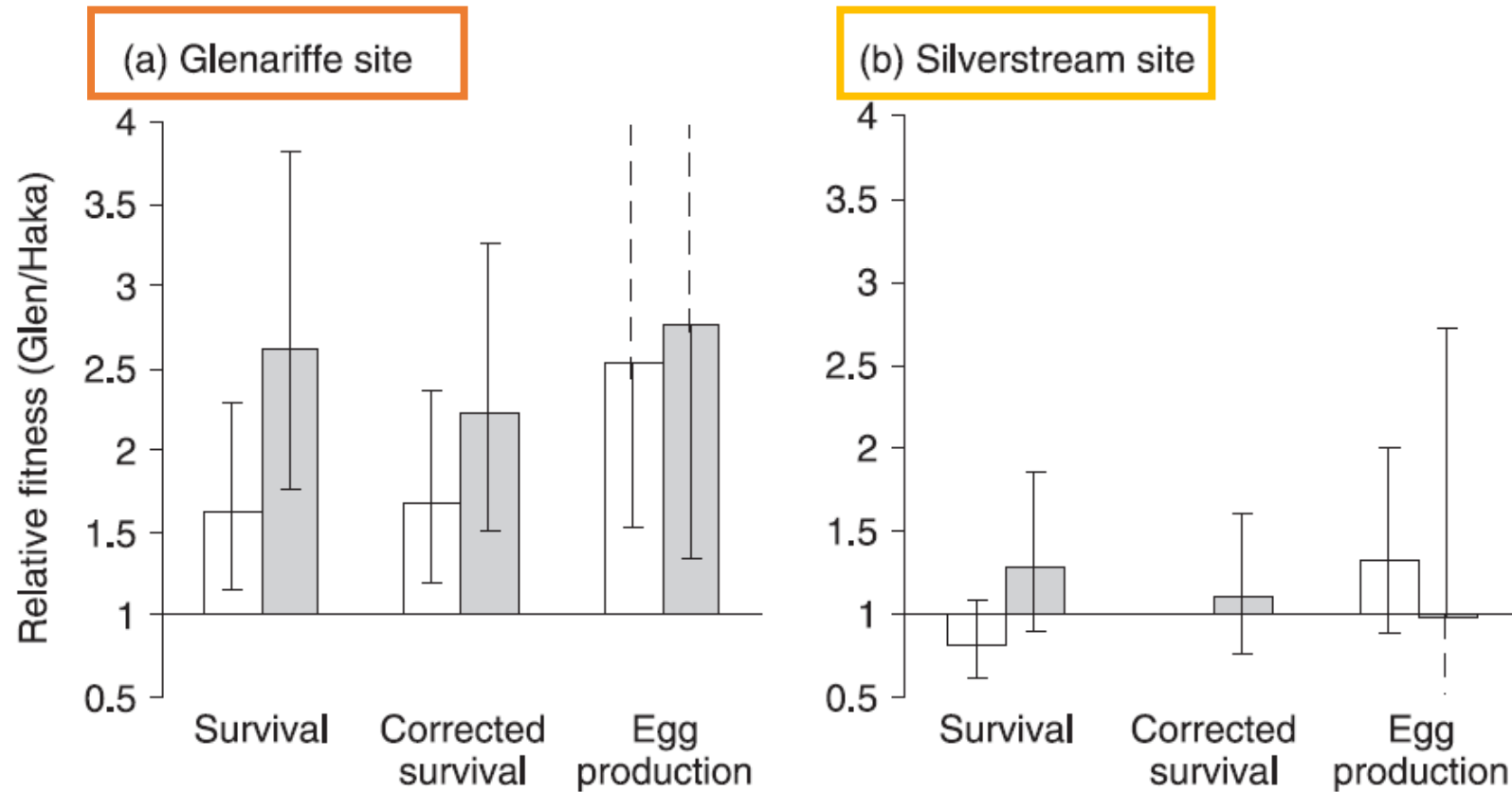
- 1901 and 1907: introduction of chinook salmon from California to New Zealand
- Common-garden studies revealed adaptive trait divergence between two populations (**Hakatemara**/**Glenariffe**) with different migration distances

Quinn *et al.* 2001 Kinnison *et al.* 2001, 2003

# Q2. To what extent/ how rapidly, does adaptation increase individual fitness?



## Q2. To what extent/how rapidly, does adaptation increase individual fitness?



Relative fitness of **Glenariffe** to **Hakataramea** genotypes released at two experimental sites (Glenariffe and Silverstream)

➤ “Reciprocal” transplant:

(a) Glenariffe genotypes outperform Hakataramea genotypes at GLENA site

(b) Glenariffe and Hakataramea genotypes perform similarly at SILVER site where neither has had the opportunity to adapt and where relative migratory (habitat) effects are minimized

