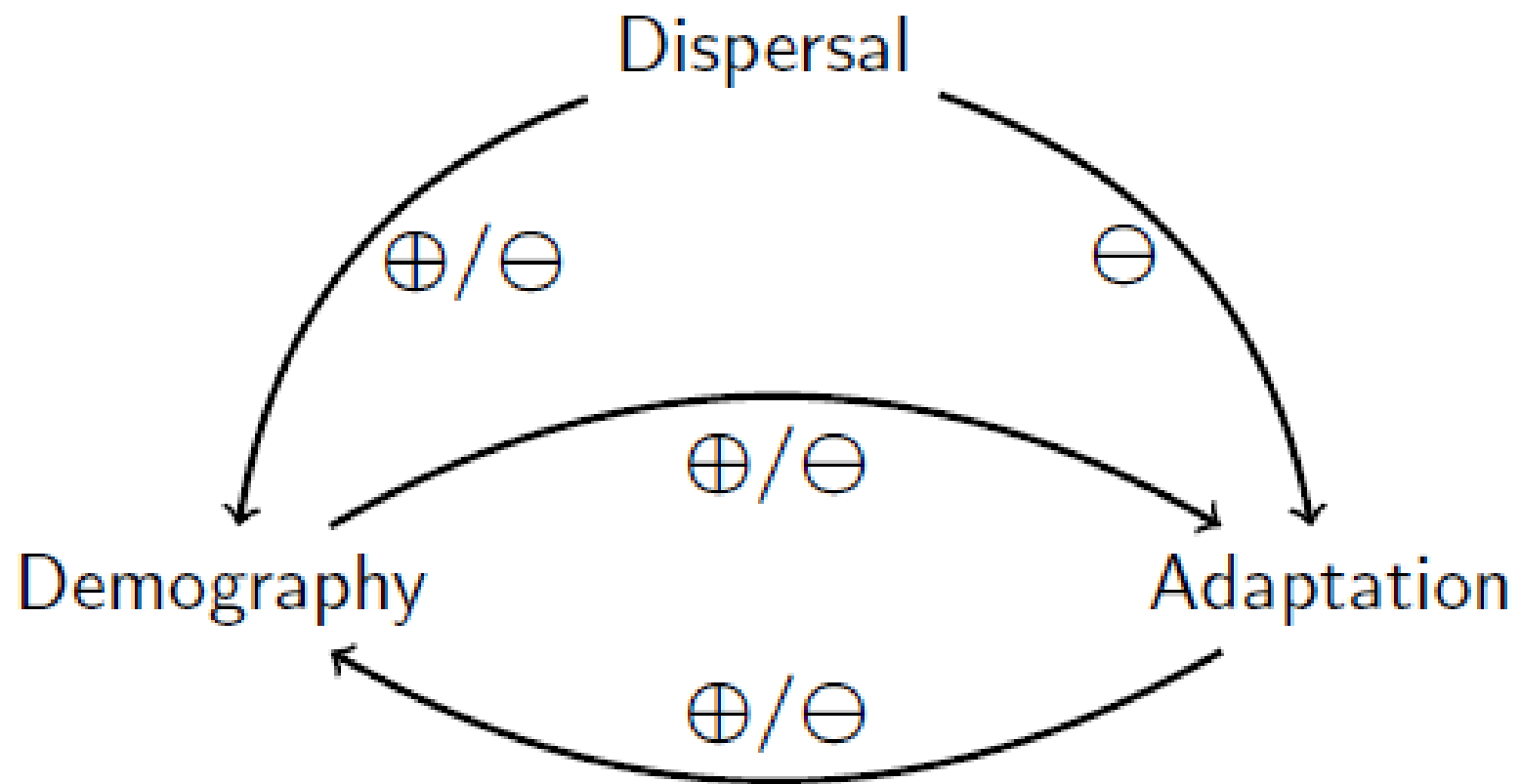




Evolution of species ecological niche and geographical range

Ophélie Ronce





Fundamental niche

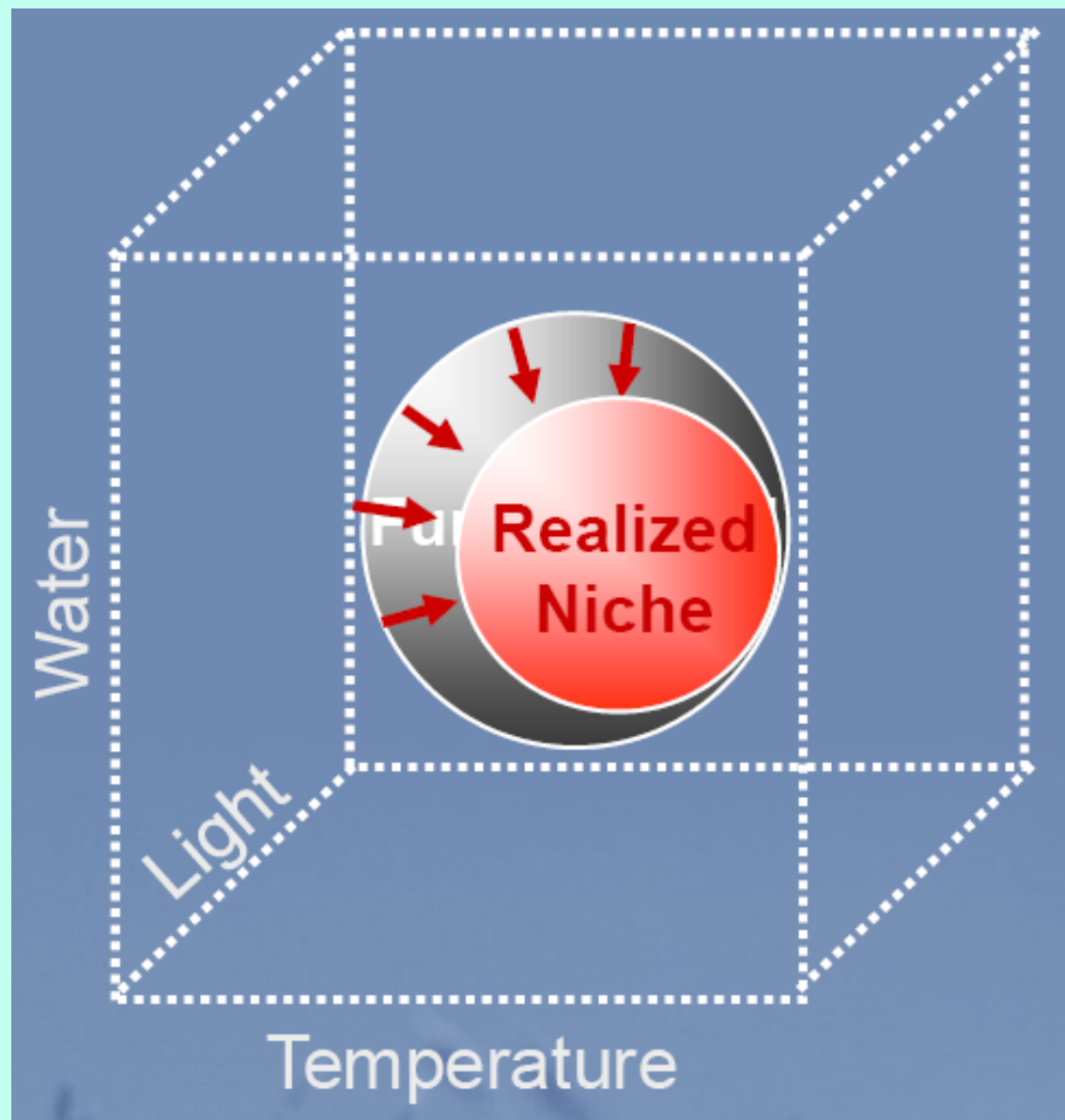
Hutchinson 1957 : the set of environmental conditions where the species can persist

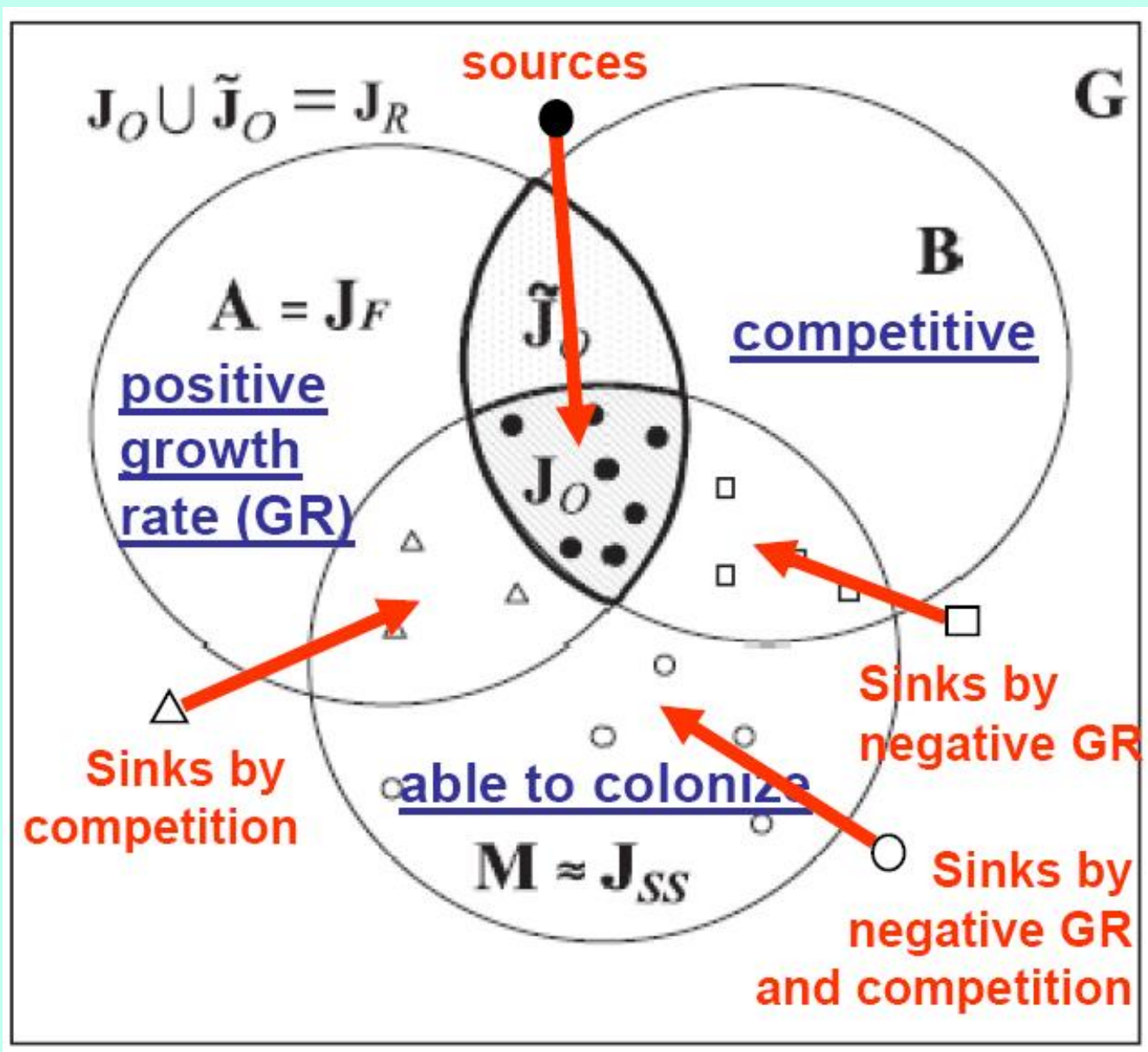
Realized niche:

Hutchinson 1957 : the set of environmental conditions where the species is found.

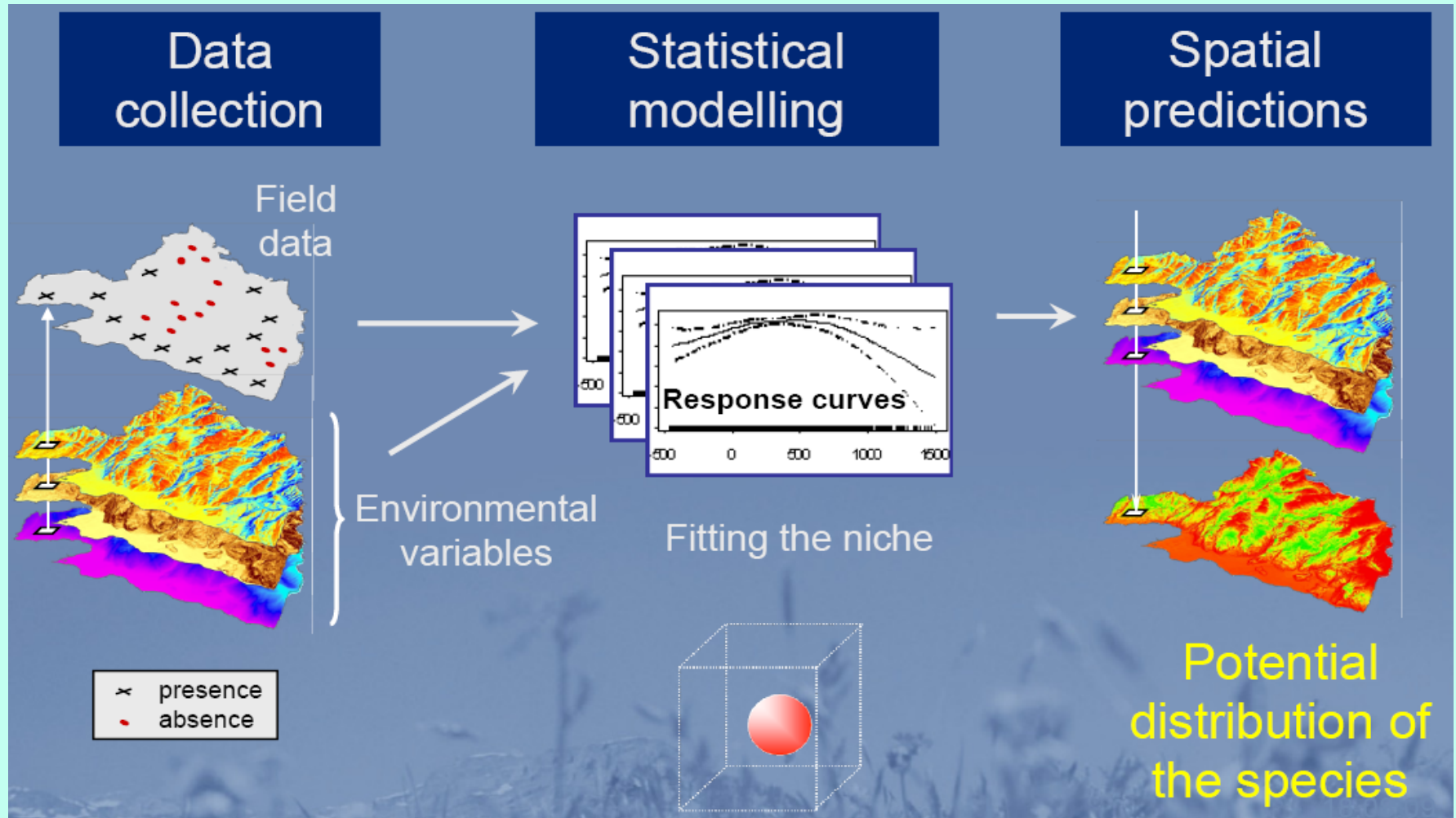
Geographical range:

The set of geographical localities where the species is found



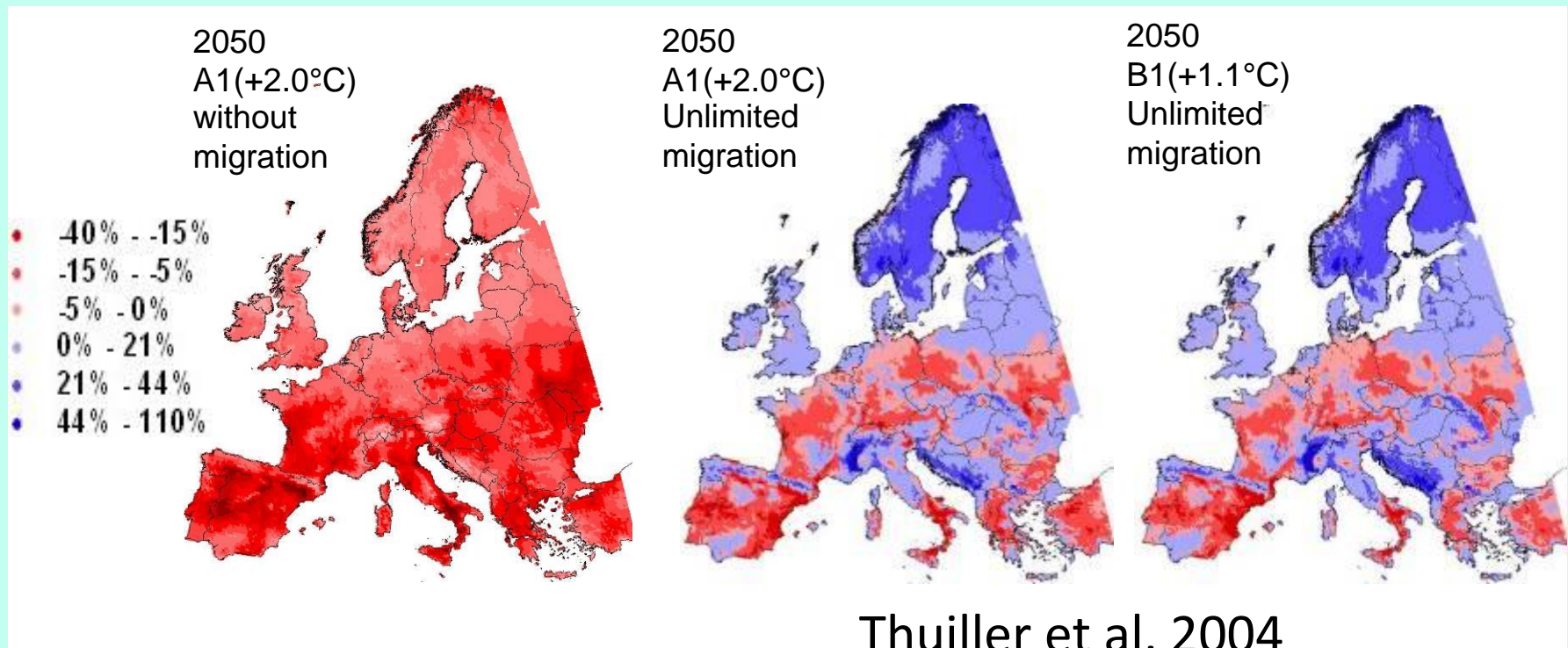


Species Distribution Models (SDM)



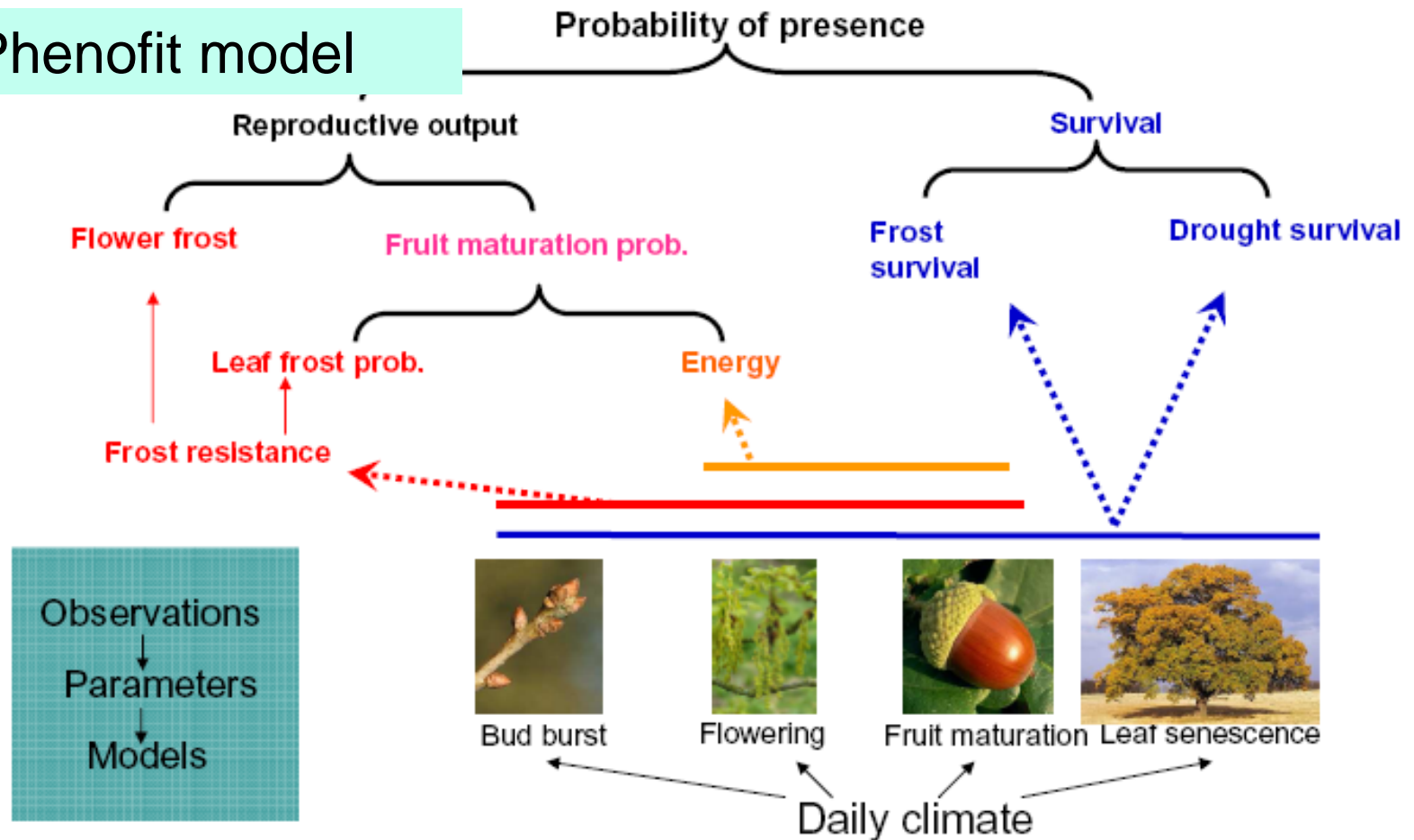
Scenarios for future biodiversity under climate change

- Forecasted biodiversity loss for Europe in 2050



Phenology as a major determinant of species range

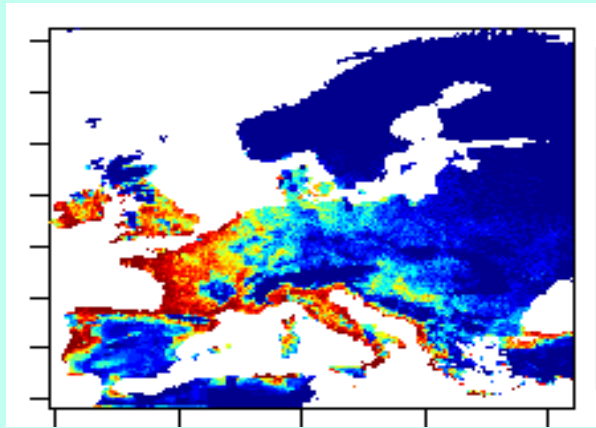
Phenofit model



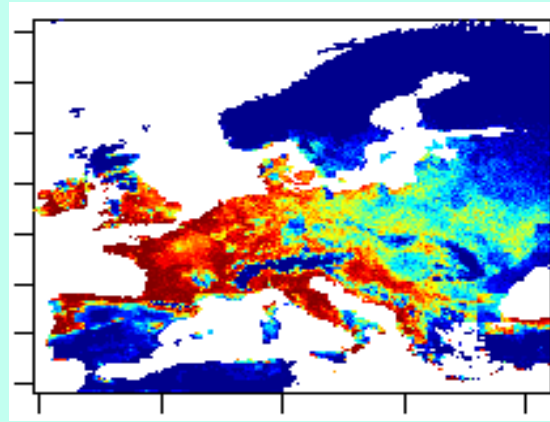
Phenology as a major determinant of species range

Phenofit model

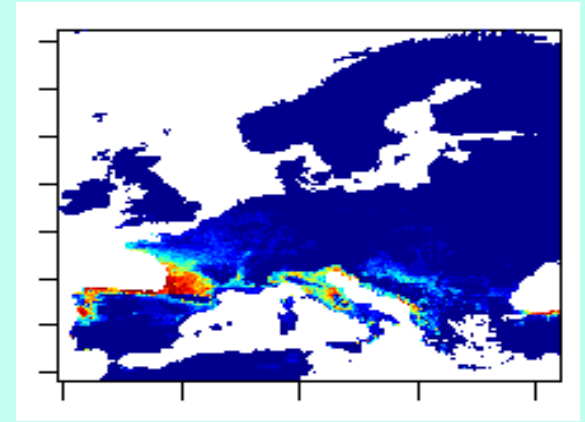
We fix bud burst date and compute average reproductive success in each location



60 days



100 days



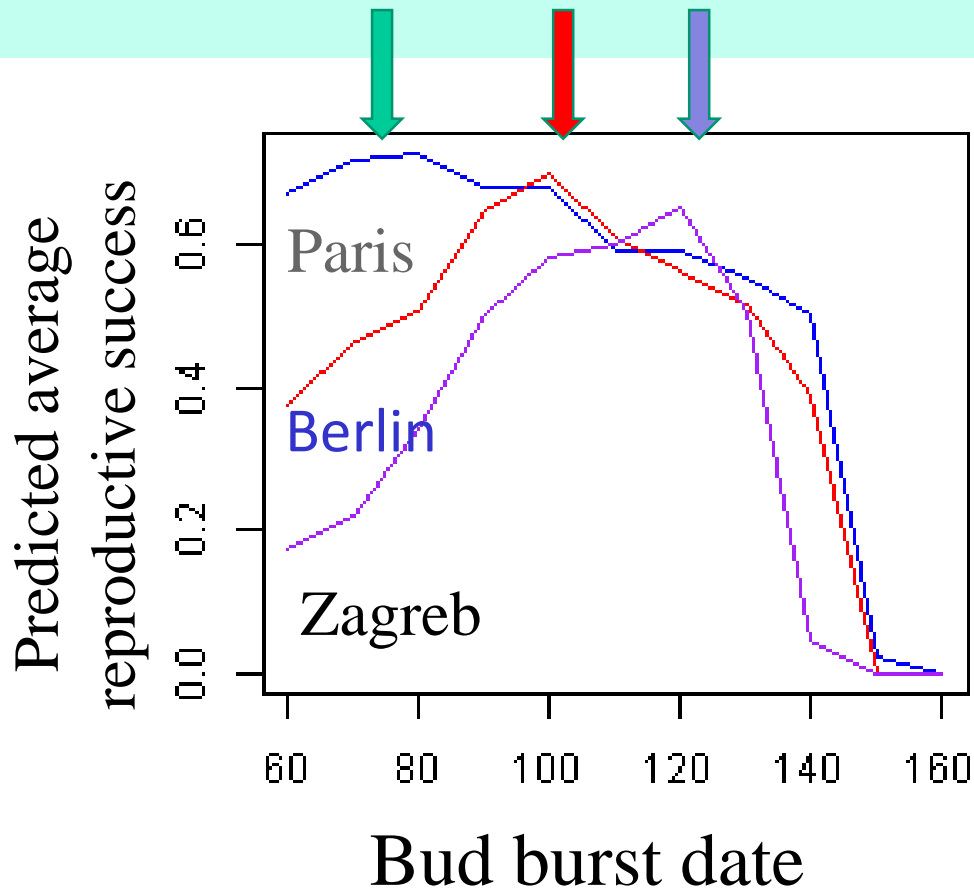
150 days

1981-2000

Quercus petraea

Selection on phenology

1981-2000

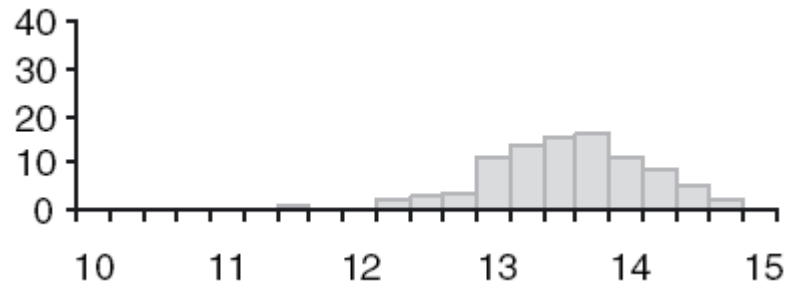


Quercus petraea

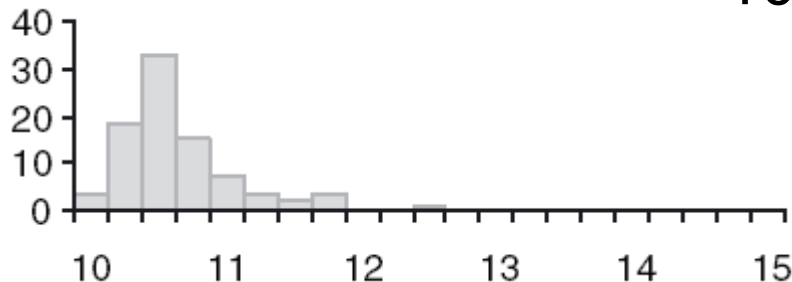
Phenology can evolve fast

Artificial selection

Van Dijk &
Hautekee 2007



10 generations



Number of daylight hours necessary
to trigger flowering

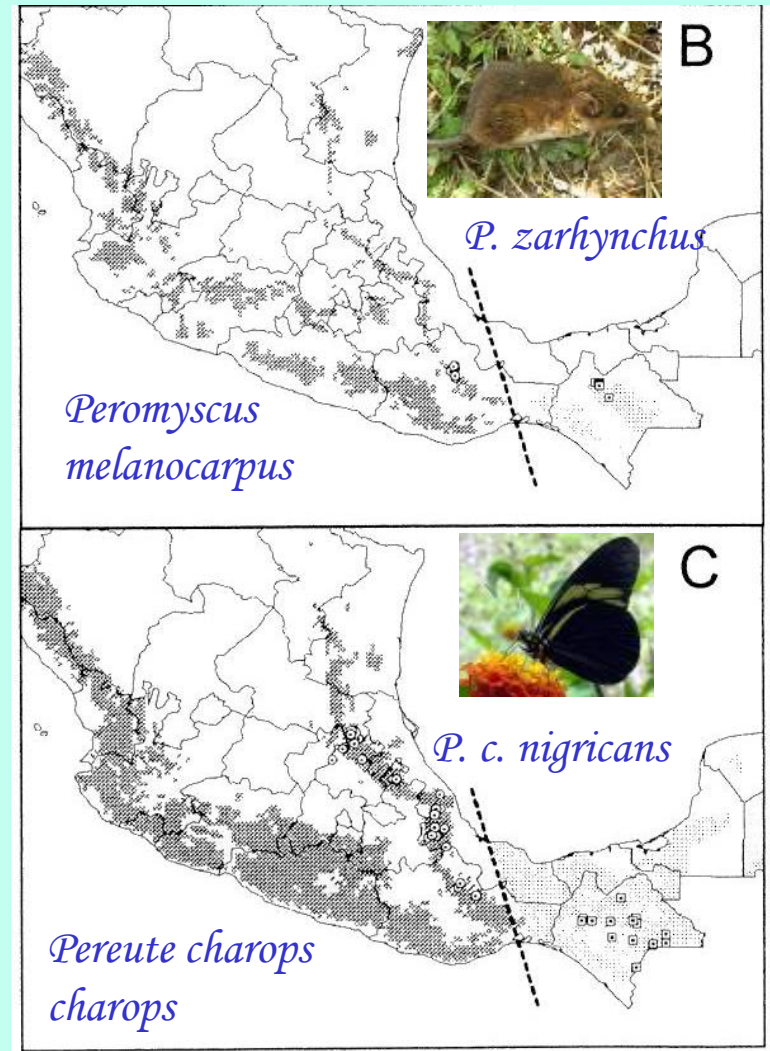
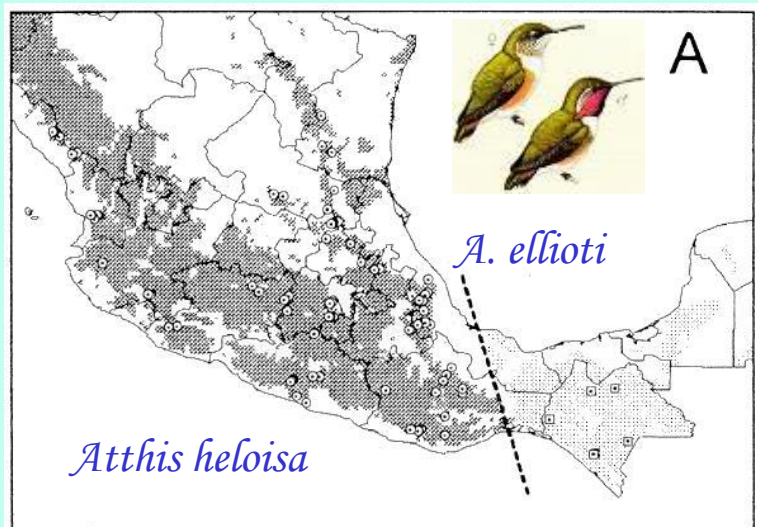


$$h^2 = \frac{\sigma_g^2}{\sigma_p^2} = 0.56$$

Evidence for niche conservatism

Peterson et al. 2002

37 pairs of sister species having diverged for 2-10 millions years on each side of Tehuantepec isthma, Mexico



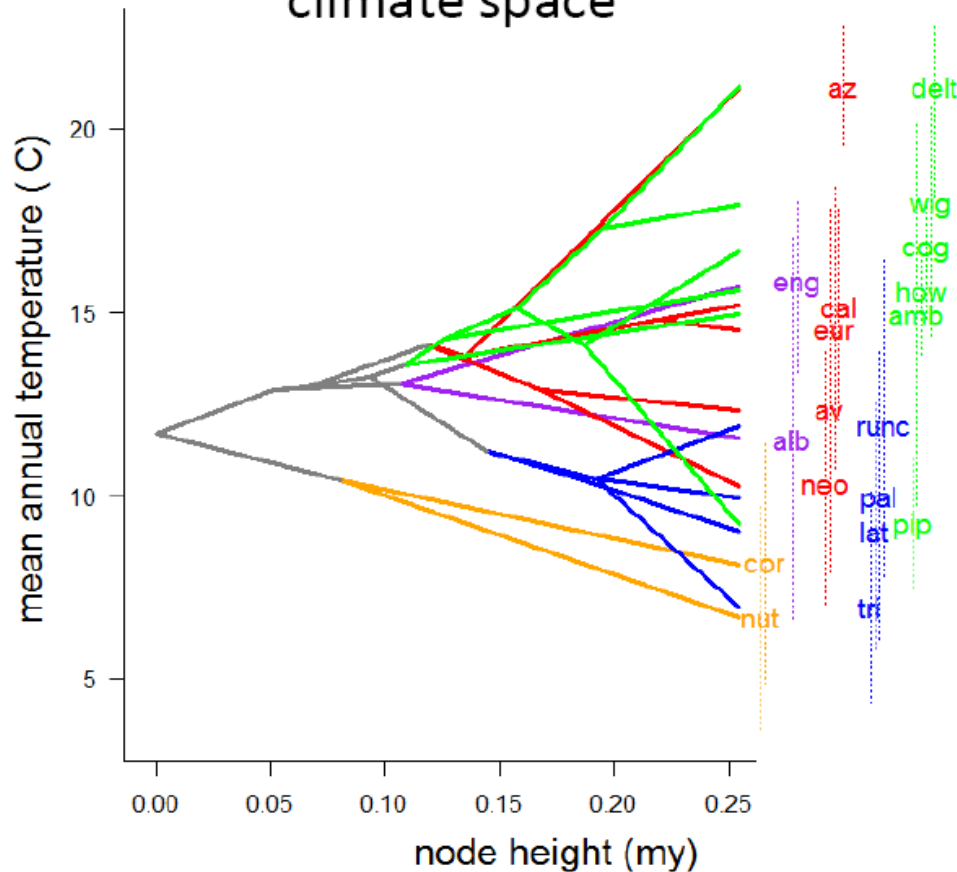
Niche evolution



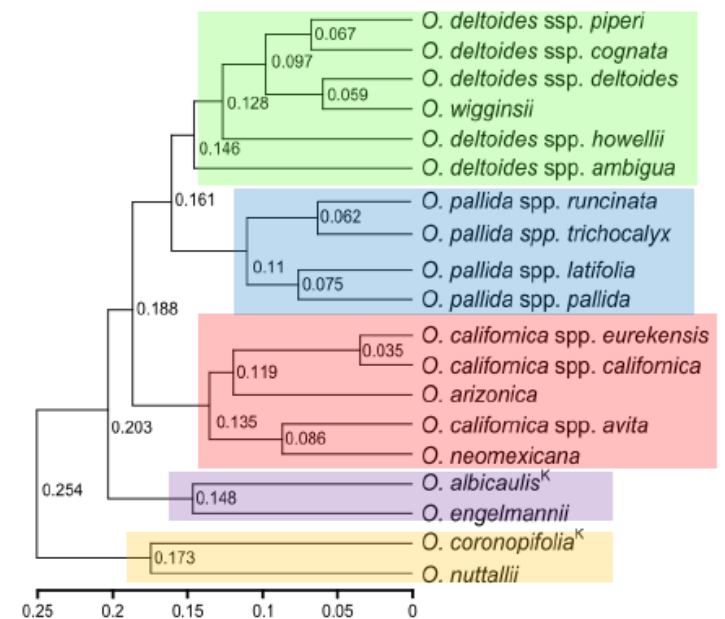
Oenothera

19 taxa, Western
North America

phylogeny in
climate space



phylogeny



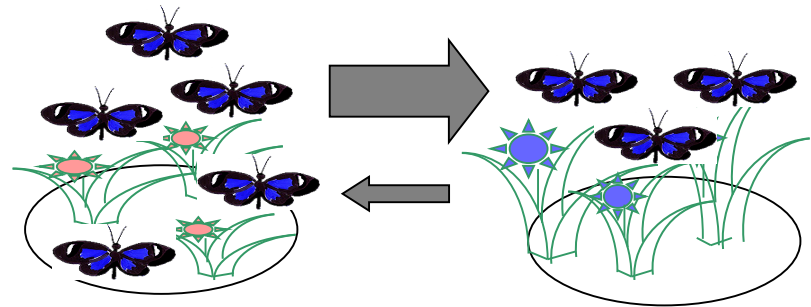
Rapid shifts in host use and source-sink dynamics



*Euphydryas
editha*

Singer and
Thomas
1996,
Boughton
1999

1979-1989:



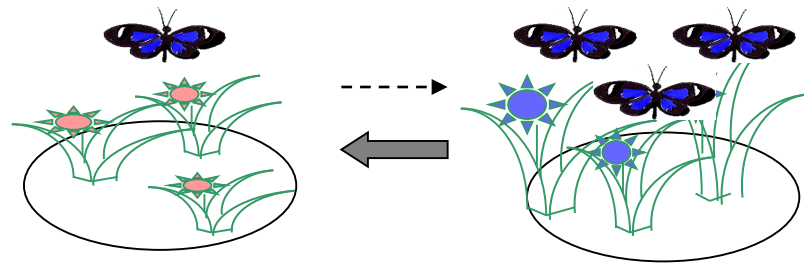
Collinsia

Pedicularis

1989-1992:

extinction on *Collinsia*

1992-1997:



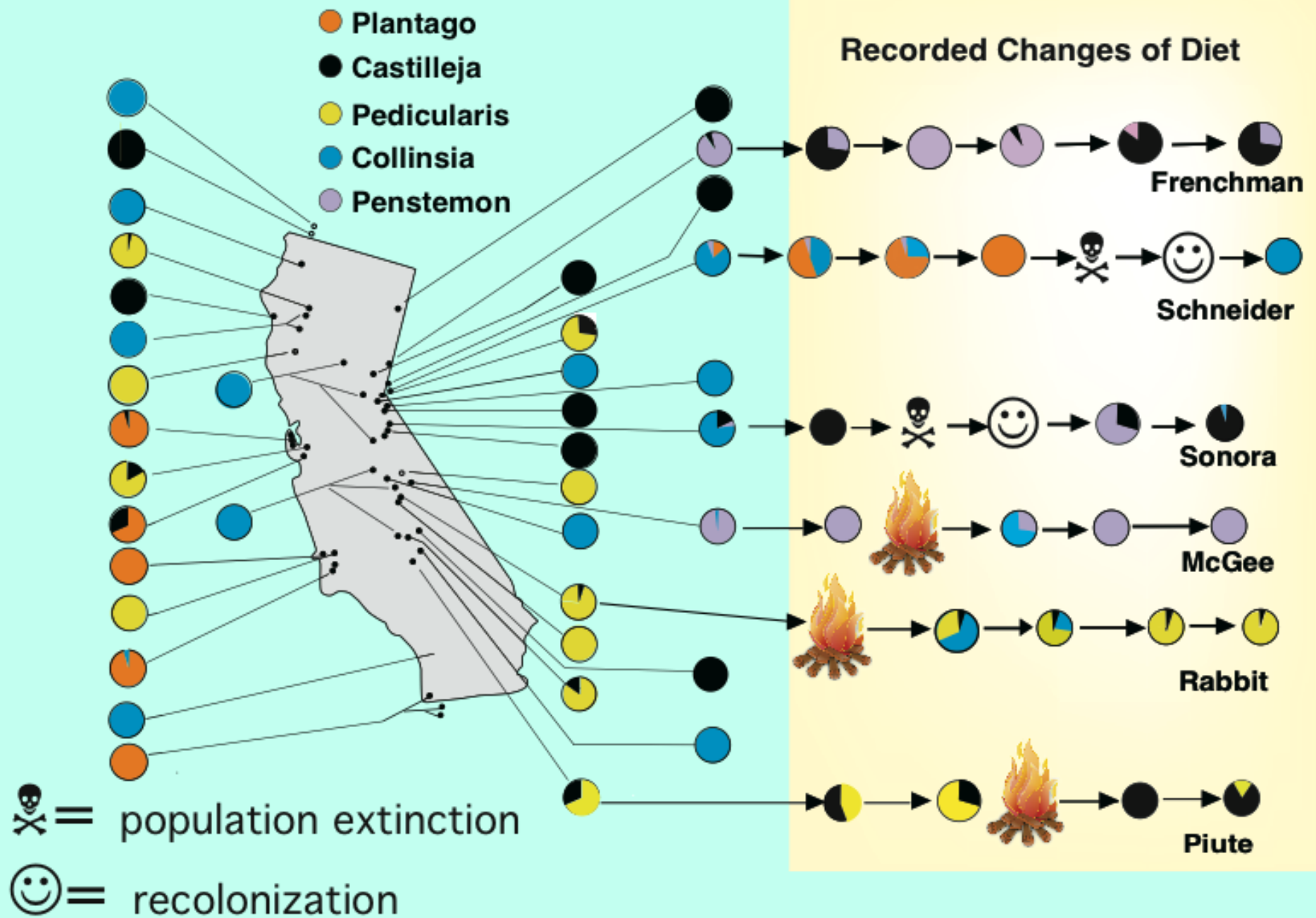
Collinsia

Pedicularis

Rapid shifts in host use



Mike C. Singer



Theoretical questions

What rules the evolution of ecological specialization/ ecological niche?