### *Q3. To what extent does adaptation influence population growth ?*

A partitioning approach for the rate of change in population growth

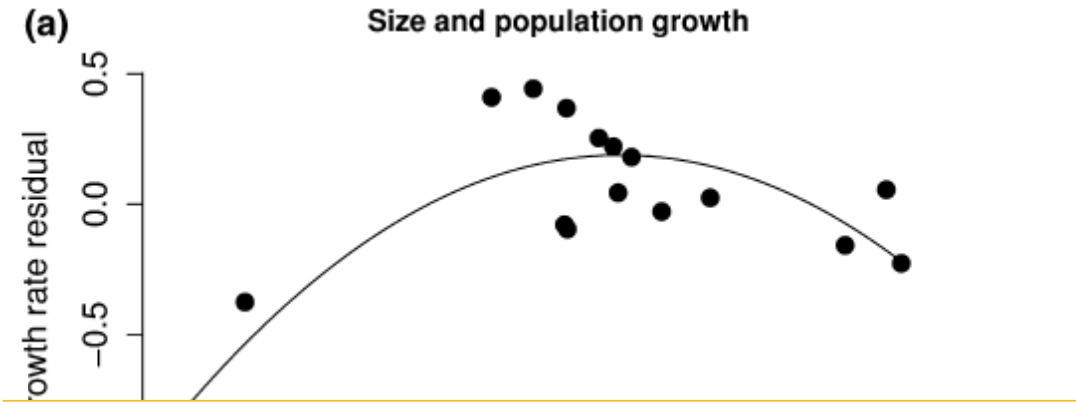
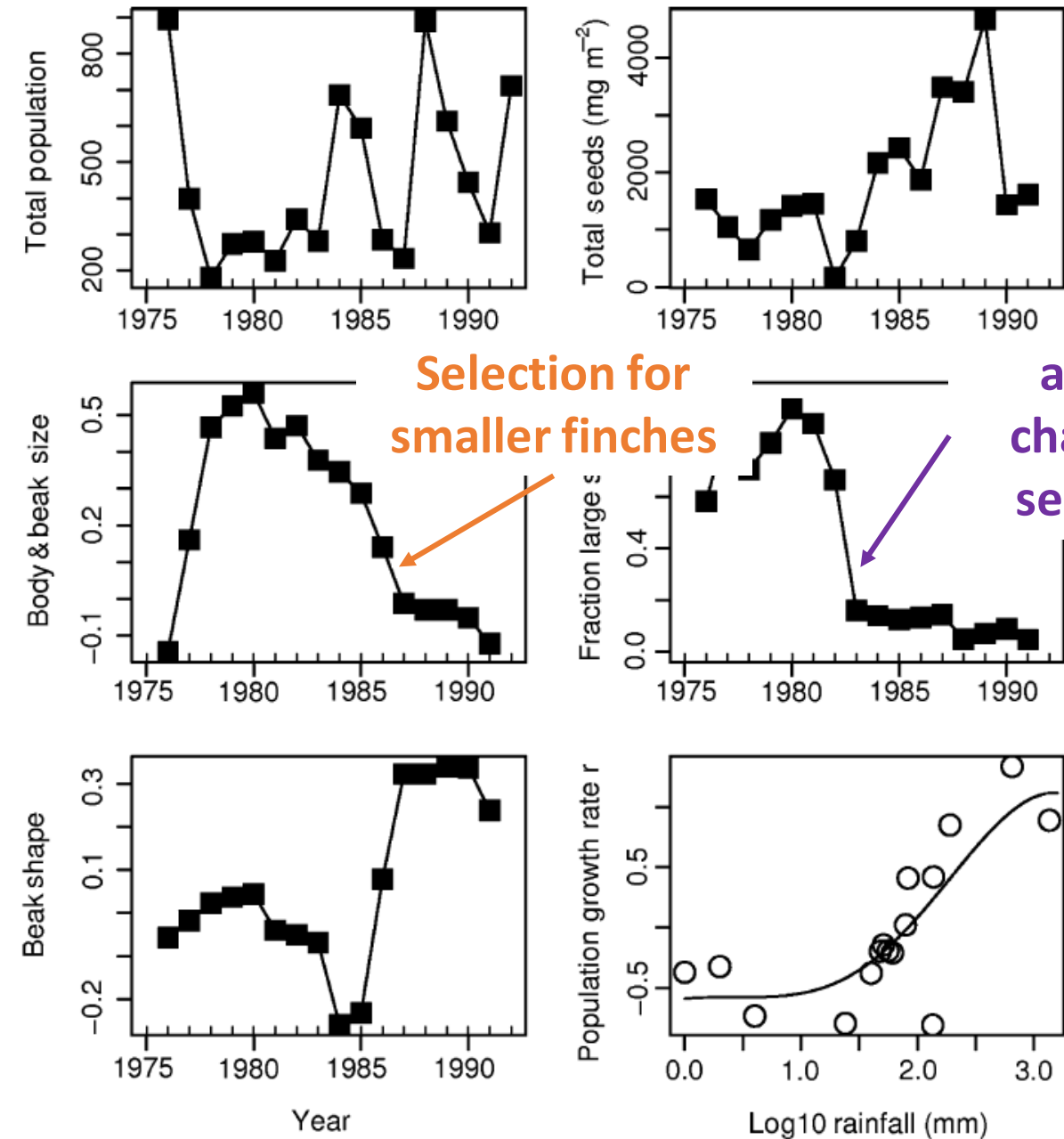
$$r(t) = r(z(t) + n(t))$$

$$\frac{dr}{dt} = \frac{\partial r}{\partial z} \frac{dz}{dt} + \frac{\partial r}{\partial n} \frac{dn}{dt}$$

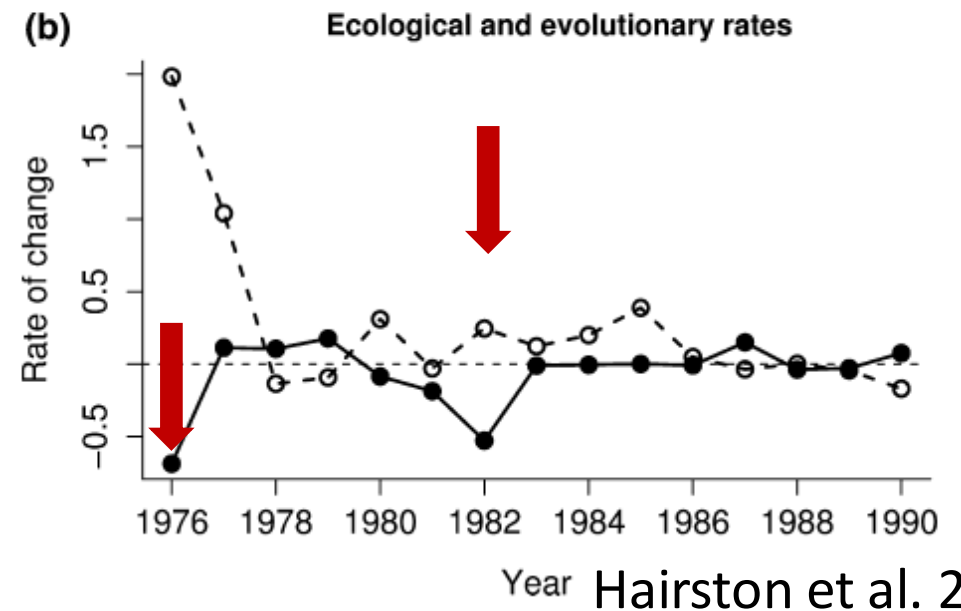
Actual rate of change  
in  $r$  resulting from the  
changes in  $z$

Actual rate of change  
in  $r$  resulting from the  
changes in  $n$

# Q3. To what extent does adaptation influence population growth?



Changes in population growth were twice as strongly influenced by evolution (changes in beak size) as by ecology (changes in rainfall).



### *Q3. To what extent does adaptation influence population growth ?*

#### Limitations of the partitioning approach

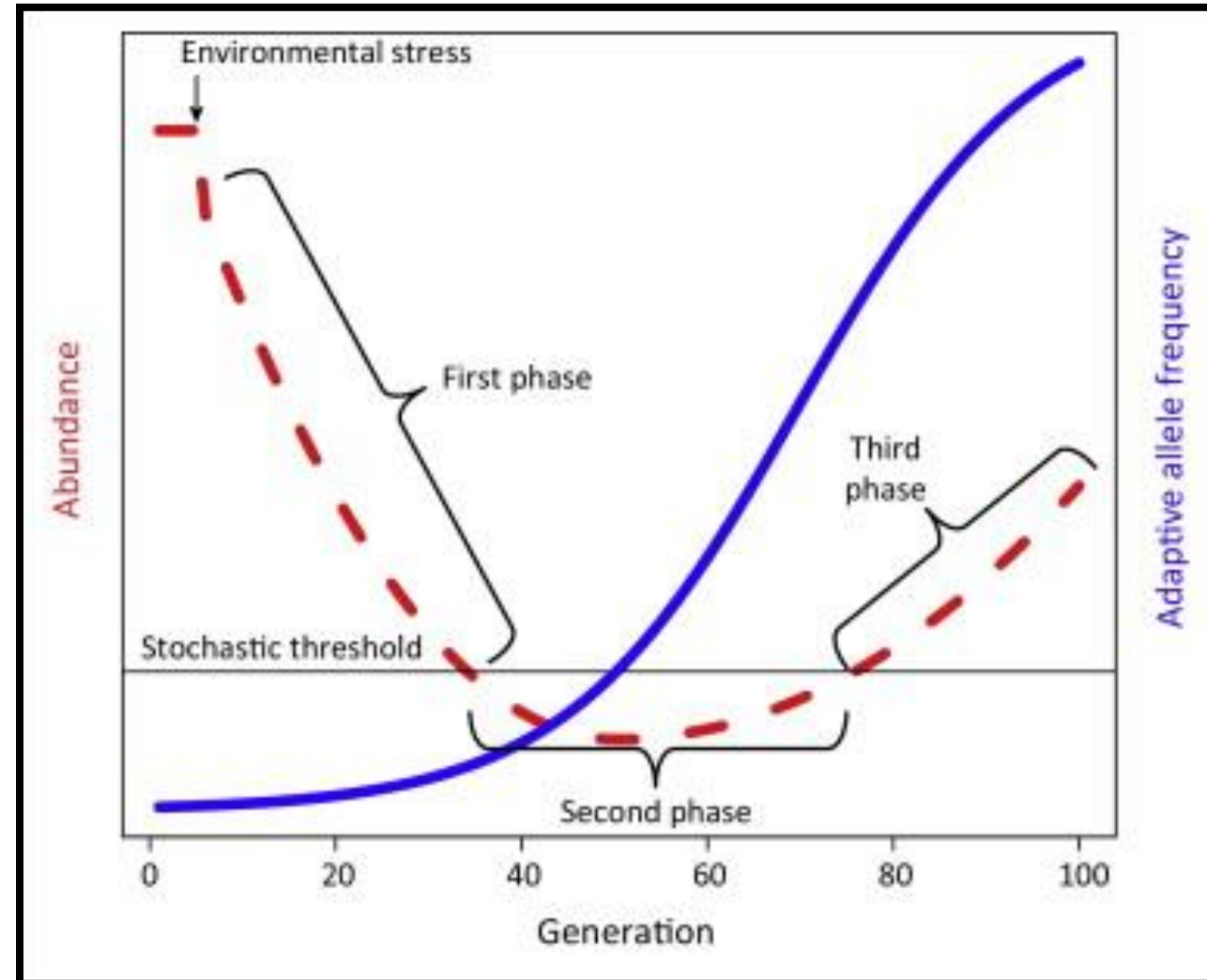
- ✓ Many phenotypic traits and ecological variables need to be considered
- ✓ The equation can incorporate an interaction term between ecology and evolution, but what about feedback ?
- ✓ Most applications consider that phenotypic change is entirely genetically based, whereas it can be influenced by plasticity
- ✓ Need for long-term data on population size, traits/genotypes and ecological variables