When can we expect shifts in source-sink dynamics?

What are the evolutionary consequences of such shifts?

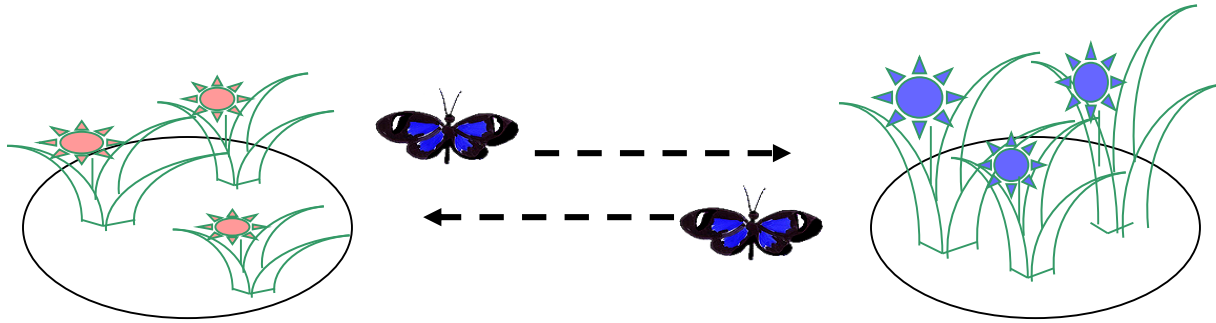
Migrational meltdown in an heterogeneous environment



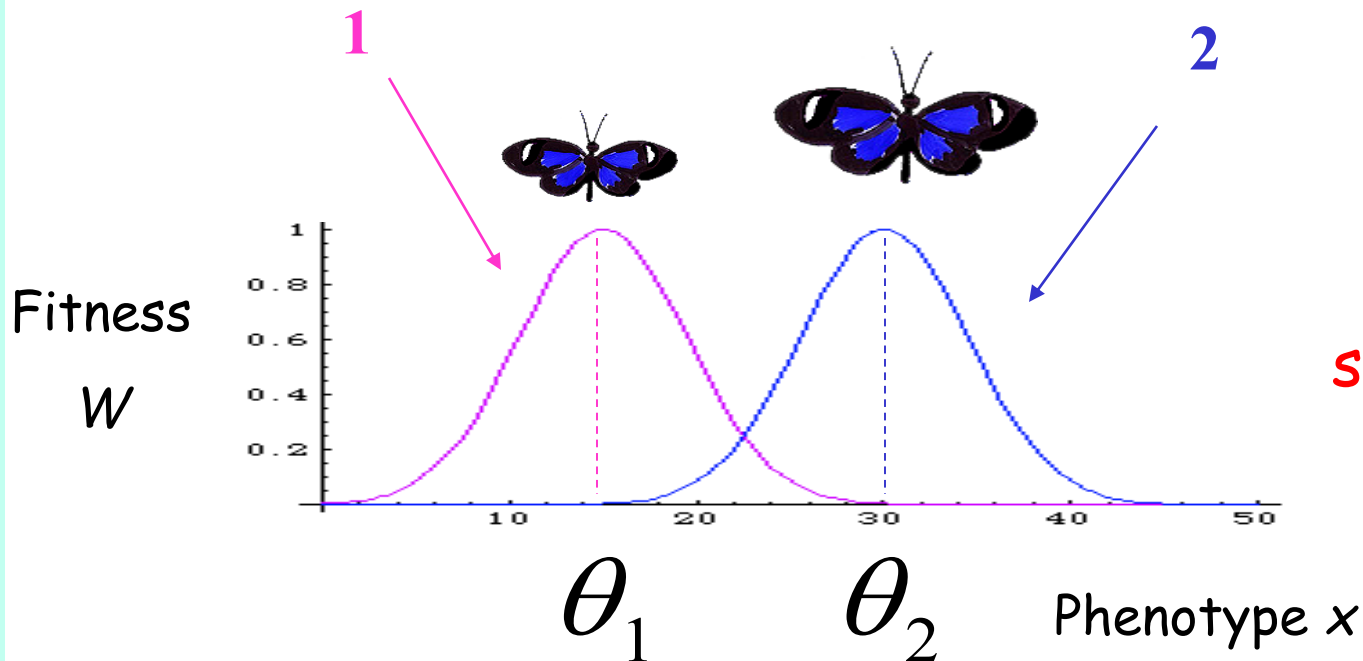
*Ronce and
Kirkpatrick,
Evolution 2000*



A quantitative genetics model



Symmetric
movement rates
between host
plants



Stabilizing
selection within
host plants

Assumptions of the quantitative genetic model

Constant genetic variance

Gaussian distribution of phenotypes

/ Hypergeometric model

n equivalent loci

Selection after recombination

The dynamical variables:

Density N_1

Maladaptation $Z_1 = \frac{\theta_1 - \bar{x}_1}{\sigma_g}$

optimum θ_1

mean phenotype \bar{x}_1

genetic standard deviation σ_g

The parameters:

Habitat heterogeneity

$$H = \frac{\theta_1 - \theta_2}{\sigma_g}$$

Movement rate

$$M$$

Intensity of stabilizing selection Γ

Feed-backs between demography and adaptation

1) Population growth depends on maladaptation

$$\frac{dN_1}{dT} = M(N_2 - N_1) + \left(1 - N_1 - \frac{\Gamma}{2} Z_1^2 \right) N_1$$

migration

local growth

2) Gene flow depends on relative population sizes

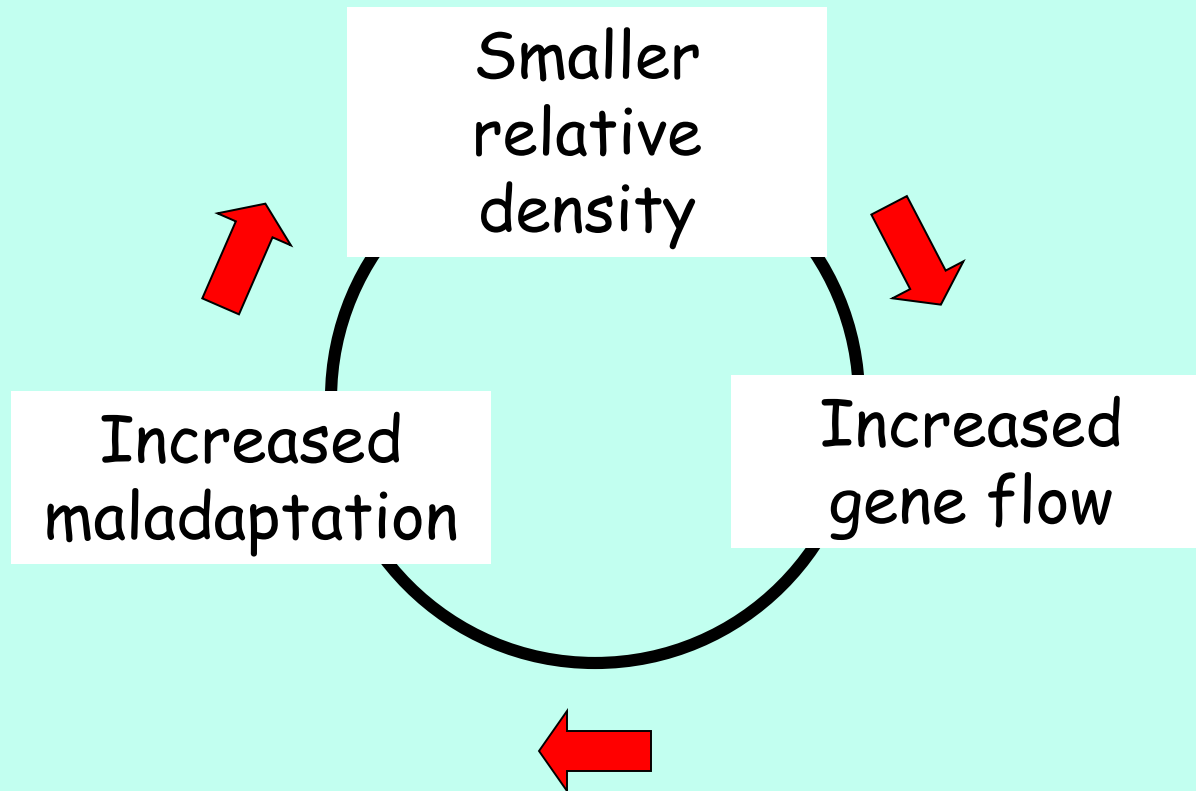
$$\frac{dZ_1}{dT} = M \frac{N_2}{N_1} (H + Z_2 - Z_1) - \Gamma Z_1$$

migration

local selection

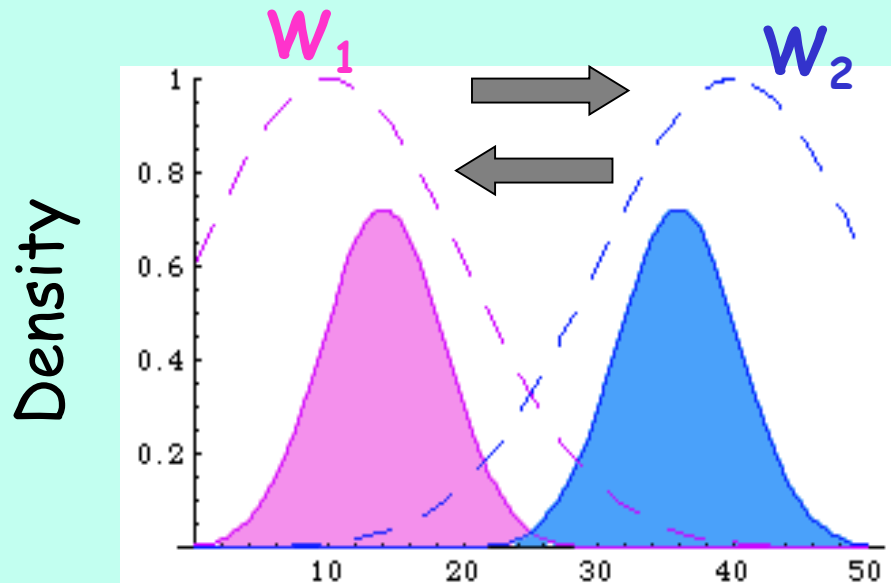
Feed-backs between demography and adaptation

An evolutionary trap for smaller populations



Several outcomes for the joint evolution of maladaptation and population size

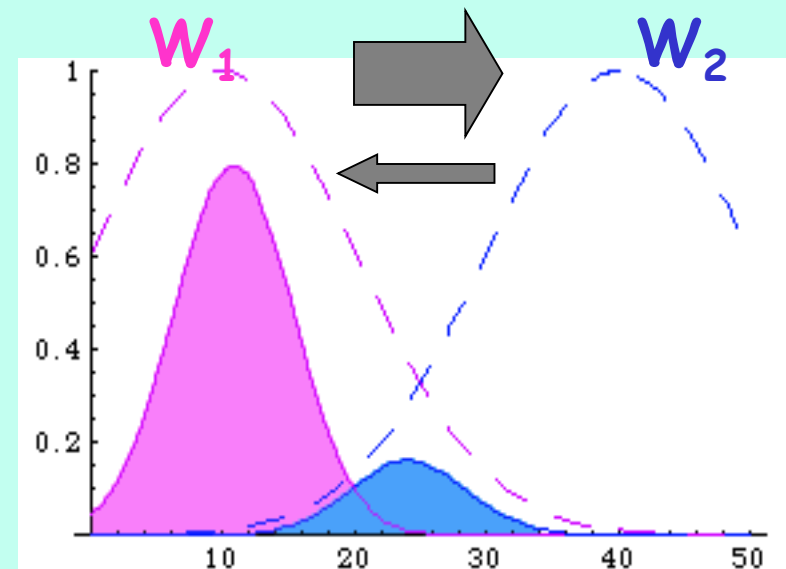
A symmetric equilibrium



generalist

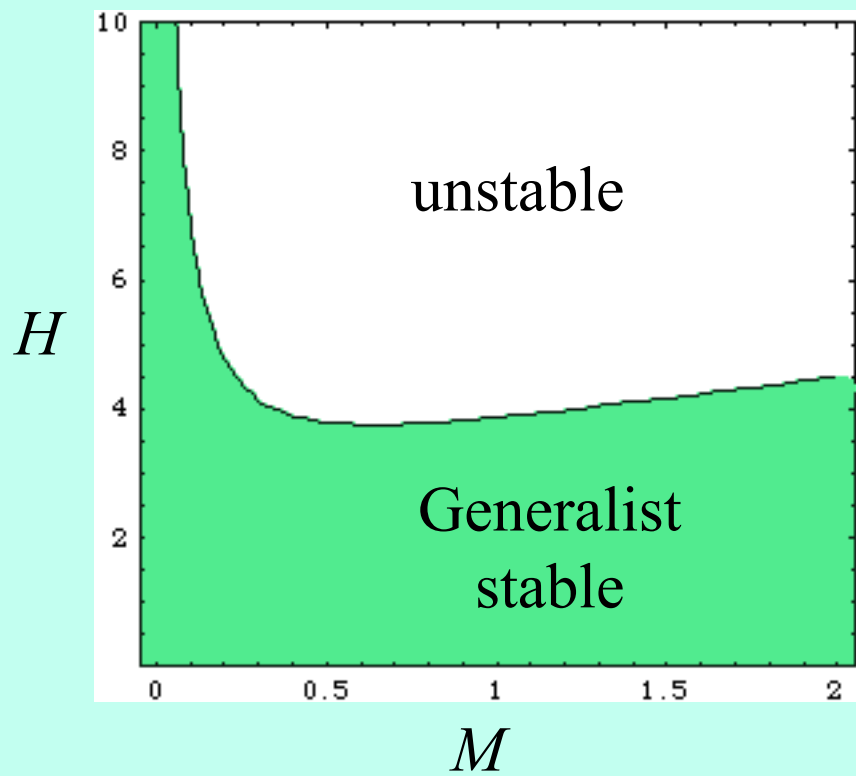
Phenotype

Two asymmetric equilibria

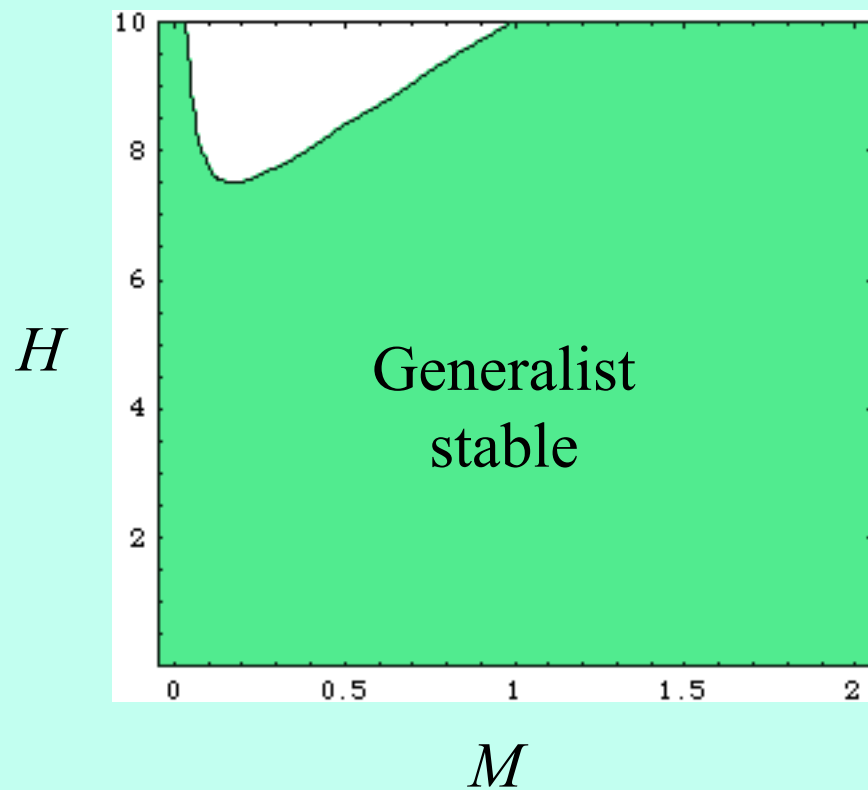


specialists

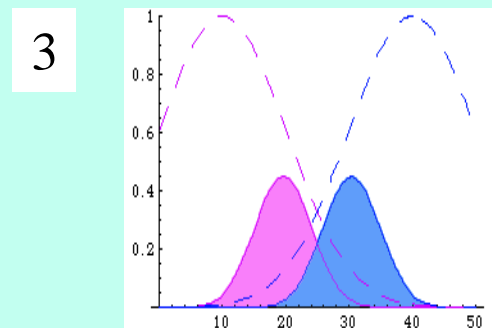
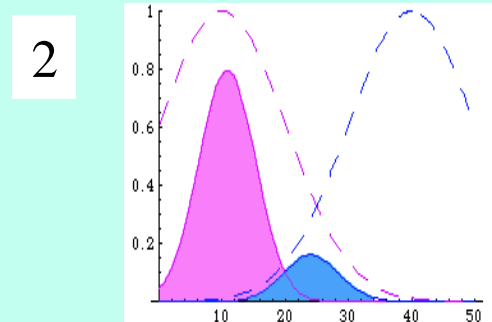
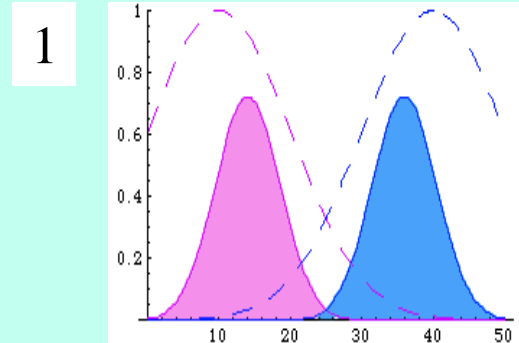
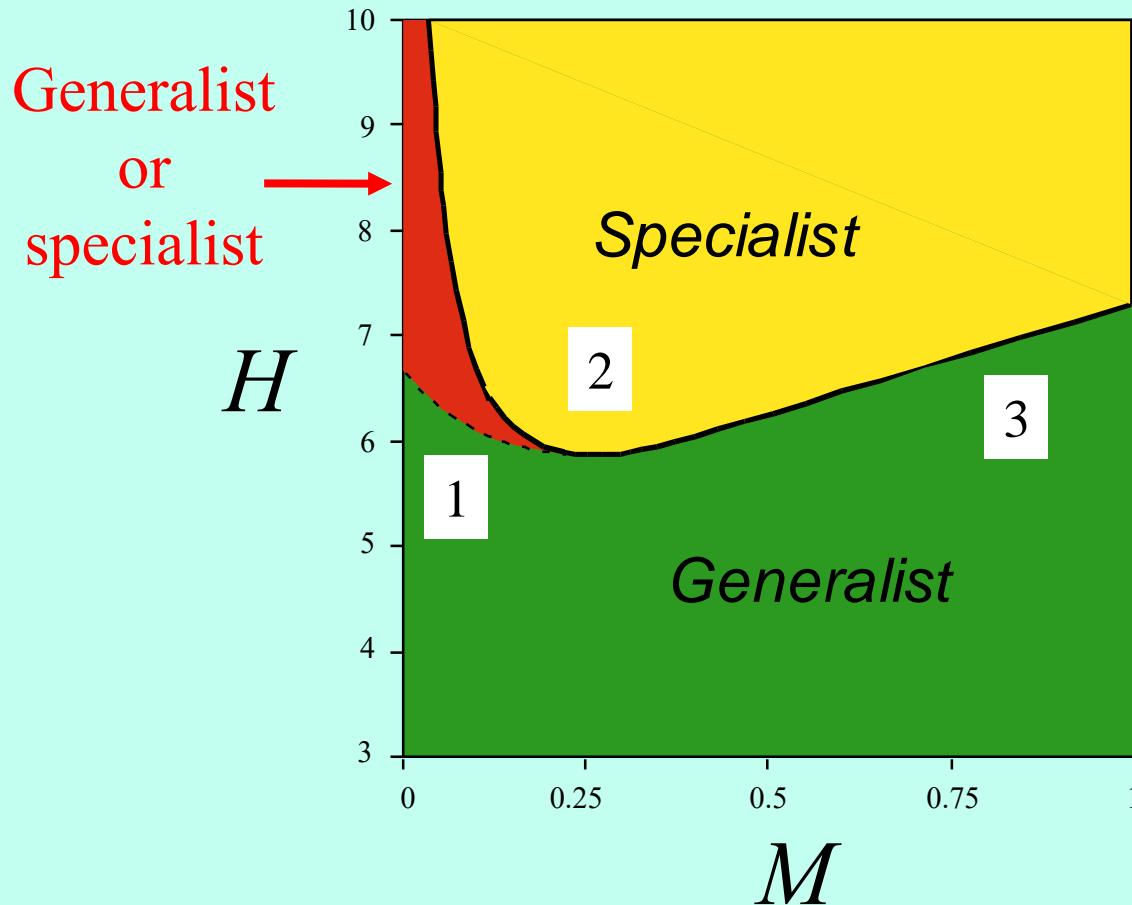
$$\Gamma = 0.5$$



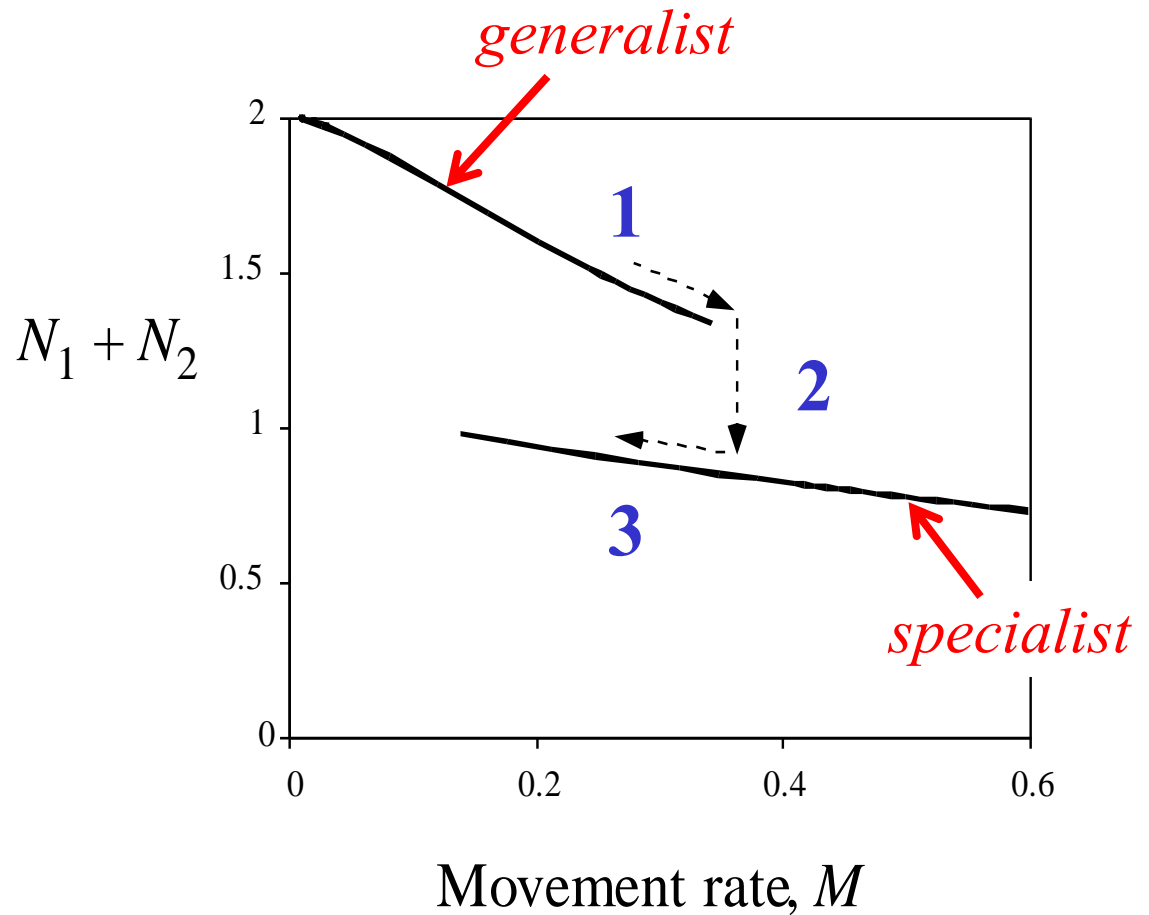
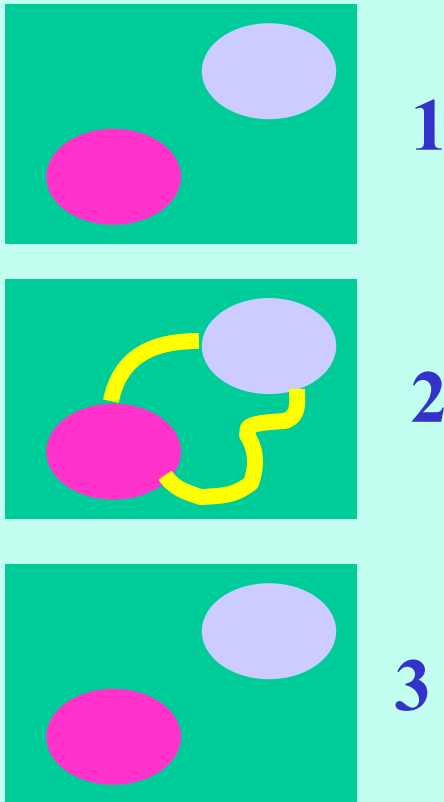
$$\Gamma = 0.05$$



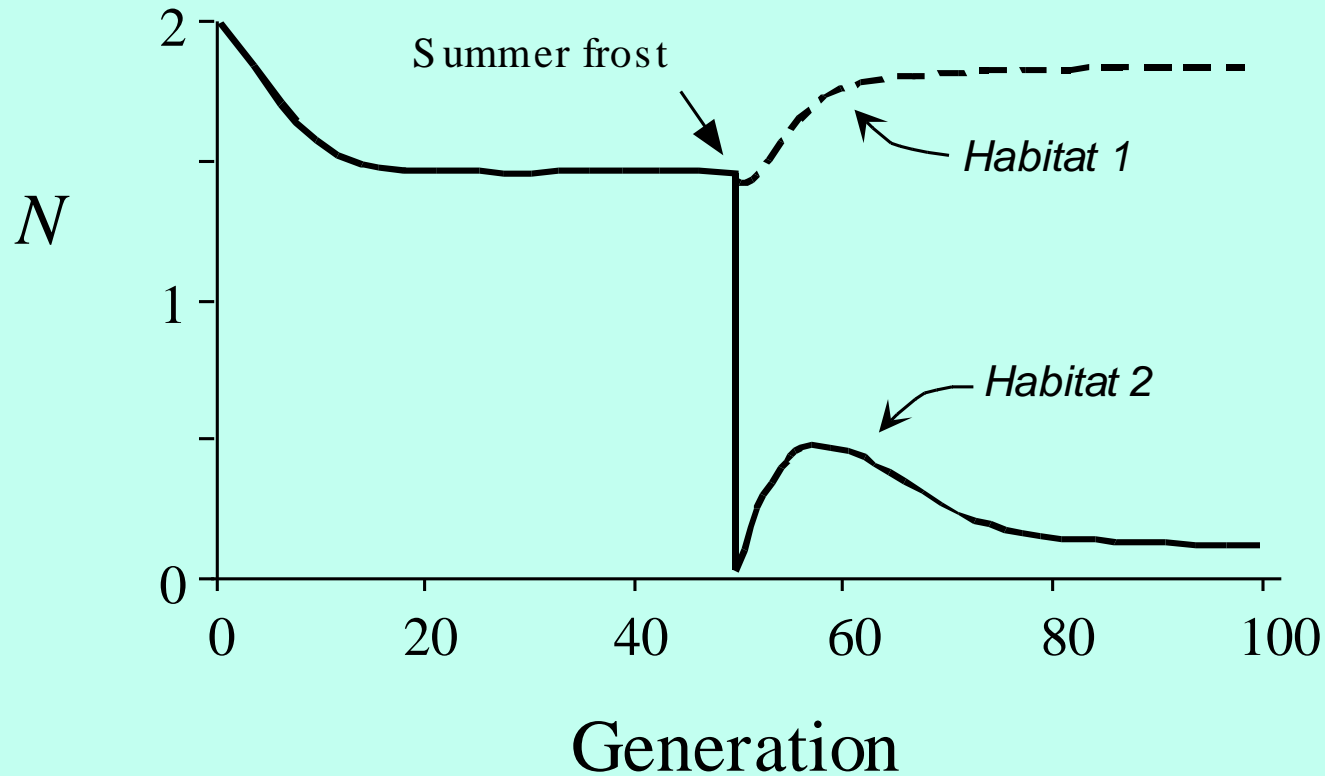
Stability of the different equilibria



Irreversible consequences of transient changes in the landscape



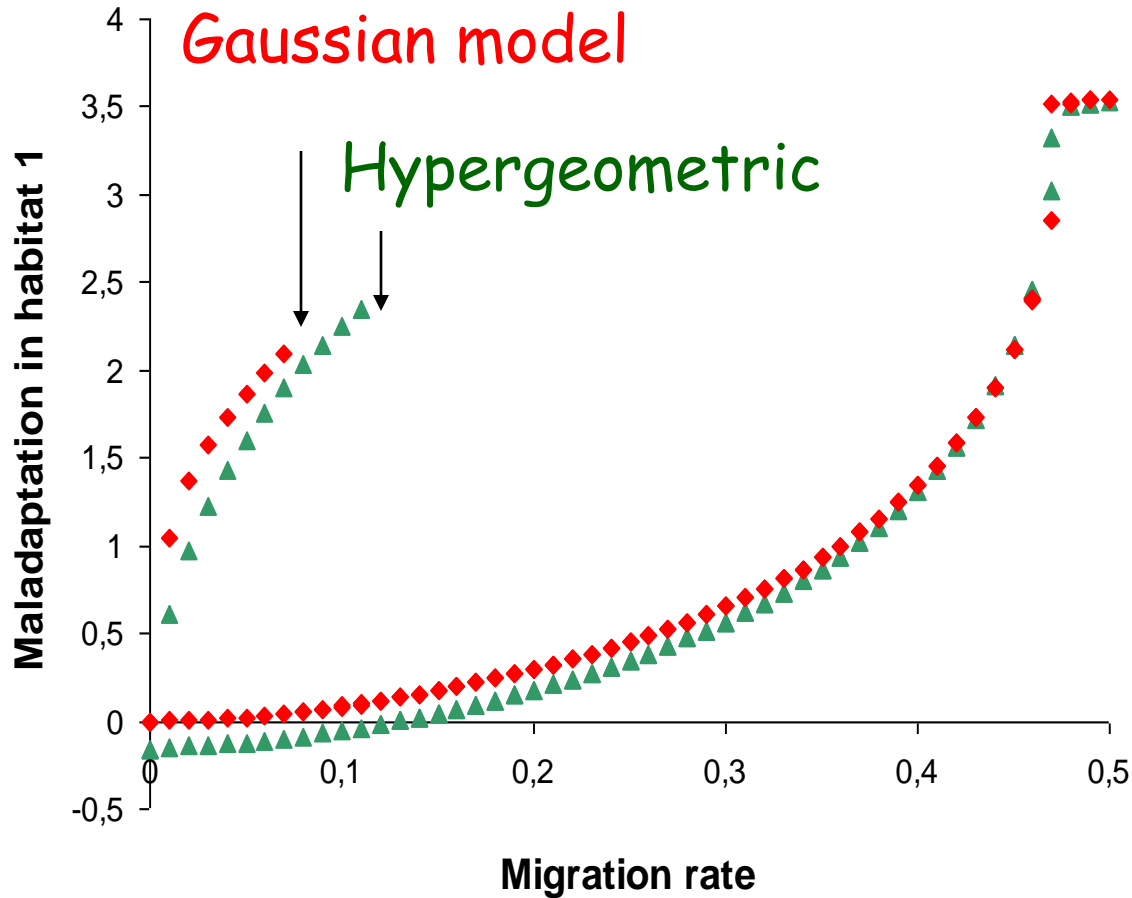
Effect of demographic disturbances



balanced

Source - Sink

Checking on our assumptions



30 equivalent loci

Free
recombination

Selection after
recombination

Conclusions

Generalist : Low habitat heterogeneity
 Weak selection
 Low or high movement rates

Specialist : Strong habitat heterogeneity
 Strong selection
 Intermediate movement rates

Kawecki 2000 (single locus)

Meszéna et al. 1997 (clonal)

Conclusions

When is specialization a labile trait?

Multiple equilibria

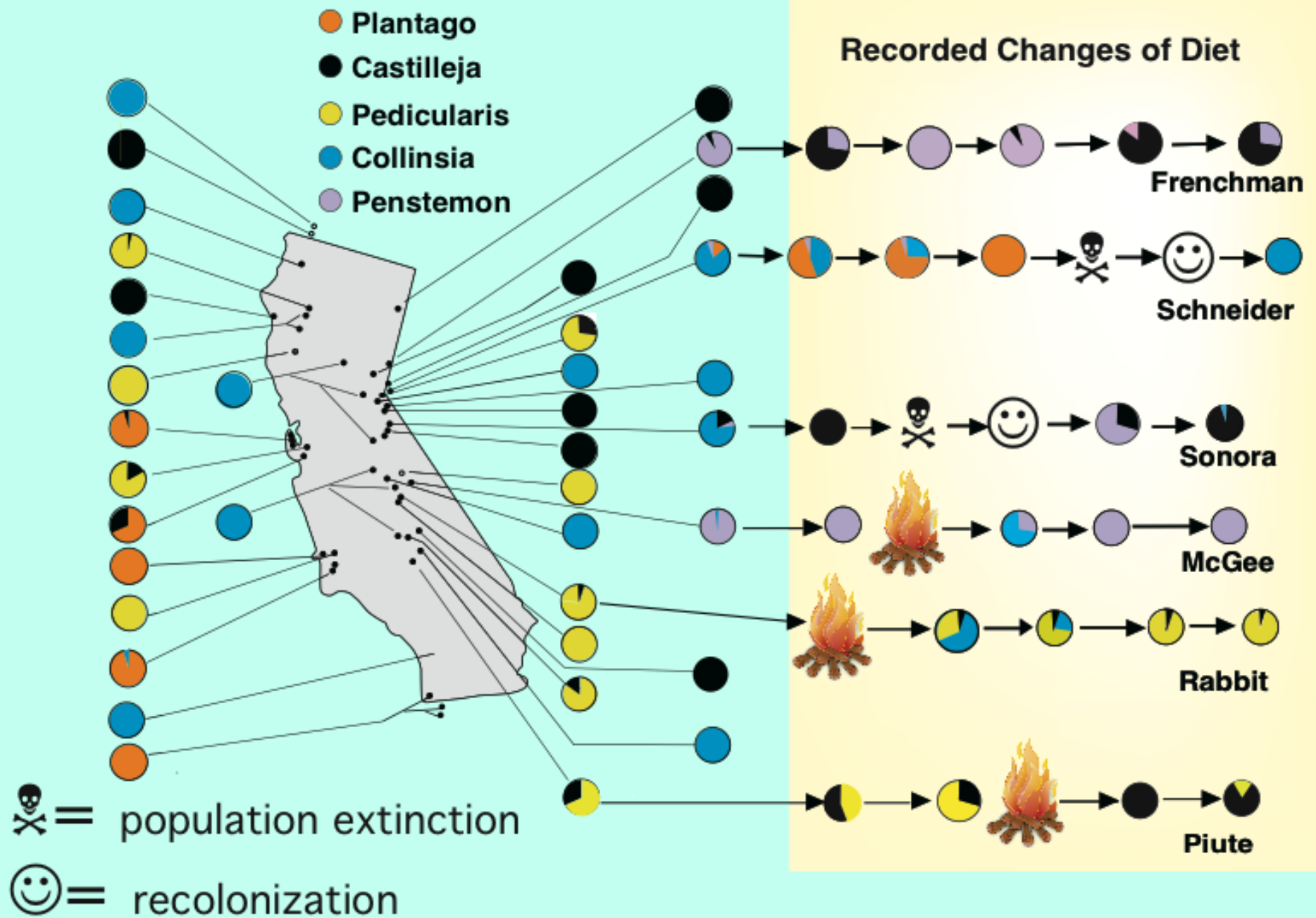


Historical factors
& Disturbances

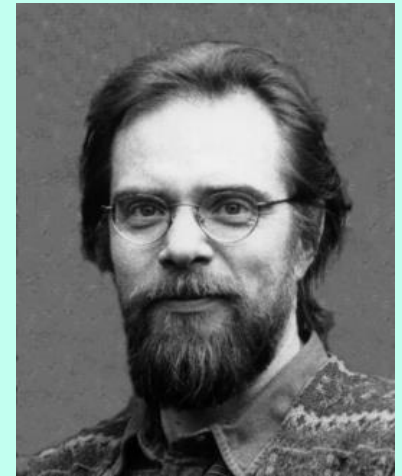


Geographical variation in host use

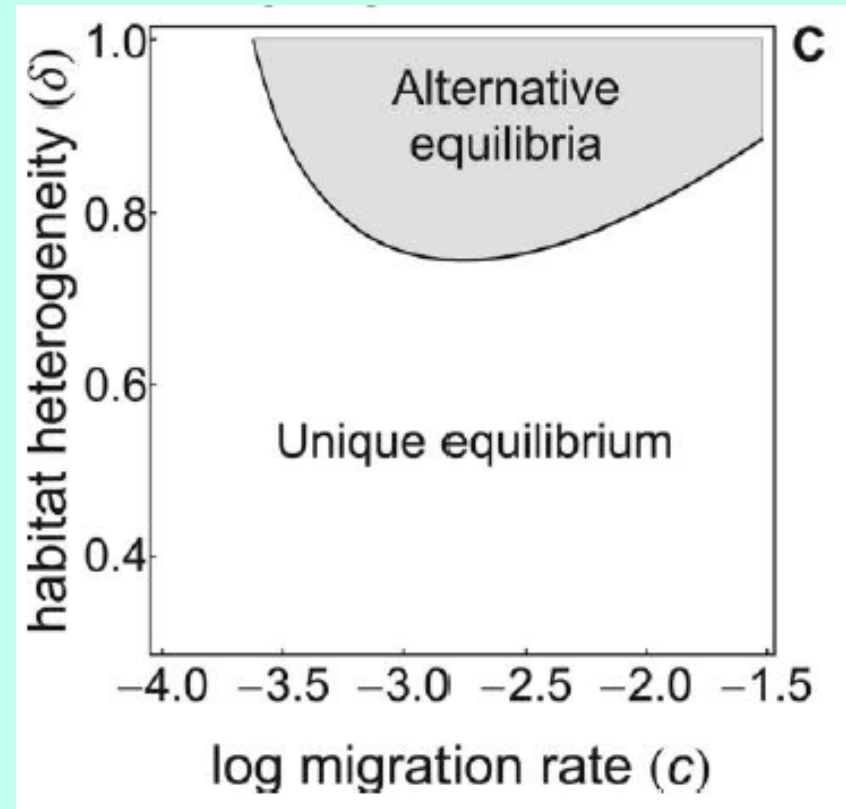
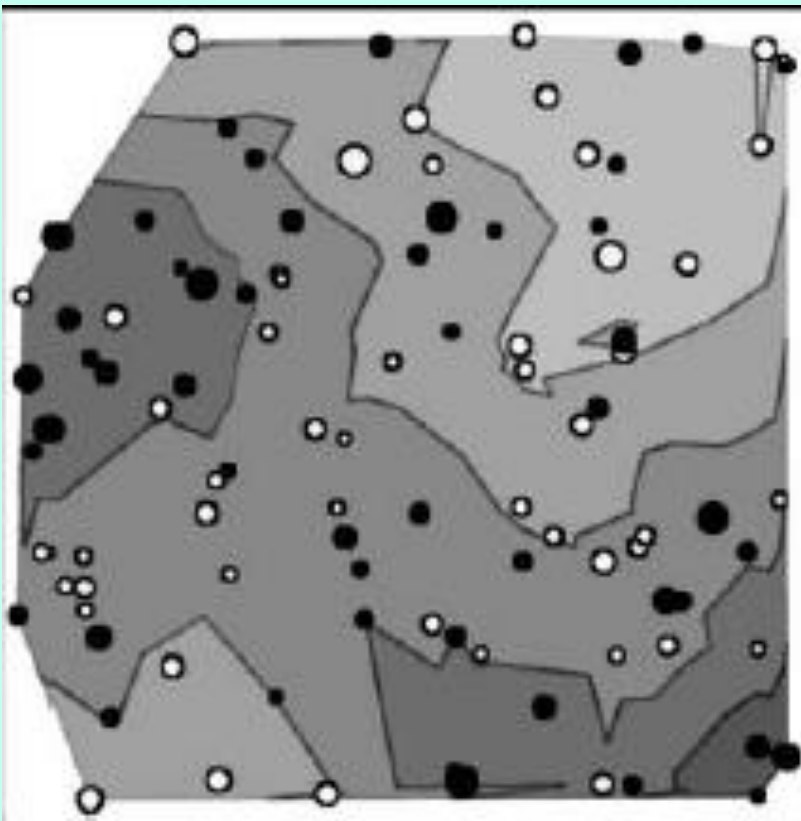
Temporal variation in host use



A spatially realistic model of niche evolution



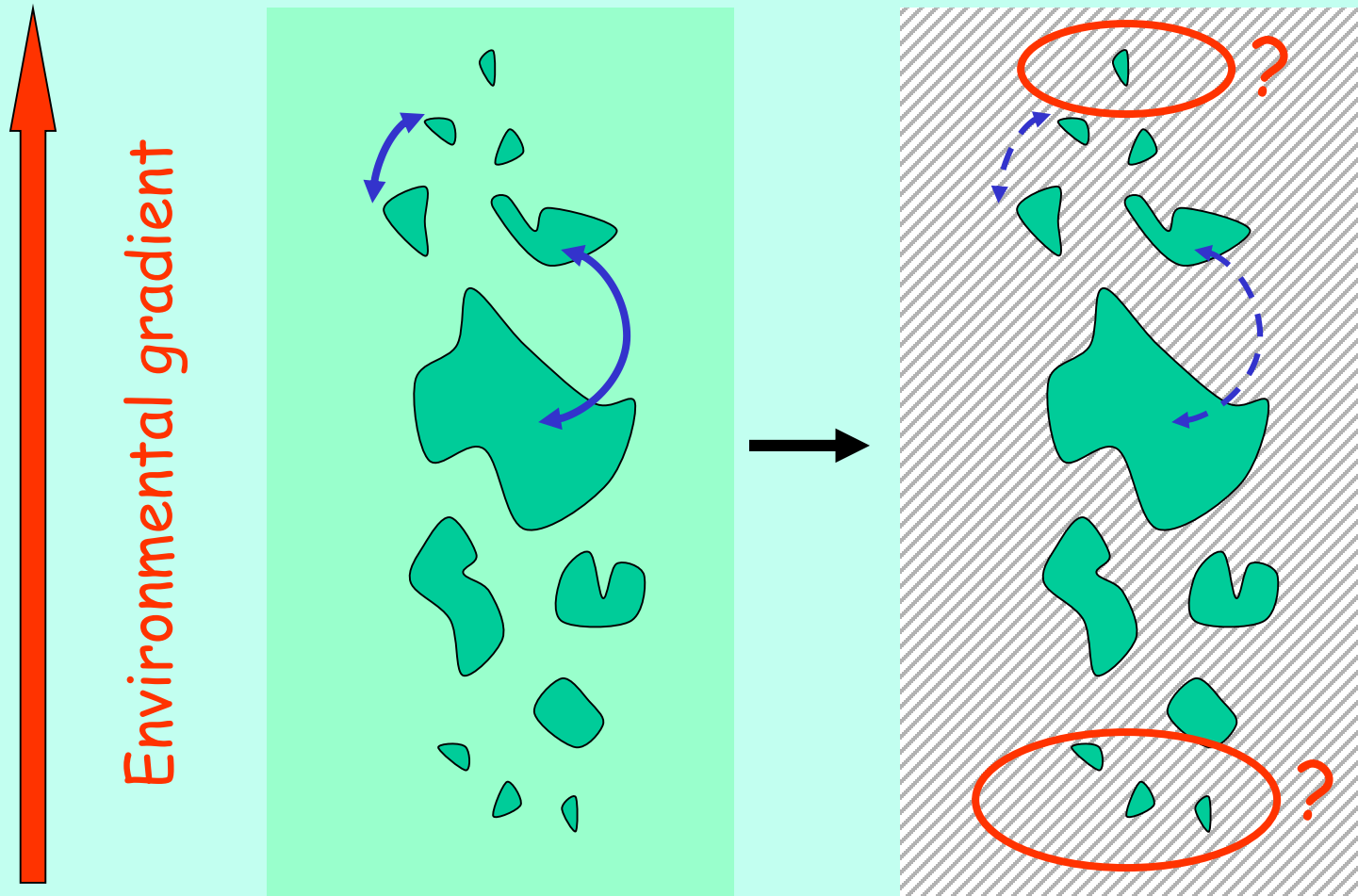
Hanski et al. 2011



Is migration always constraining adaptation?