# Q4. Does adaptation allow evolutionary rescue?

## Evolutionary rescue

1. Rapid environmental change can cause maladaptation that reduces population size
2. This maladaptation should impose selection on phenotypes and thus promote adaptive evolution that improves individual fitness
3. Such adaptive evolution may increase population size

**To what extent can adaptive evolution arrest population declines that would lead to extinction and instead stabilize /recover population size ?**



Carlson *et al.* 2014

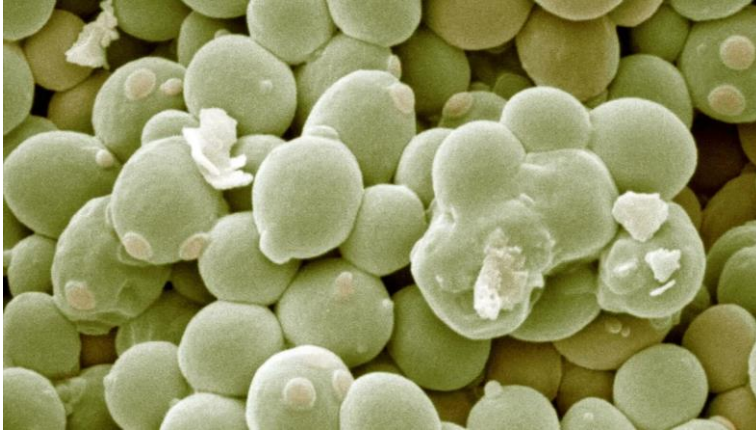
## *Q4. Does adaptation allow evolutionary rescue?*

### Conditions for evolutionary rescue

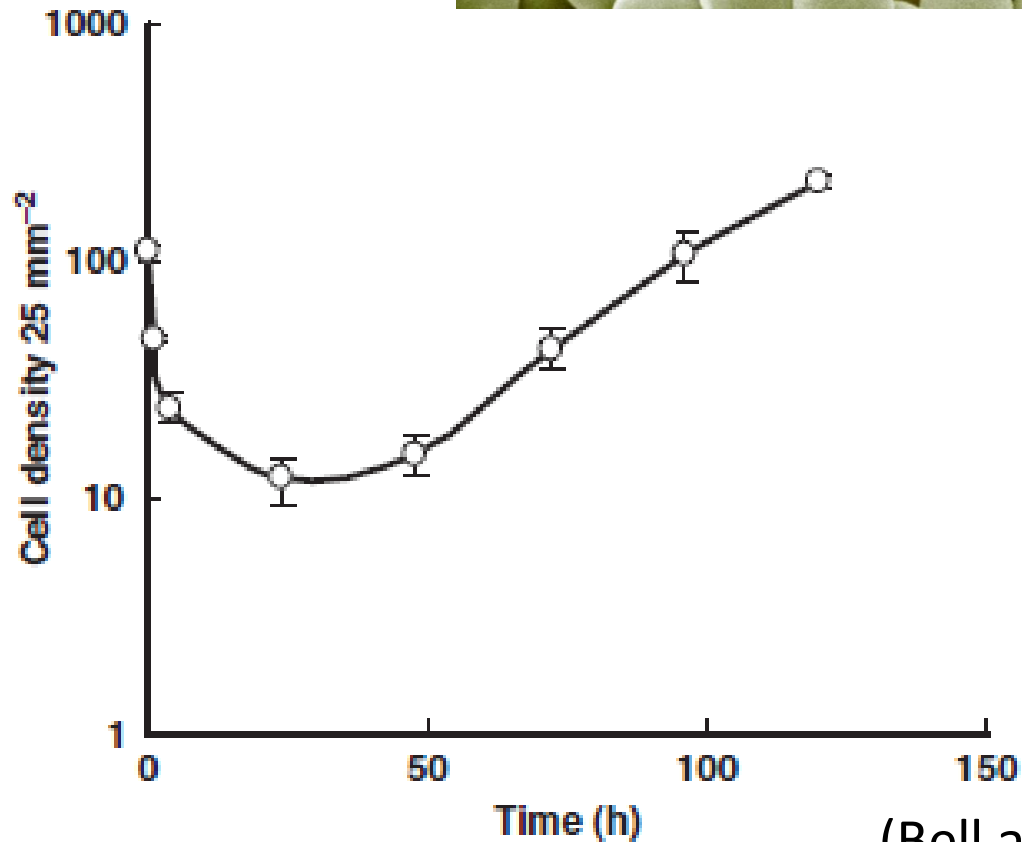
1. larger initial population sizes
2. less dramatic environmental change (lower initial maladaptation),
3. weaker stabilizing selection around the “optimum” trait value,
4. higher additive genetic variance in the direction of selection
5. shorter generation times