Alleaume et al. 2006

The scenario



Previous theoretical predictions

Garcia-Ramos and Kirkpatrick 1997

Disrupted migration → Increased adaptation in peripheral populations !

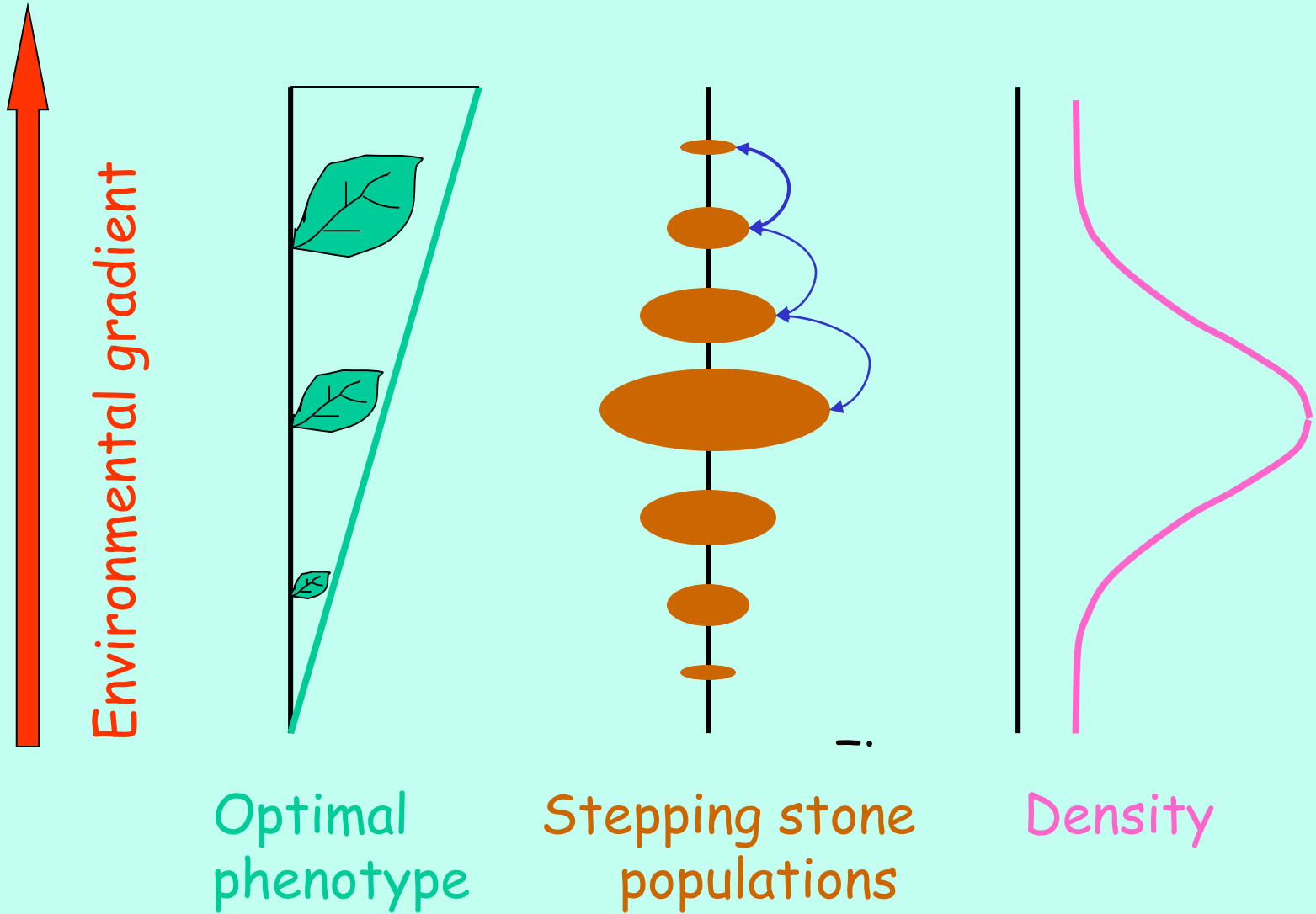
Because...

Gene flow opposes local selection

Gene flow is asymmetric

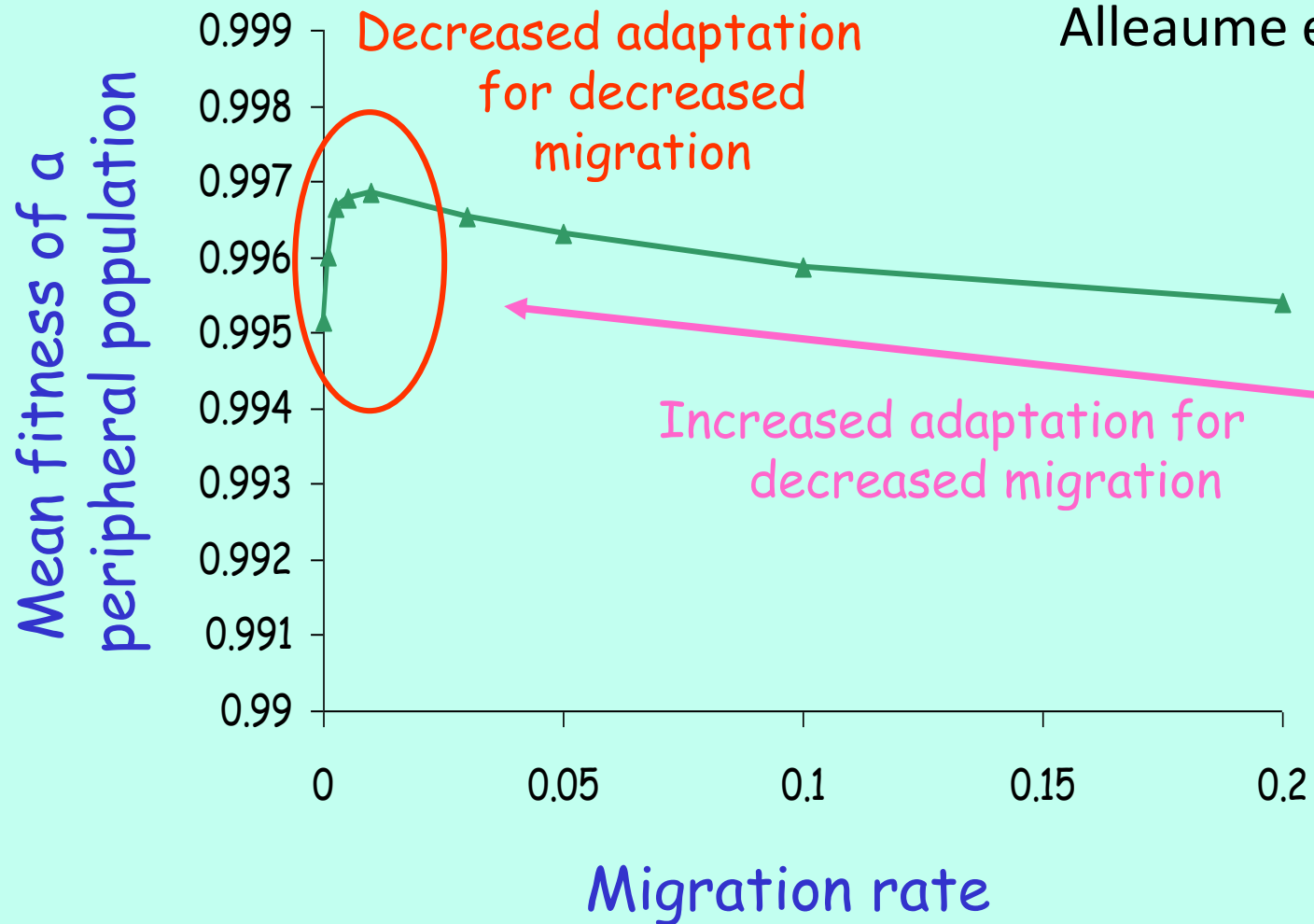
What about drift?

The model



Results

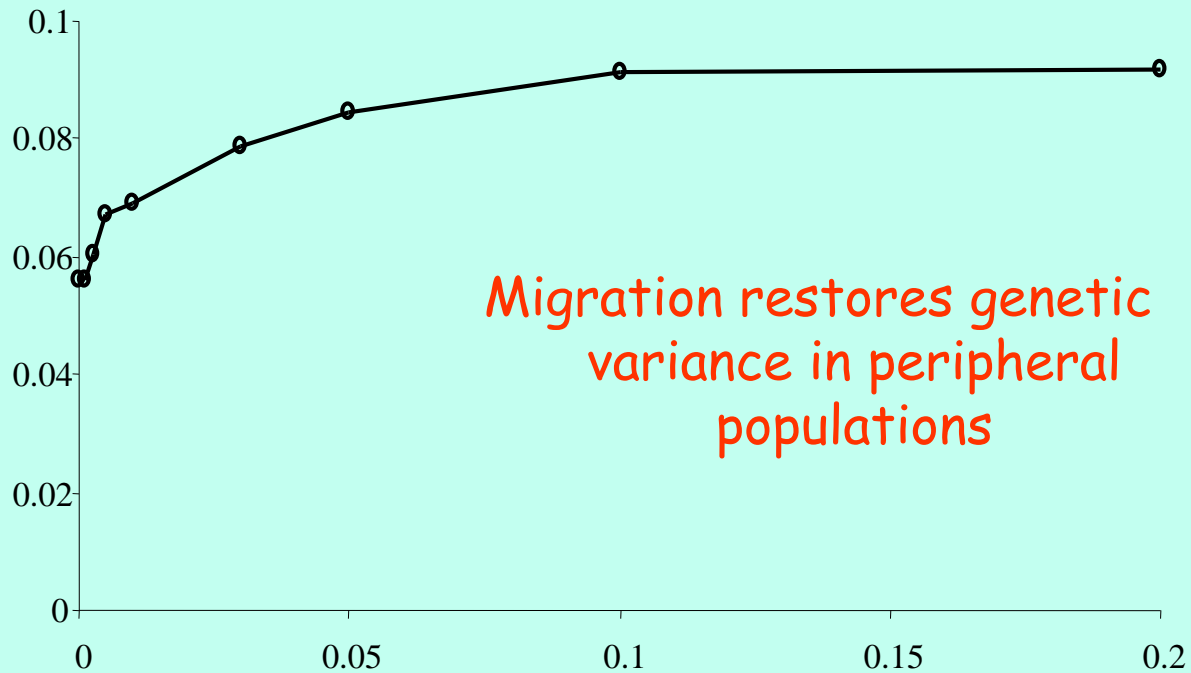
Alleaume et al. 2006



Results

Genetic variance in a
peripheral population

Alleaume et al. 2006



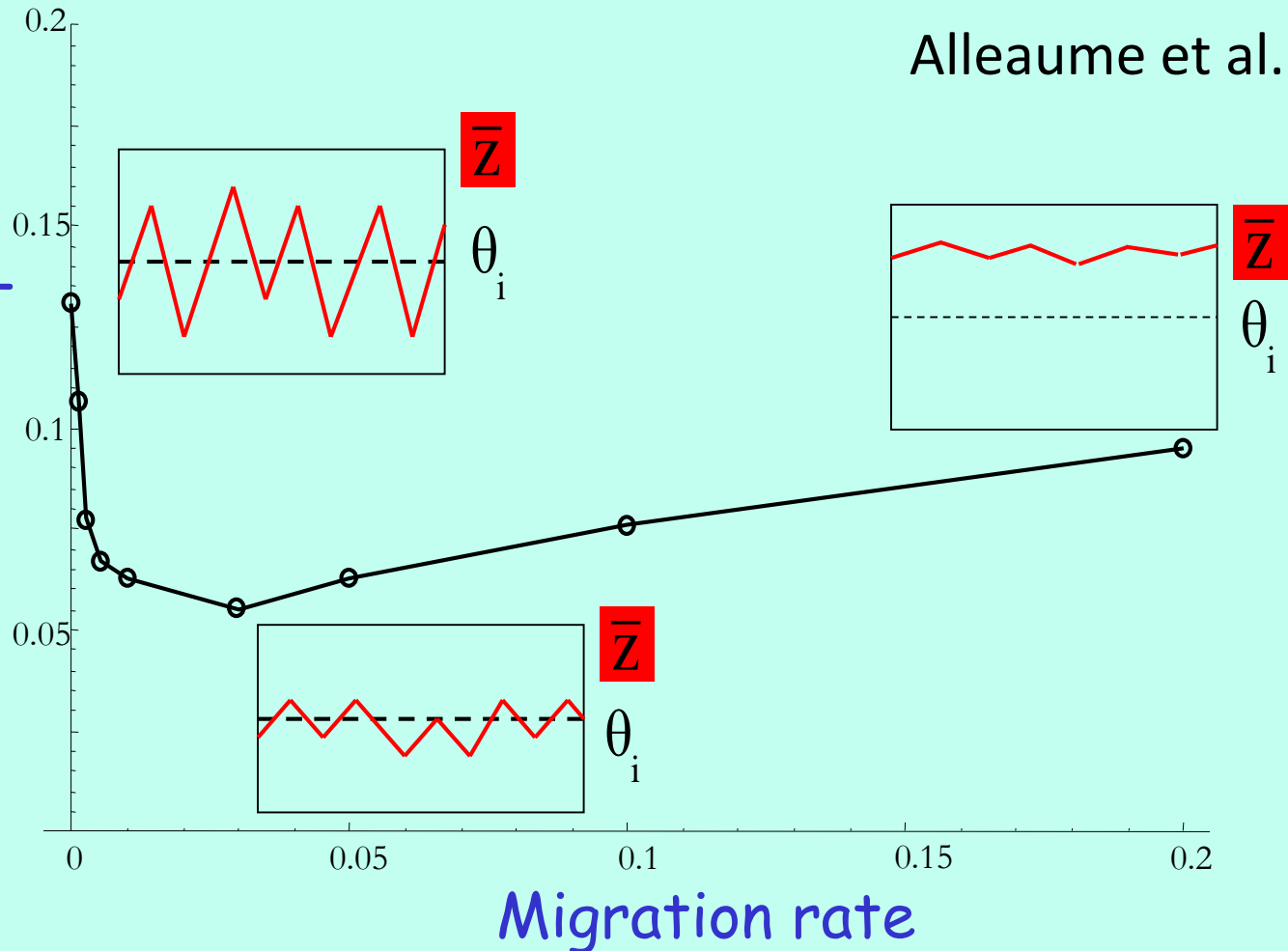
Migration restores genetic
variance in peripheral
populations

Migration rate

Results

Alleaume et al. 2006

Square distance between
the mean phenotype
and local optimum



Interpretation

1) No migration: drift-selection balance

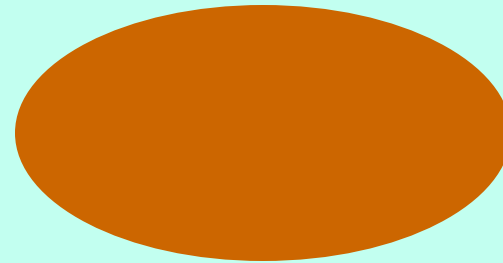


Strong drift

Low genetic variance

Selection inefficient

Deleterious
mutations fixed



Weaker drift

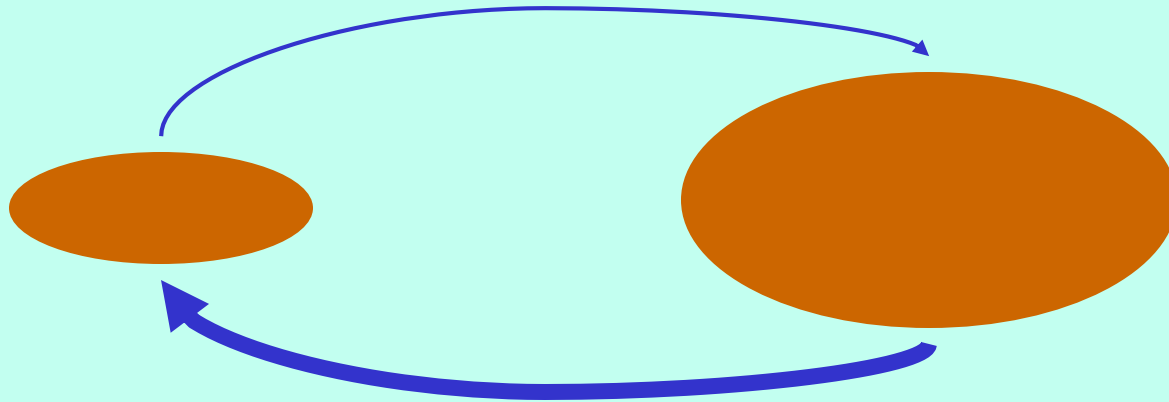
Higher genetic variance

Efficient selection

Mean phenotype close to
the local optimum

Interpretation

2) Low migration



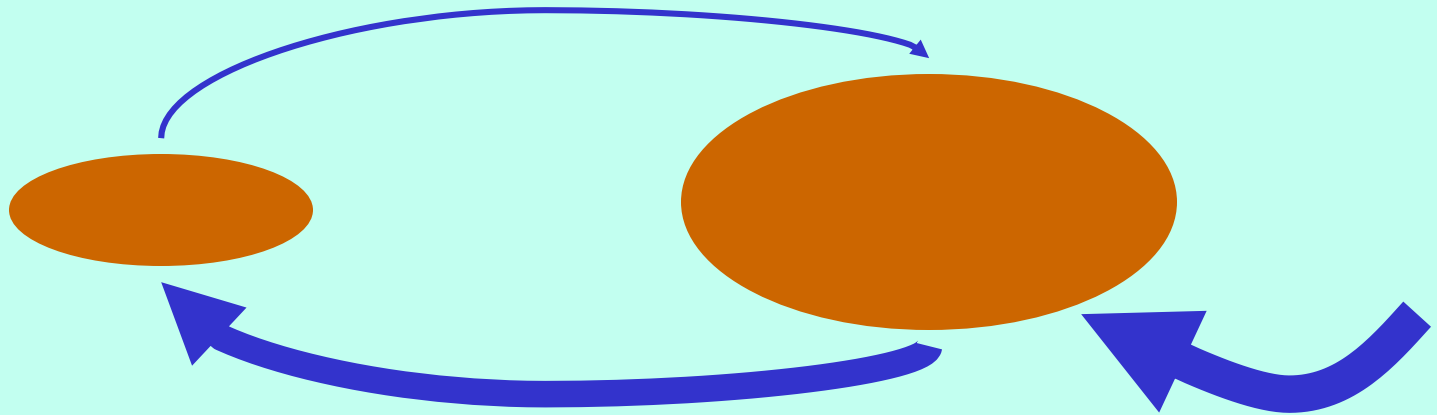
Immigration from larger adjacent populations...

...restores genetic variance

...introduces better adapted genotypes

Interpretation

2) High migration: migration-selection balance

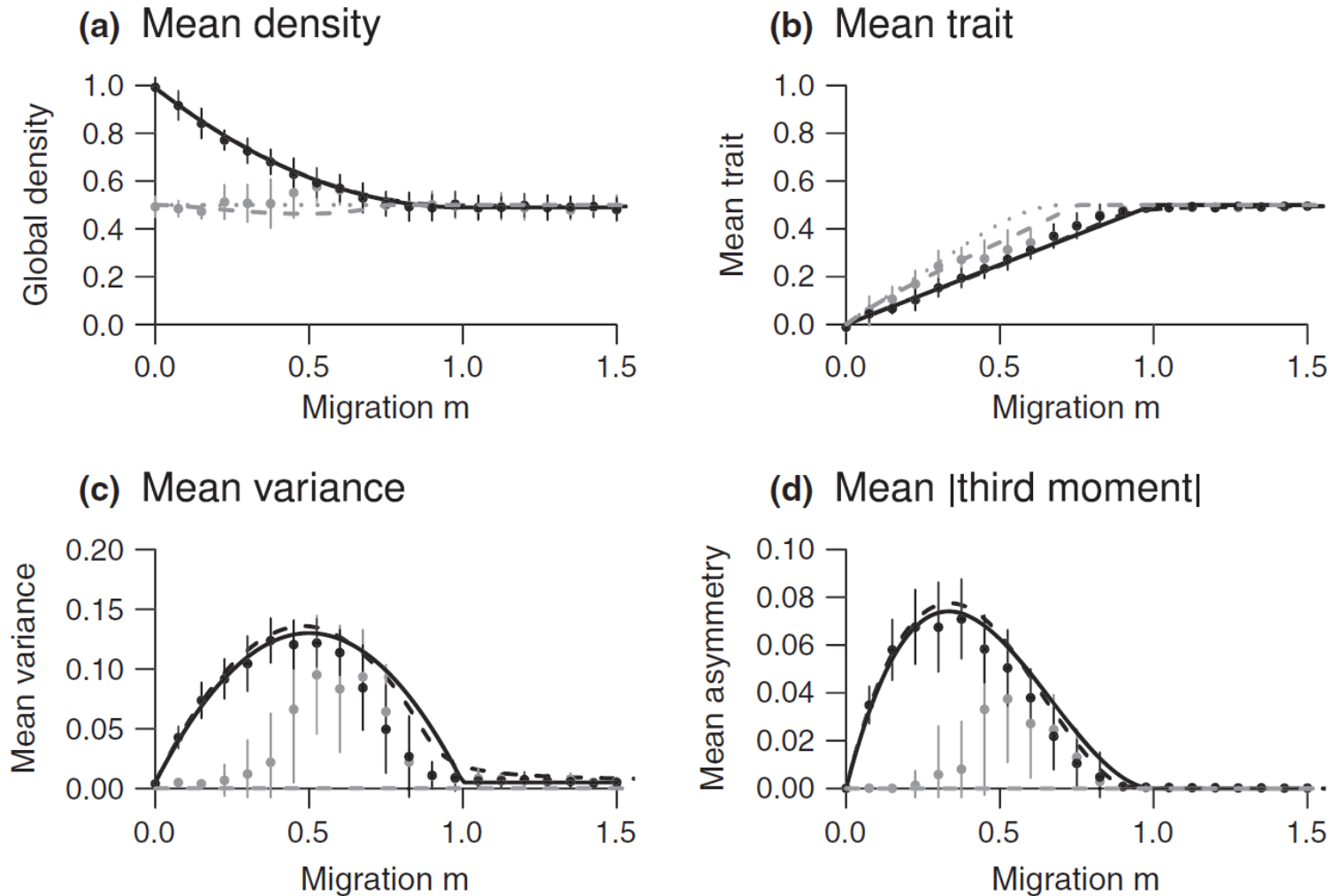


Gene swamping

Maladapted adjacent populations

Mean phenotype close to the central population optimum

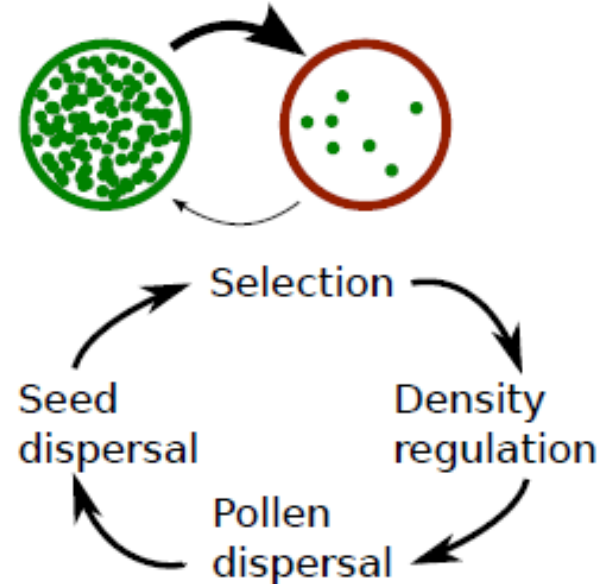
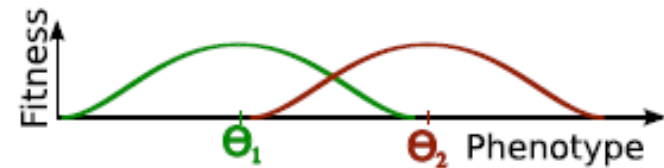
What me normal?



Débarre et al. 2013; Yeaman & Guillaume 2009; Huismann & Tufto 2012

Models of niche expansion with pollen dispersal

- 2 habitats, 2 optimal phenotypes
- Initial state: source-sink
- Discrete time, non-overlapping generations



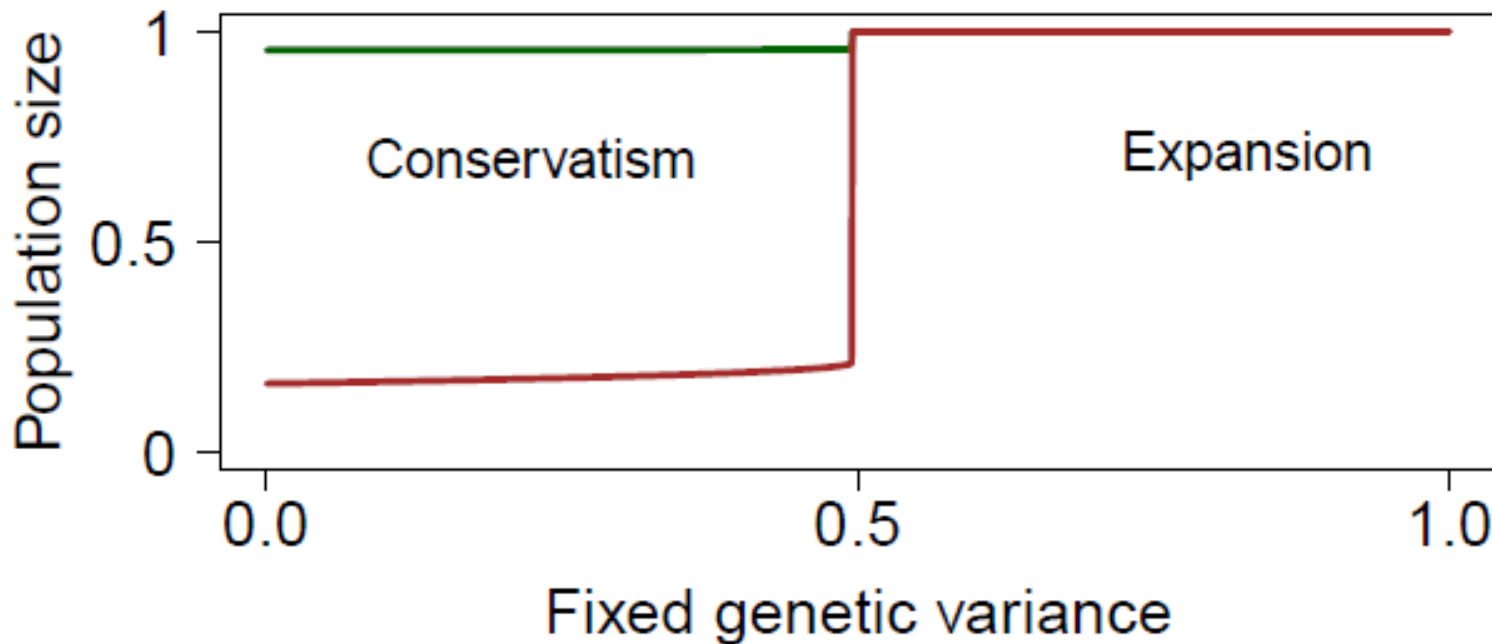
Analytical model: **fixed** genetic variance
Simulation model: **evolving** genetic variance

Aguilée et al.
2012 Evolution

Models of niche expansion with pollen dispersal

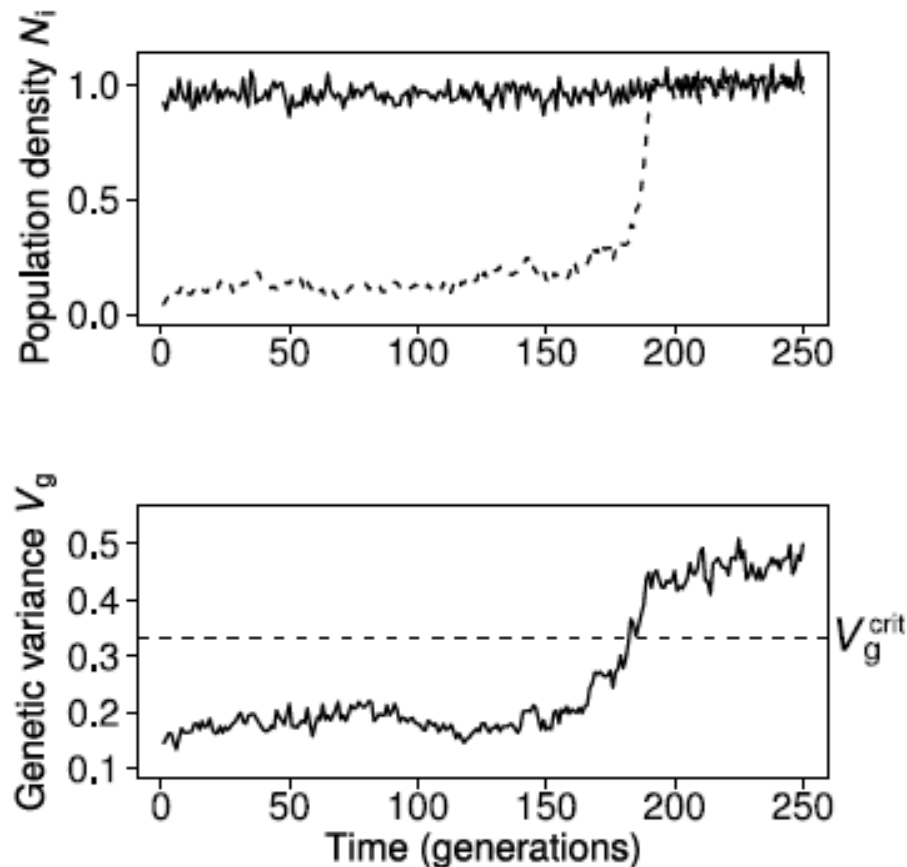
Critical genetic variance
needed for niche expansion

At equilibrium:

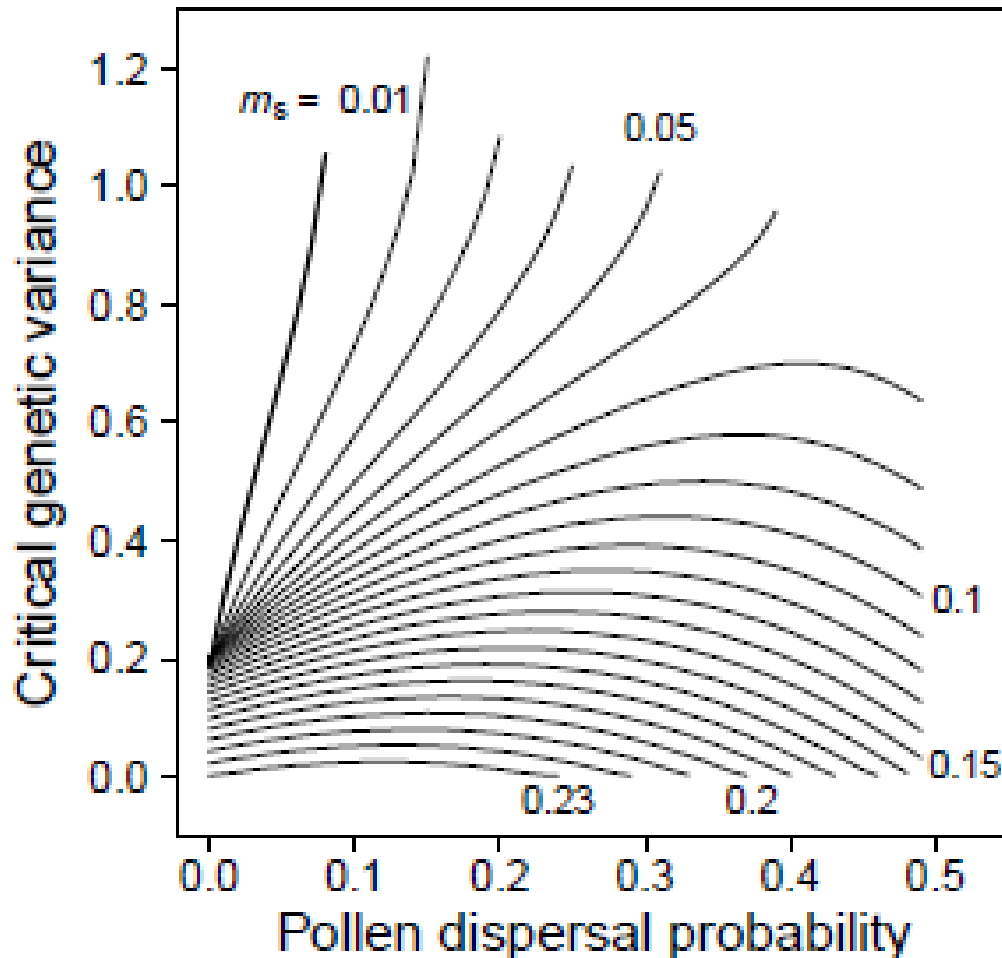


Critical genetic variance **reached**: niche expansion

(simulation model, **evolving** genetic variance)



Models of niche expansion with pollen dispersal

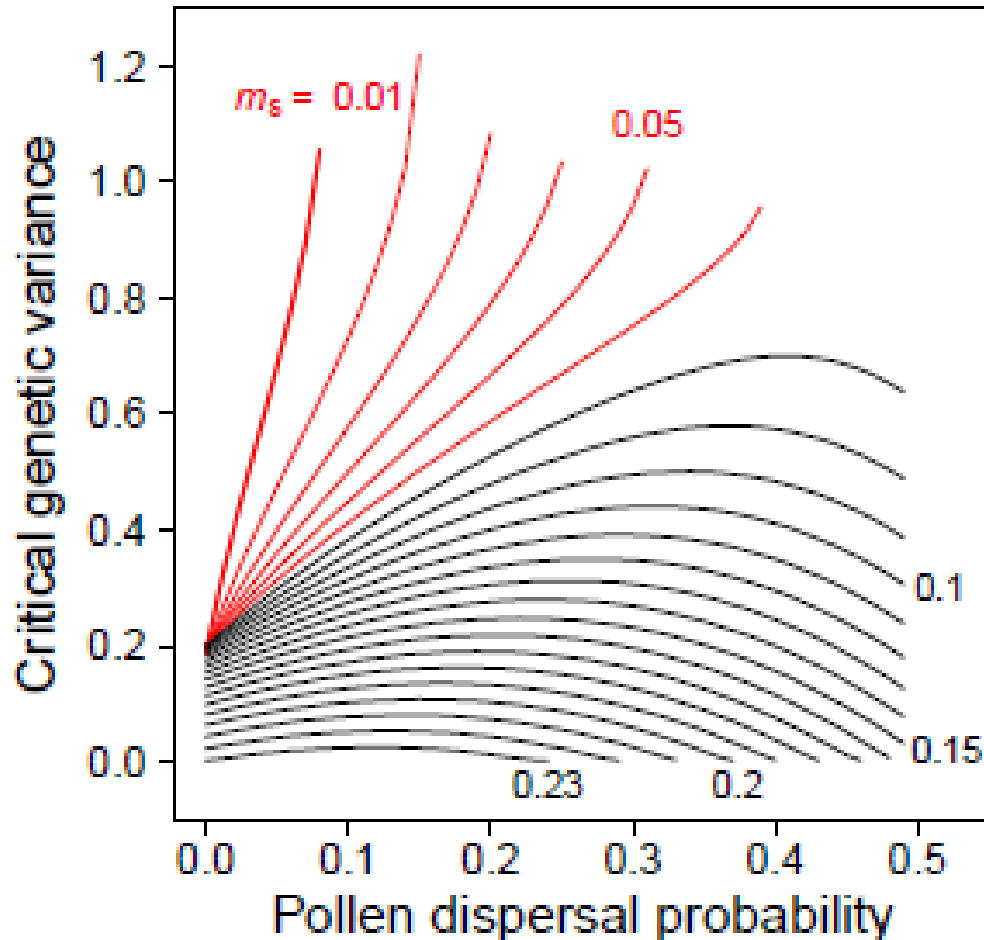


Critical genetic variance decreases with higher seed dispersal

Seed dispersal:

- demographic effect: easier niche expansion

Models of niche expansion with pollen dispersal



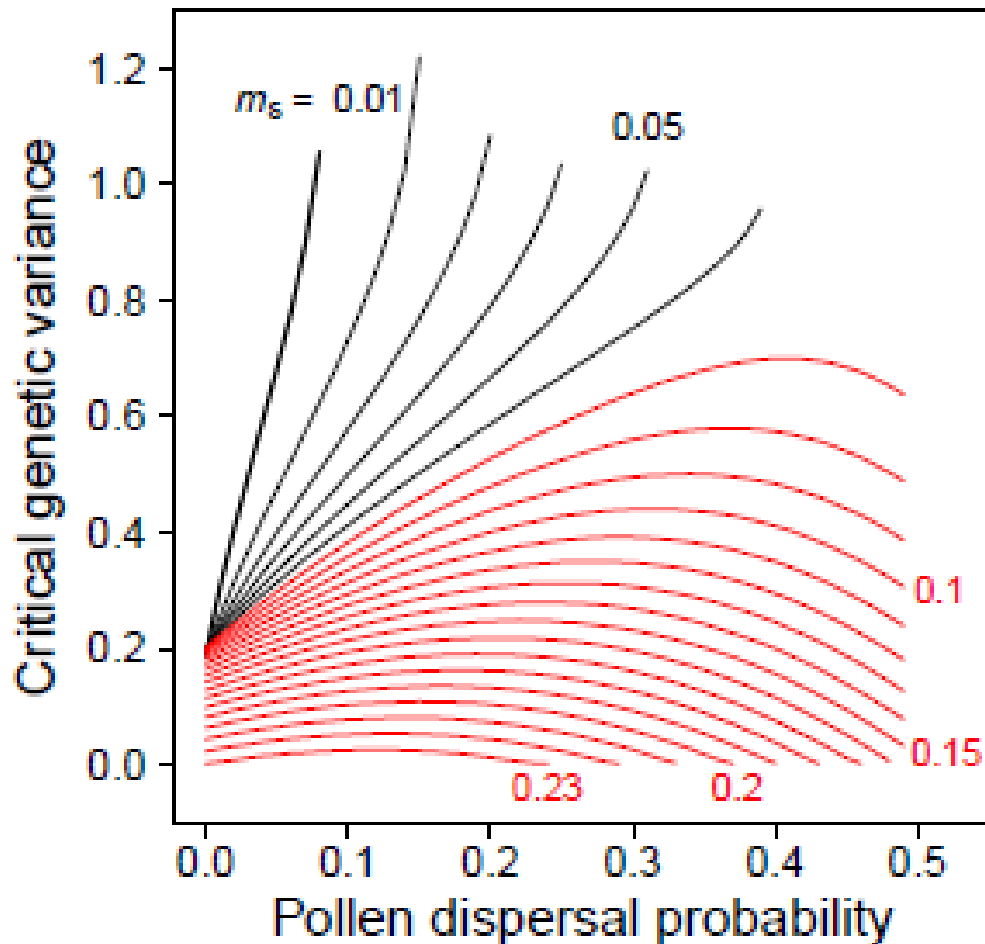
When seed dispersal is low

Critical genetic variance increases with higher pollen dispersal

Pollen dispersal:

- genetic effect: harder niche expansion
- indirect genetic effect: maladapted source, easier niche expansion