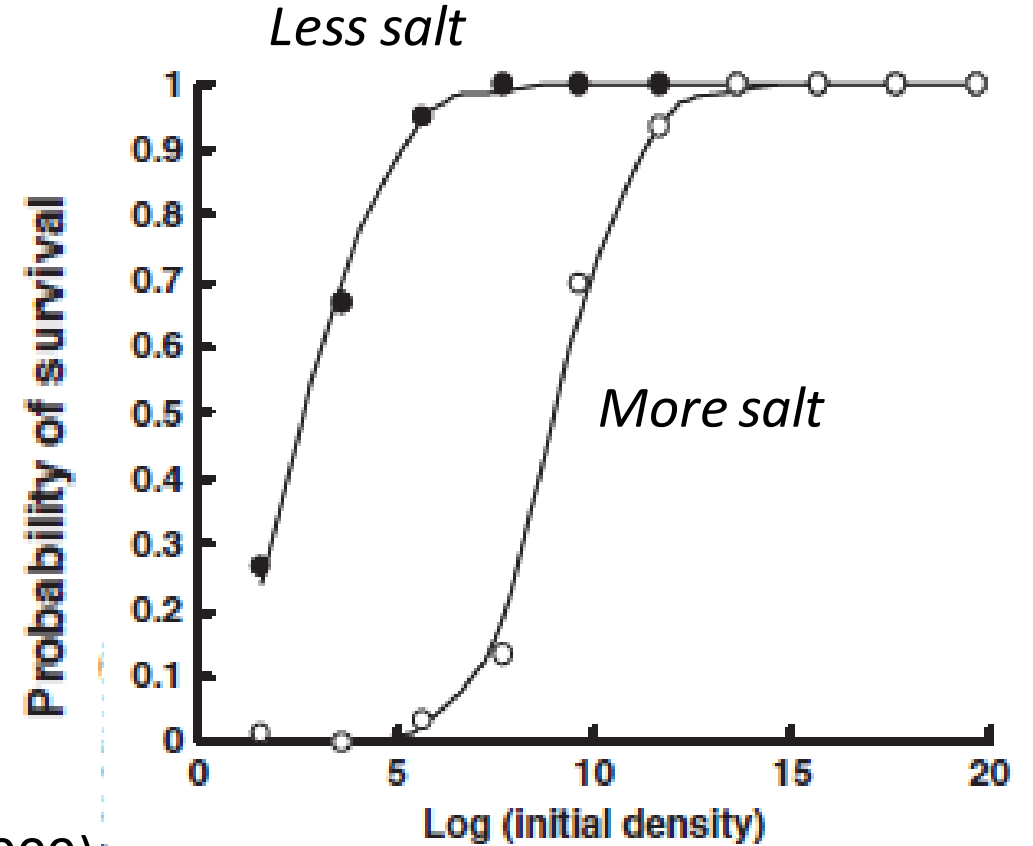
# Q4. Does adaptation allow evolutionary rescue?



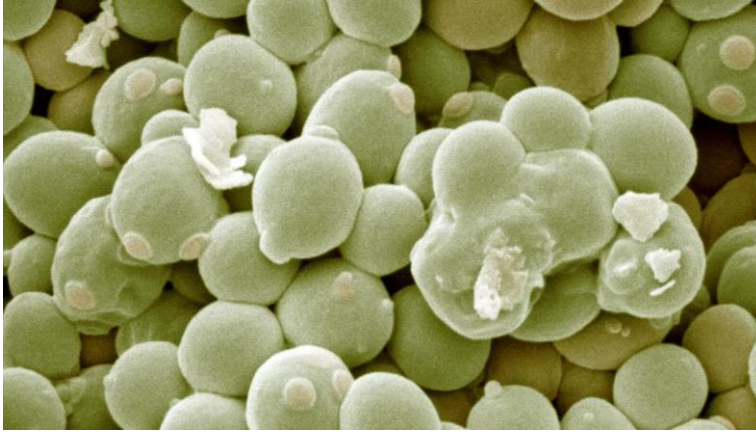
*Saccharomyces cerevisiae*



(Bell and Gonzalez 2009)



## Q4. Does adaptation allow evolutionary rescue?



*Saccharomyces cerevisiae*

- Many populations in altered environments would disappear without sufficiently rapid and effective adaptation.
- This evolutionary rescue is most likely when environmental change is small, initial population size is large, and appropriate genetic variation is high.
- These conclusions are based on theoretical models and laboratory studies, whereas we really have no idea when evolutionary rescue will or will not take place in nature.

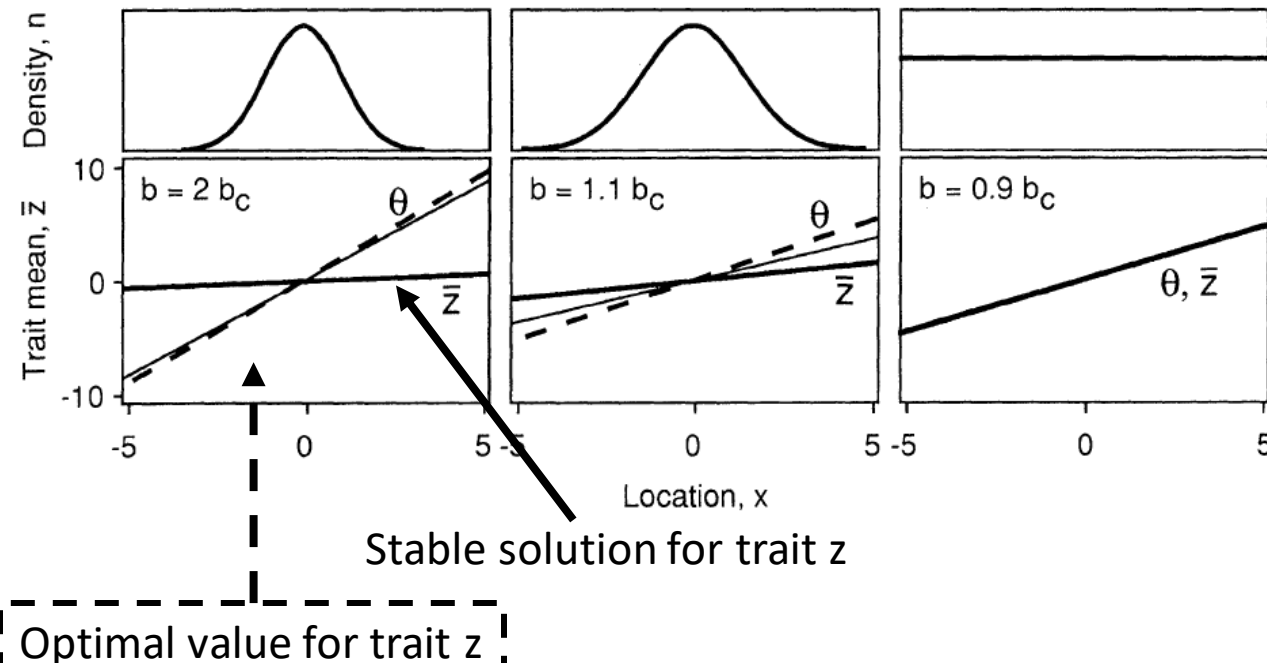
# Q5. Does adaptation aid range expansion ?