Models of niche expansion with pollen dispersal



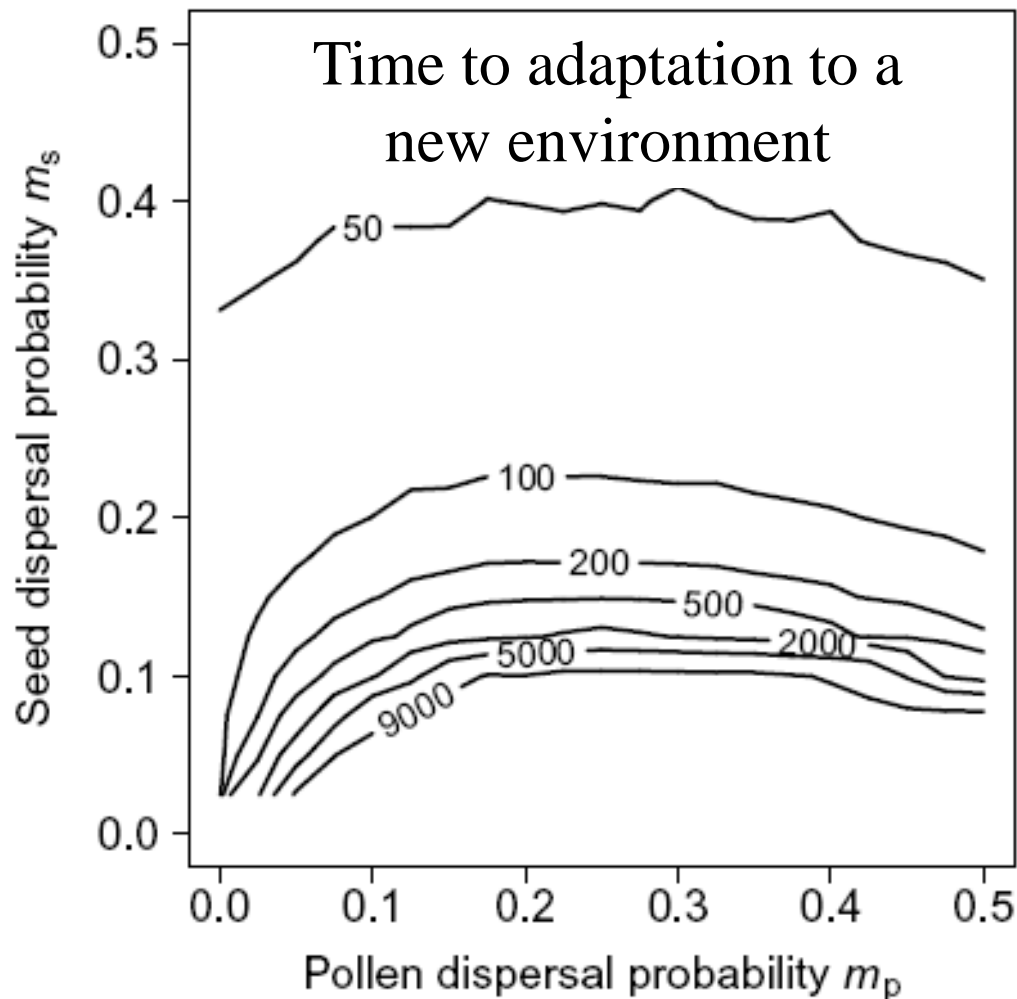
When seed dispersal is high

Non monotonic
effect of pollen
dispersal

Pollen dispersal:

- genetic effect:
harder niche expansion
- indirect genetic effect:
maladapted source,
easier niche expansion

Models of niche expansion with pollen dispersal

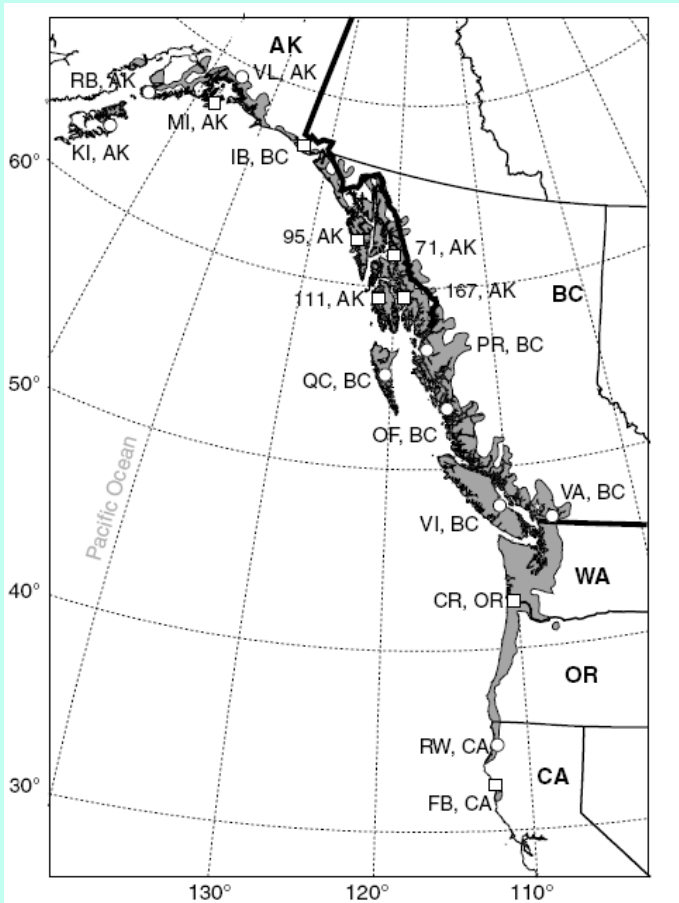


Seed dispersal accelerates adaptation to a new habitat

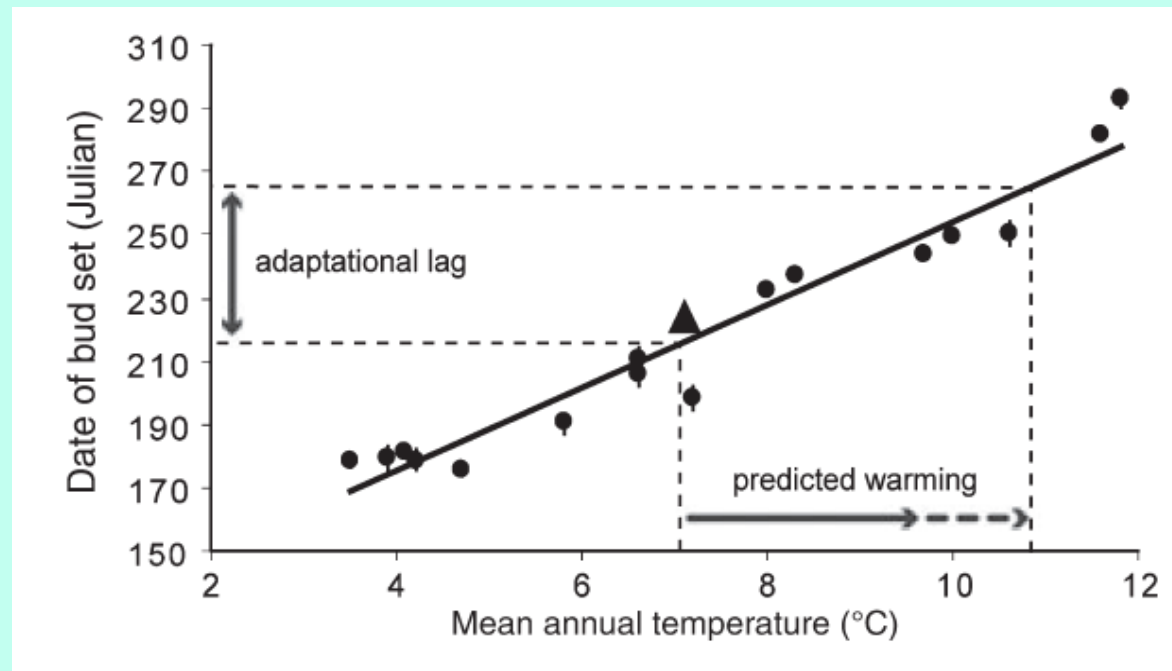
Pollen dispersal impedes it

(simulations)

Continuous environmental gradients



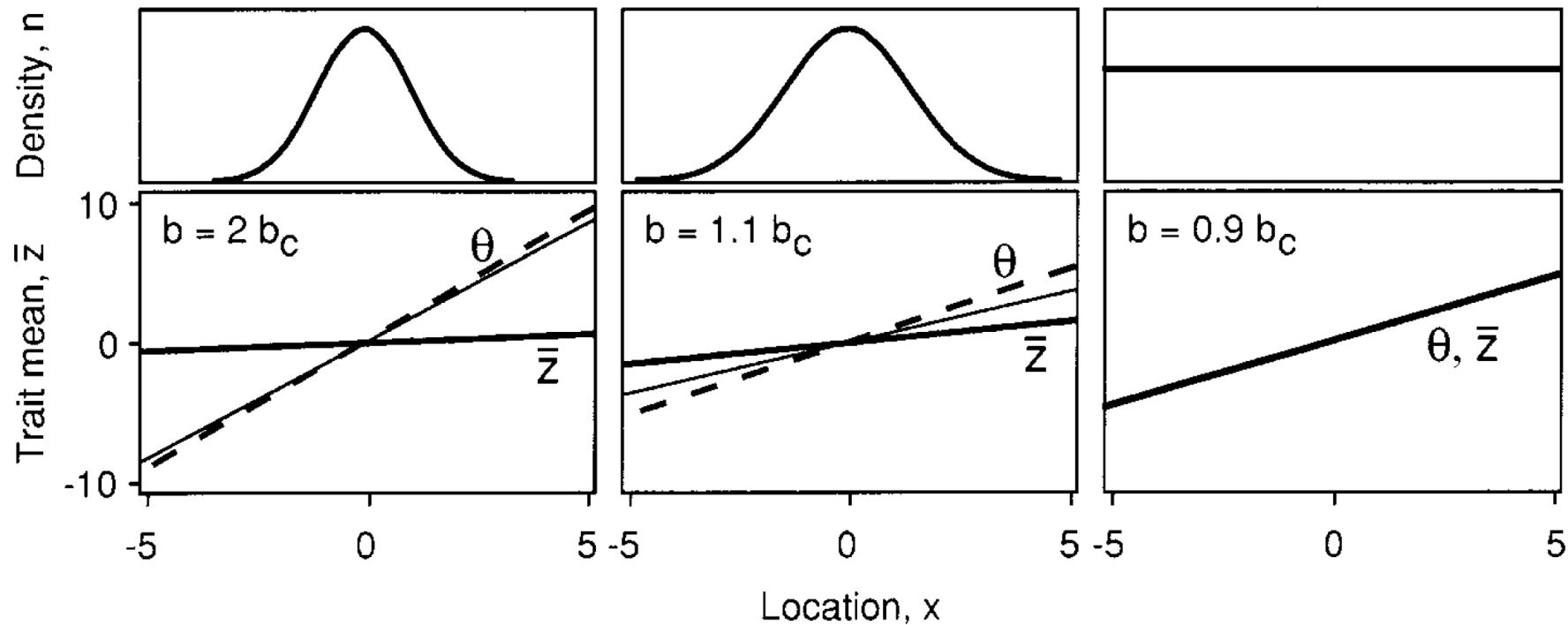
Sitka spruce



Mimura & Aitken 2007; Aitken et al. 2008

A quantitative genetics model for species range evolution

Kirkpatrick & Barton 1997

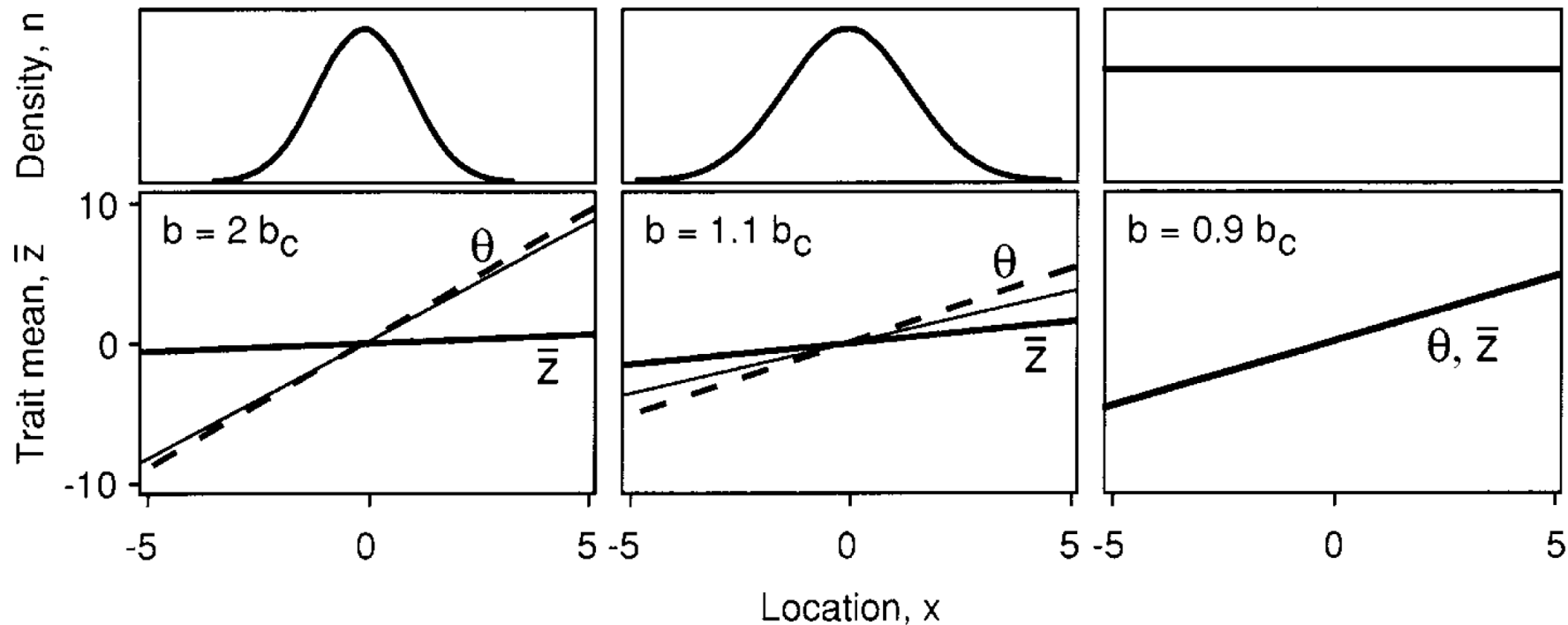


Maladaptation at the margins
Less phenotypic divergence than optimal
Limited range

Perfect adaptation
everywhere
Infinite range

A quantitative genetics model for species range evolution

Kirkpatrick & Barton 1997



Spatial gradient above a critical value

Spatial gradient below a critical value

Are marginal populations maladapted?

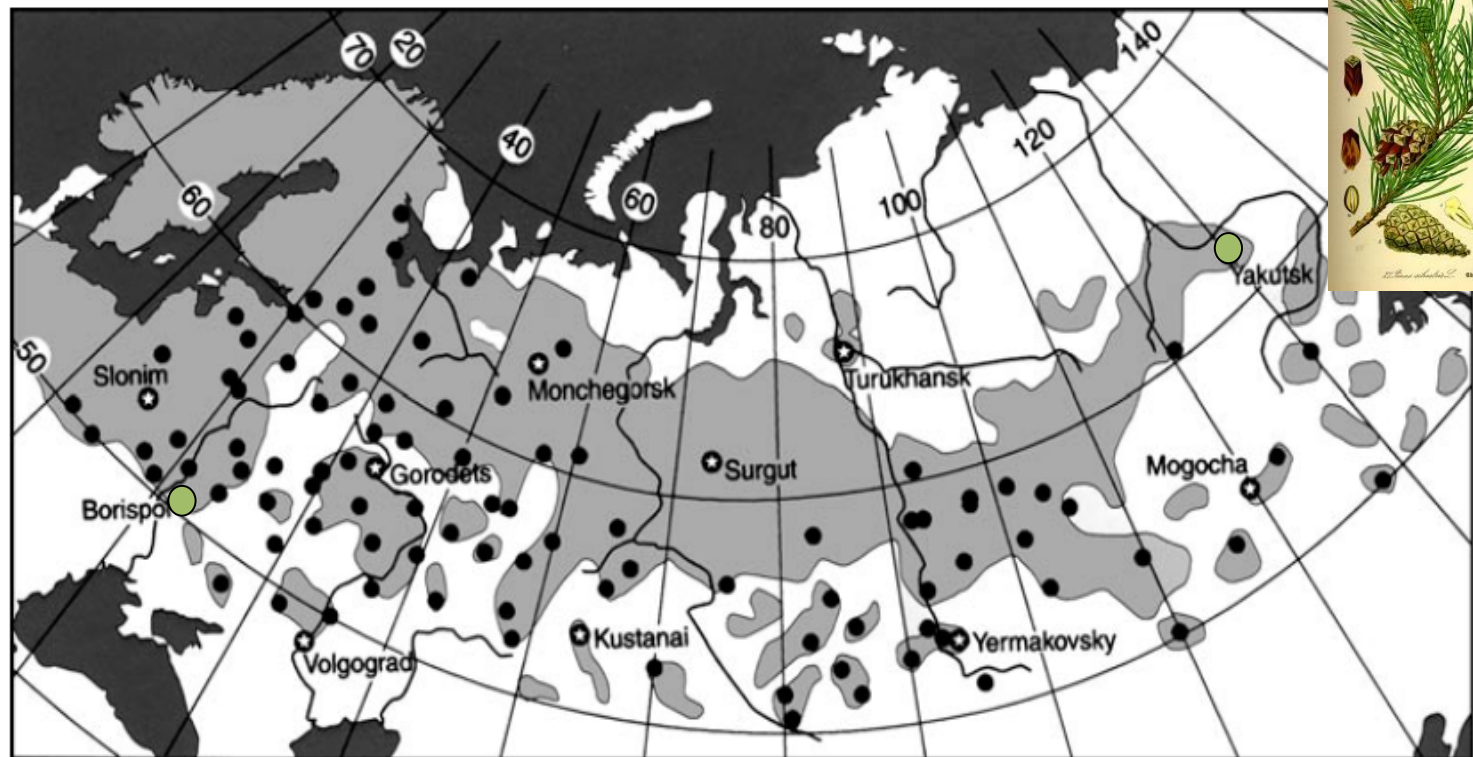
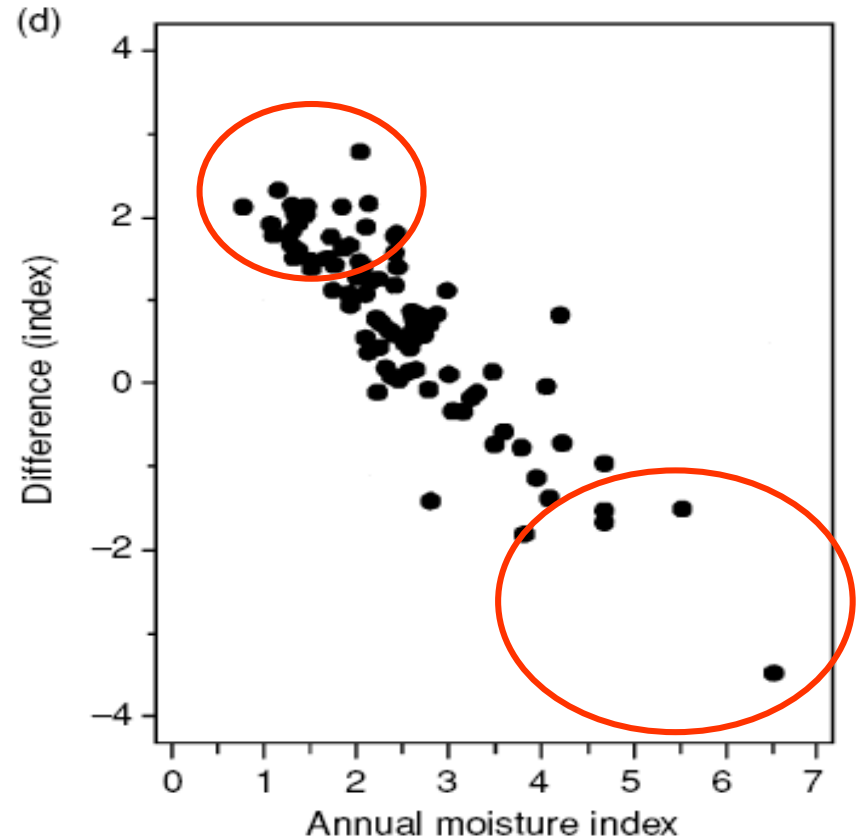
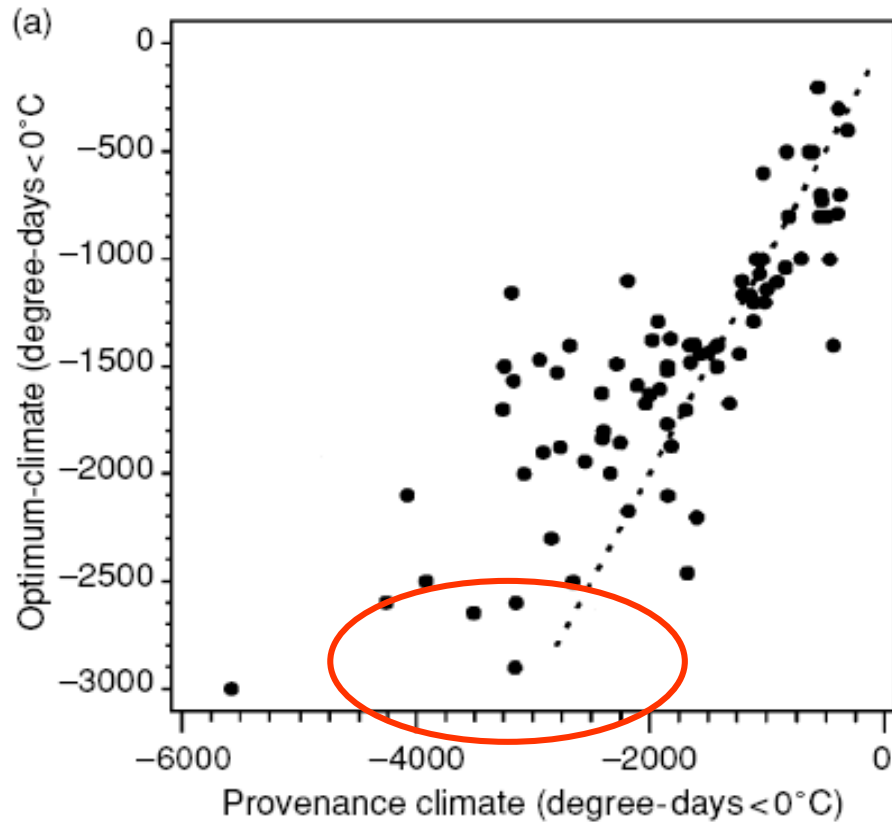


Fig. 1 Distribution (shading) of *P. sylvestris* (after Critchfield & Little, 1966) and location of populations (dots) sampled. Locations that are named are used throughout the paper to illustrate geographical effects.