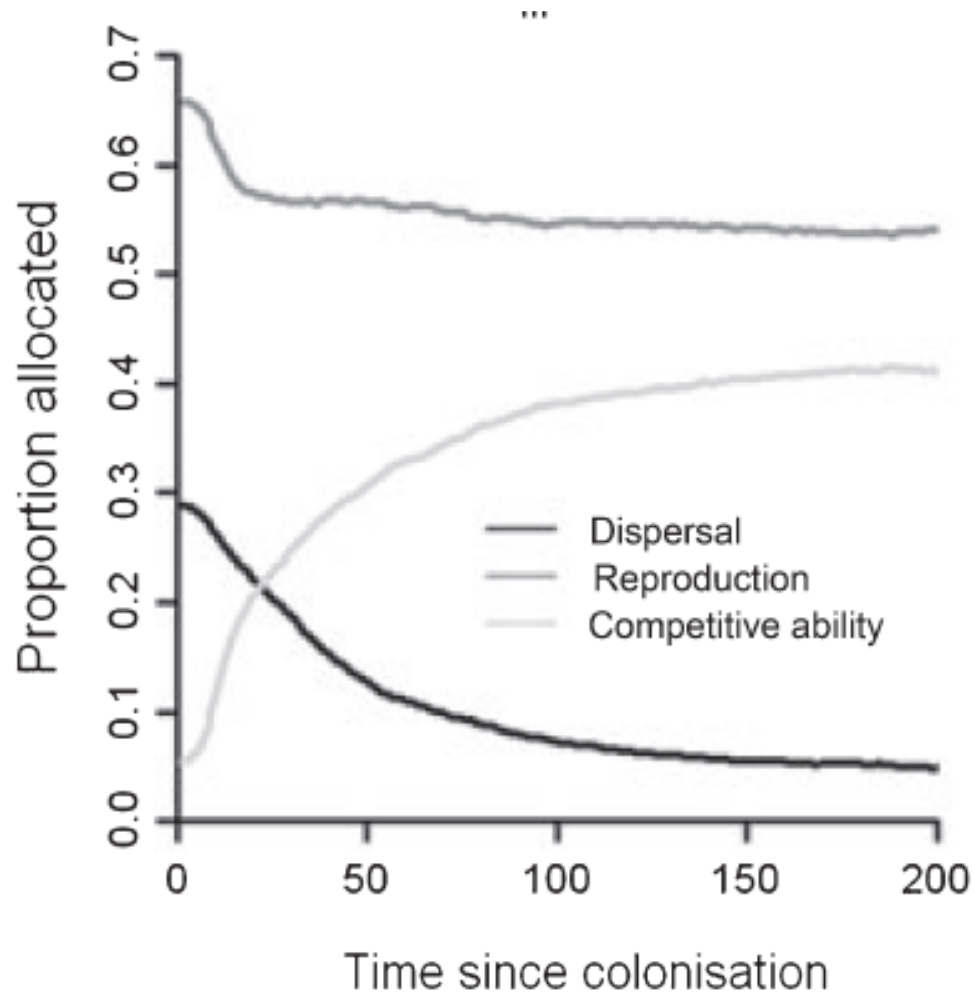
What is a species distribution range ?  
Which factors drive species distribution range ?

- **Environmental factors:** climate, habitat availability
- **Ecological interactions:** competition, predation, parasitism, mutualism
- **Anthropogenic factors**
- **Evolutionary factors**

The balance between migration, gene flow, and local adaptation determines whether a species can expand its range or remains limited to a smaller geographic area

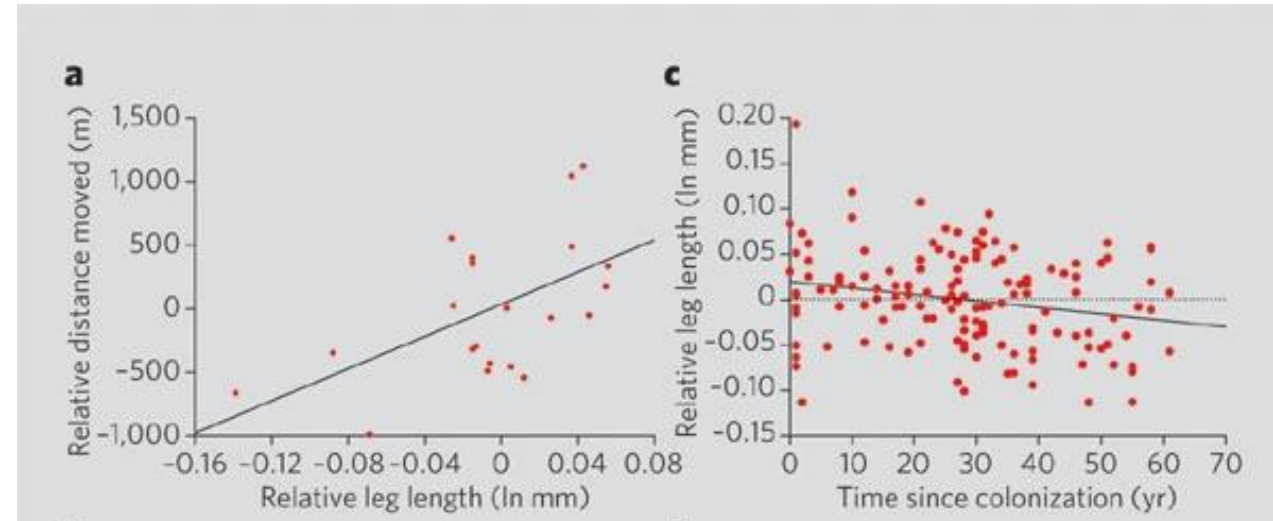
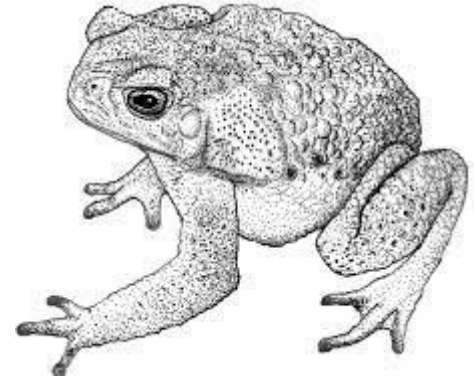


# Q5. Does adaptation aid range expansion? What can we learn from species introduction?



Burton *et al.* 2010

Cane toad, *Bufo marinus*



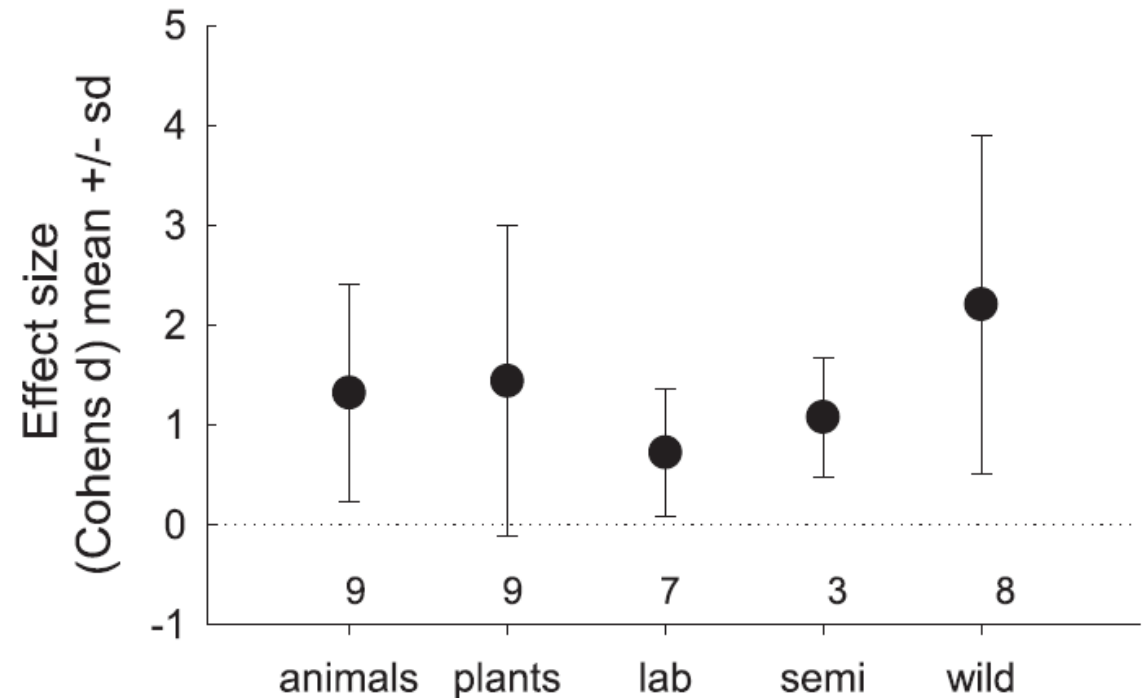
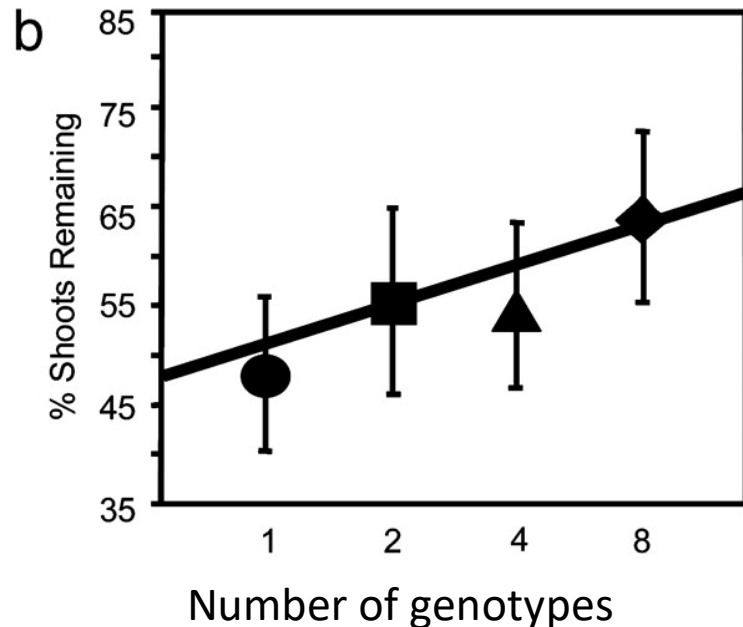
Phillips *et al.* 2006; Phillips 2009

# Q6. Does intraspecific diversity influence population dynamics ?



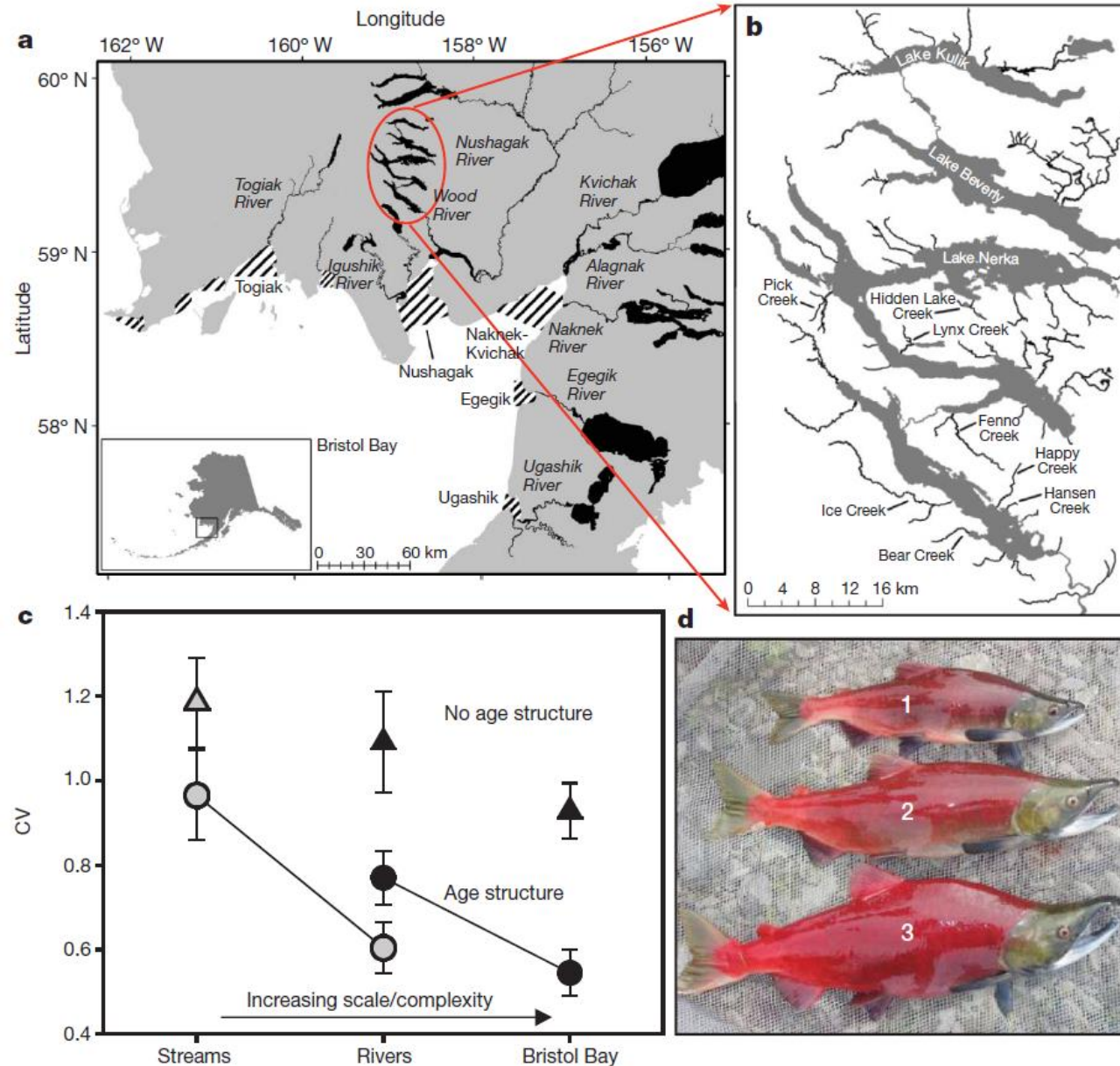
*Zoostera marina*

- ✓ In *zoostera marina*, more genetically diverse plots were more resistant to disturbance by geese (Hughes and Stachowicz 2004)
- ✓ Meta-analysis: a greater genotypic/phenotypic diversity of a founding population increases the probability of successful establishment (Forsman 2014)



# Q6. Does intraspecific diversity influence population dynamics?

Nursery lake in black



- ✓ Each year, fishery targets adult sockeye salmon returning from the open ocean to spawn in fresh water in Bristol Bay, Alaska
- ✓ High interannual variability in total returns, but it decreases with increasing spatial/temporal scale
- ✓ The size of the overall metapopulation (all fish returning to Bristol Bay) is about half as variable as would be expected if the population-specific interannual fluctuations were instead synchronized among year

➤ **Diversity among local populations within a metapopulation thus has a dramatic positive influence on reducing variation in overall population density**

(Schindler *et al.* 2010)

# *Take-home message*

- ✓ This chapter focuses on the evo-to-eco side of eco-evolutionary dynamics, exploring how evolutionary changes impact ecological processes such as population size, growth rate, and structure.
- ✓ The effects of evolutionary change on population dynamics vary based on factors like density dependence and eco-evolutionary feedback loops.
- ✓ While laboratory experiments have shown clear eco-evolutionary dynamics at the population level, evidence from natural populations remains more circumstantial.
- ✓ Maladaptation, often triggered by environmental change, leads to population declines, suggesting that evolution helps many populations maintain their abundance over time.
- ✓ Several studies have correlated population growth with evolutionary change, but direct evidence of evolutionary rescue in nature is scarce.
- ✓ Intraspecific diversity within populations plays a crucial role in traits like colonization, resistance to disturbance, and extinction risk.
- ✓ Evolution is also important for range expansion, but formal studies proving this process are still limited.

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