Pinus sylvestris

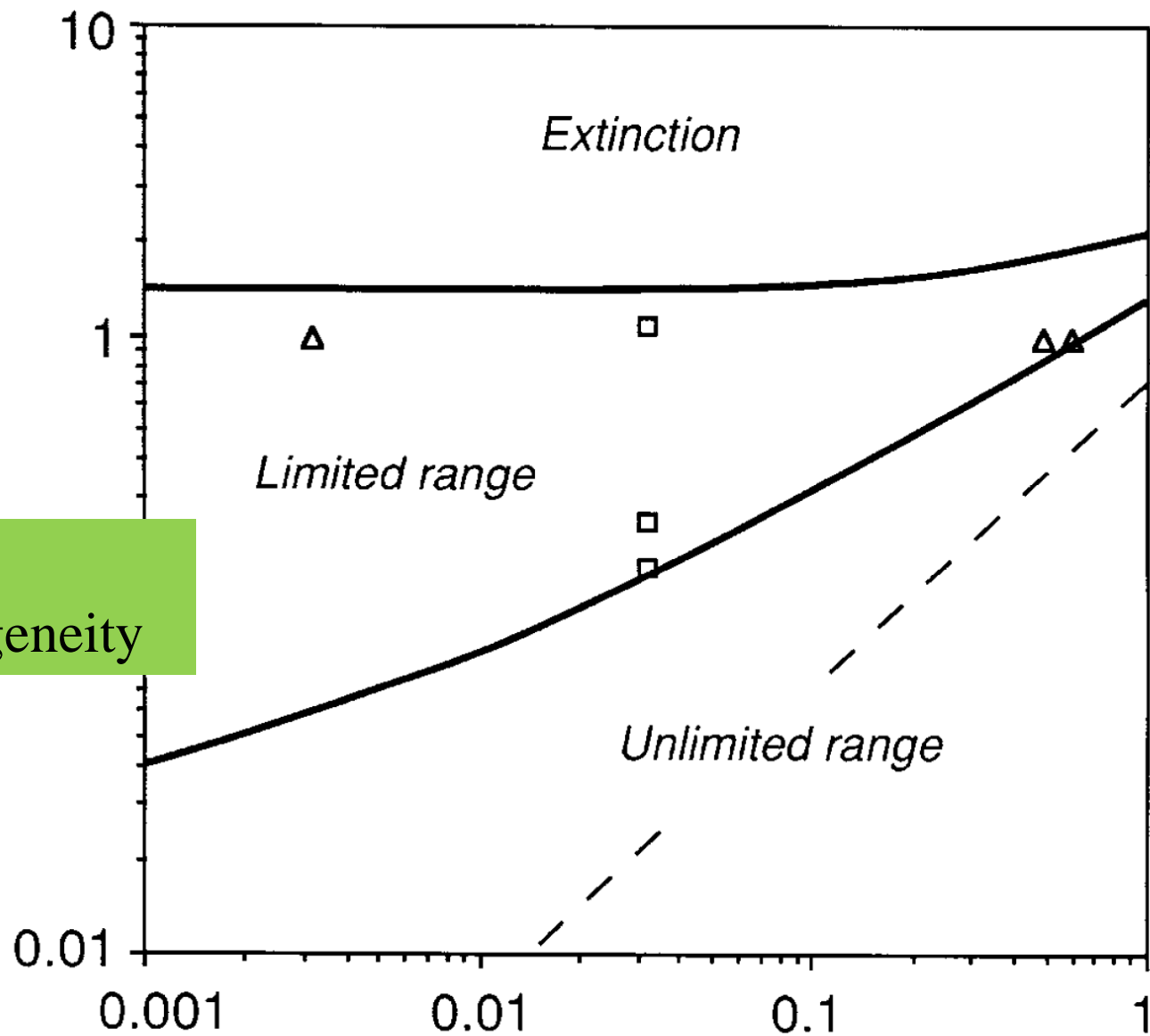
Are marginal populations maladapted?



Rehfeldt et al. 1999, 2002

B

Spatial
heterogeneity



A

Genetic variance

Deriving K&B 1997 model from structured models

Raoul 2017

Diffusion across space

Selection

Competition (local in space non local in phenotype)

$$\begin{aligned} \partial_t n(t, x, y) = & \Delta_x n(t, x, y) + \left(1 + \frac{A}{2} - \frac{1}{2}(y - y_{opt}(t, x))^2 - \int n(t, x, z) dz \right) n(t, x, y) \\ & + \gamma \left(\int \int \Gamma_{A/2} \left(y - \frac{y_* + y'_*}{2} \right) \frac{n(t, x, y_*) n(t, x, y'_*)}{\int n(t, x, z) dz} dy_* dy'_* - n(t, x, y) \right), \end{aligned}$$

Reproduction (Infinitesimal model of trait inheritance)

$$\Gamma_{A/2}(y) := \frac{1}{\sqrt{2\pi A}} e^{-\frac{|y|^2}{A}}.$$

if $\gamma > 0$ is large

$$n(t, x, y) \sim N(t, x) \Gamma_A(y - Z(t, x))$$

Relaxing the hypothesis of constant variance

Barton 2001

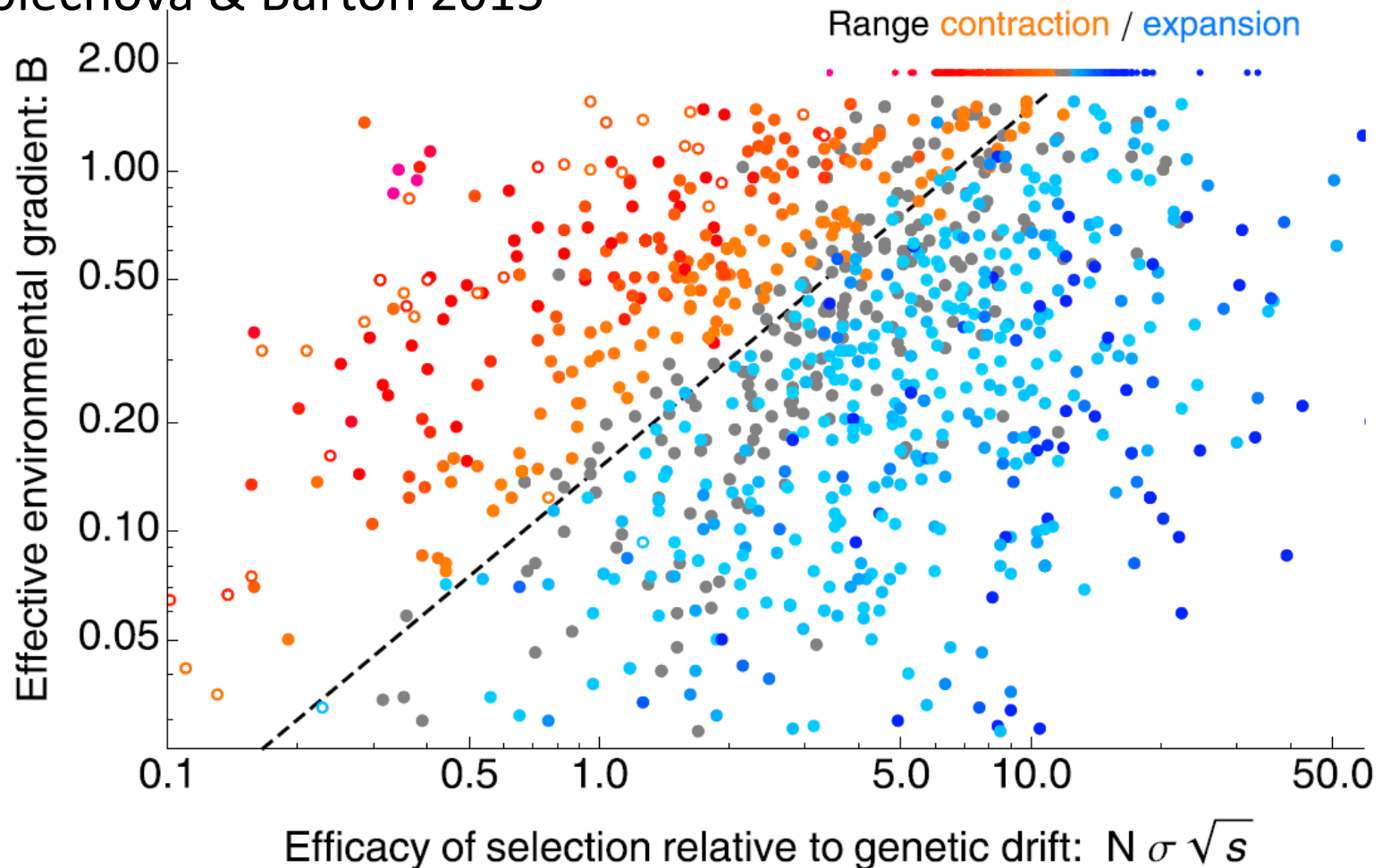
Gene flow across a phenotypic cline maintained by the environment can generate much more genetic variance than would mutation alone

Rise of genetic variance allow species to adapt to steep environmental gradients

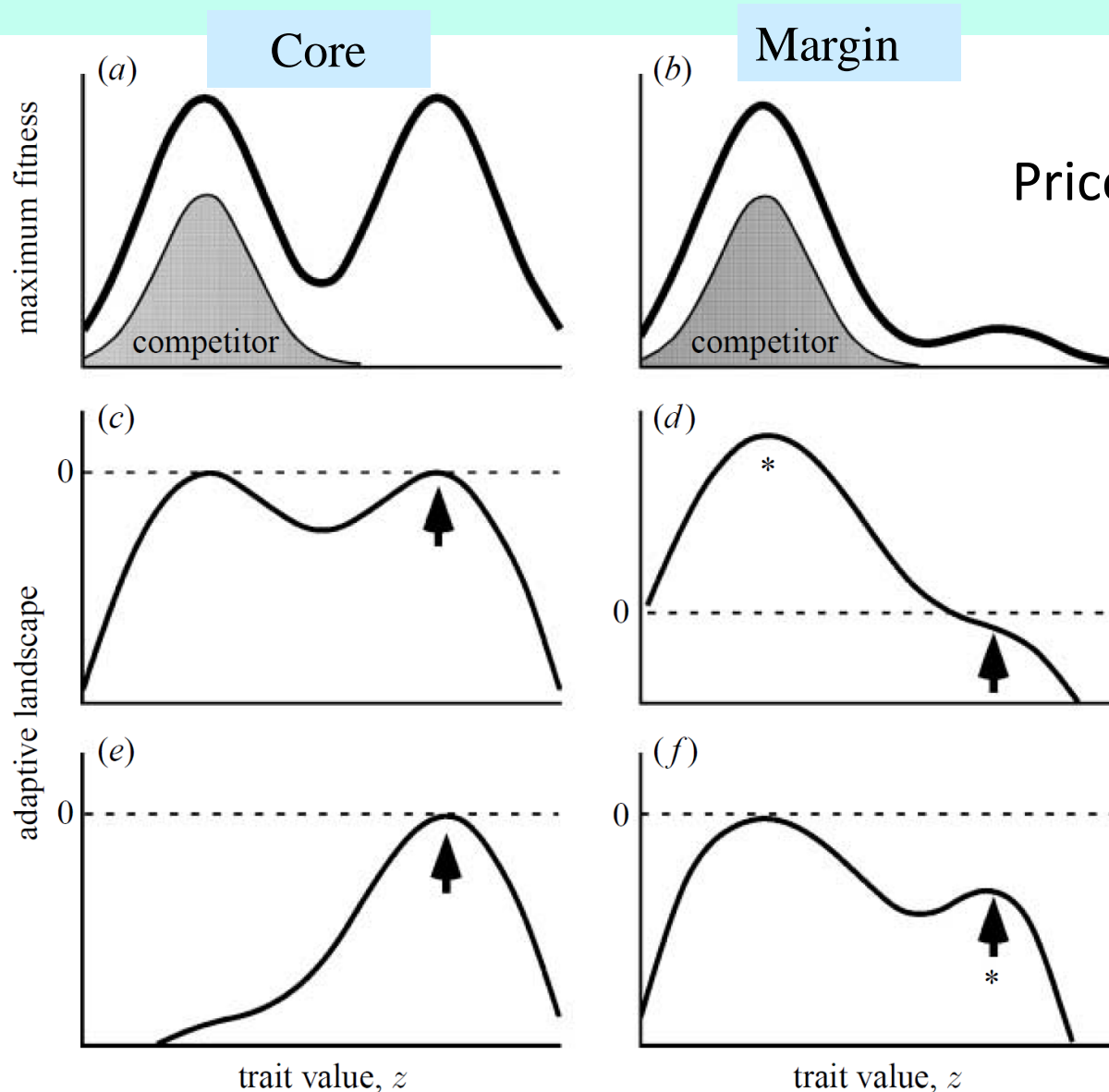
No limited range!

Relaxing the hypothesis of large population size

Polechova & Barton 2015



Evolutionarily stable range limits set by competition

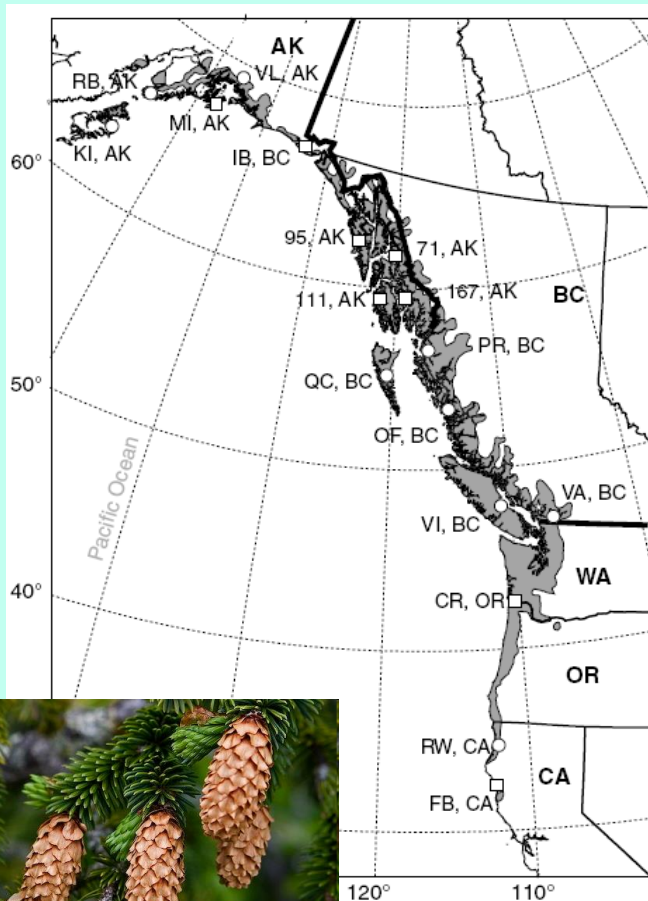


Price & Kirkpatrick 2009

Without competitor

With competitor

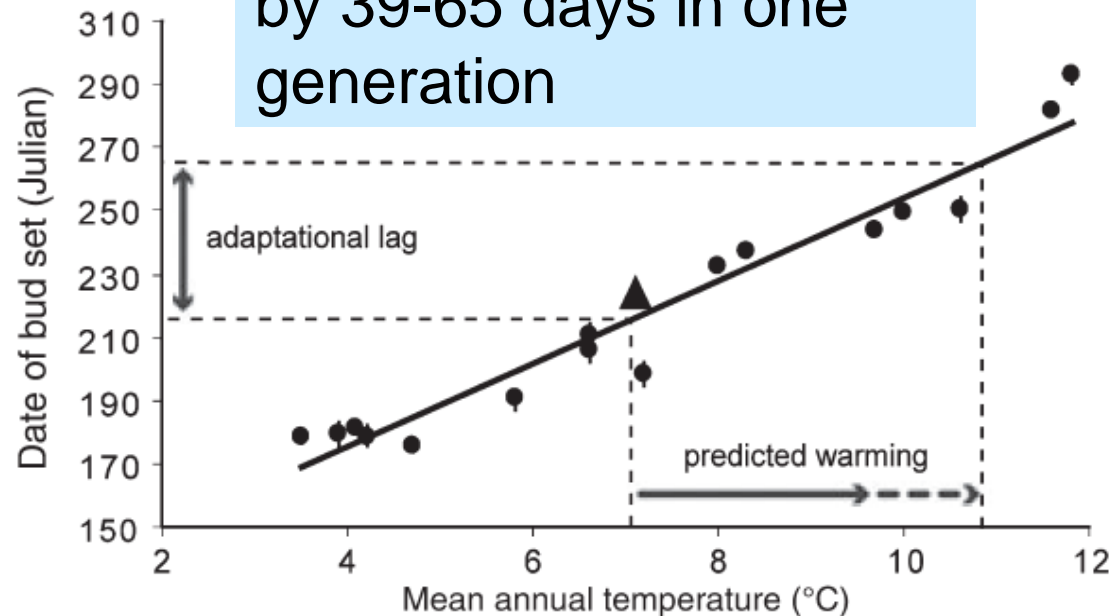
Adaptative challenges due to climate change



Sitka spruce

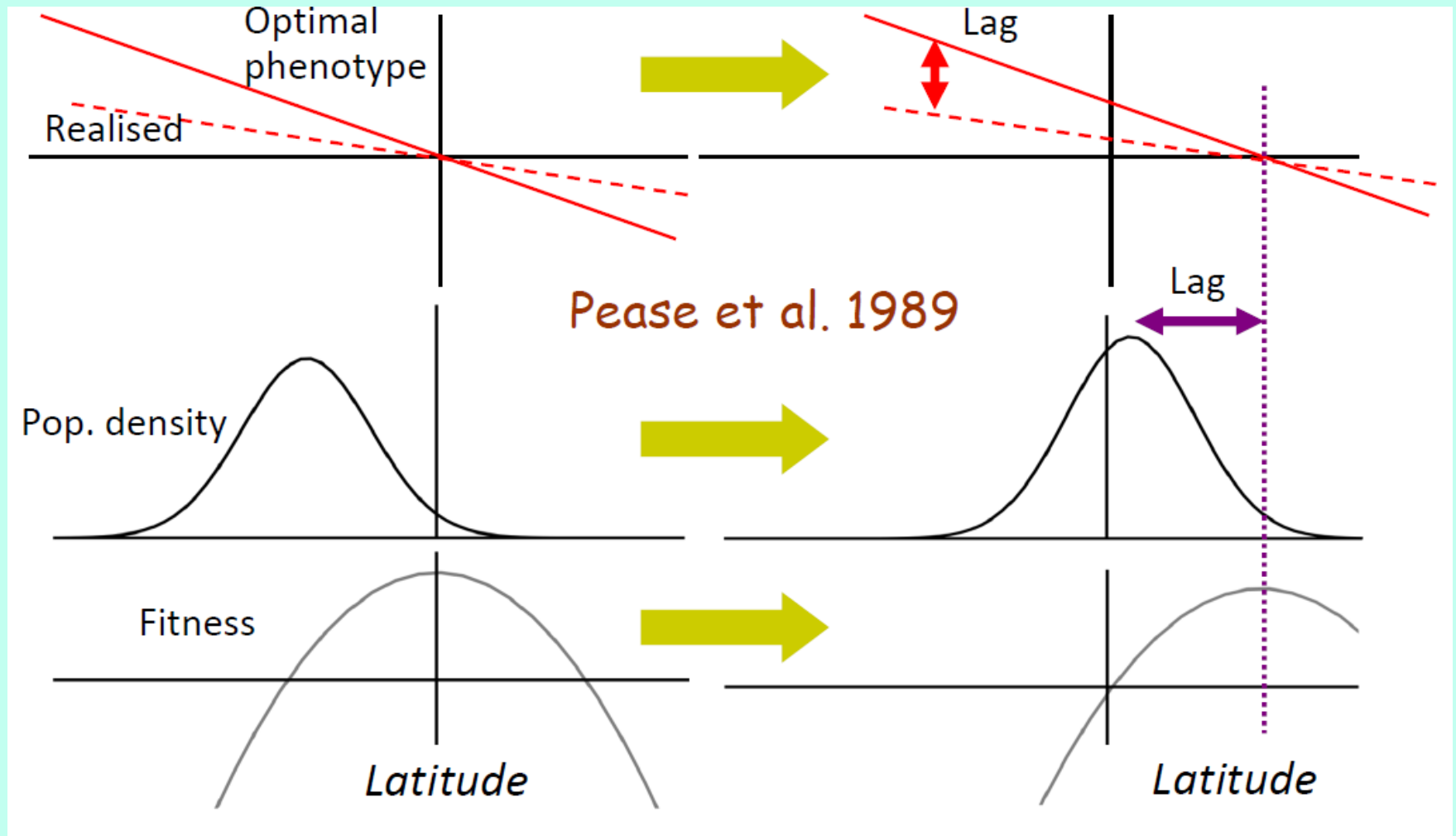
Mimura & Aitken 2007; Aitken et al. 2008

Bud set date should shift by 39-65 days in one generation

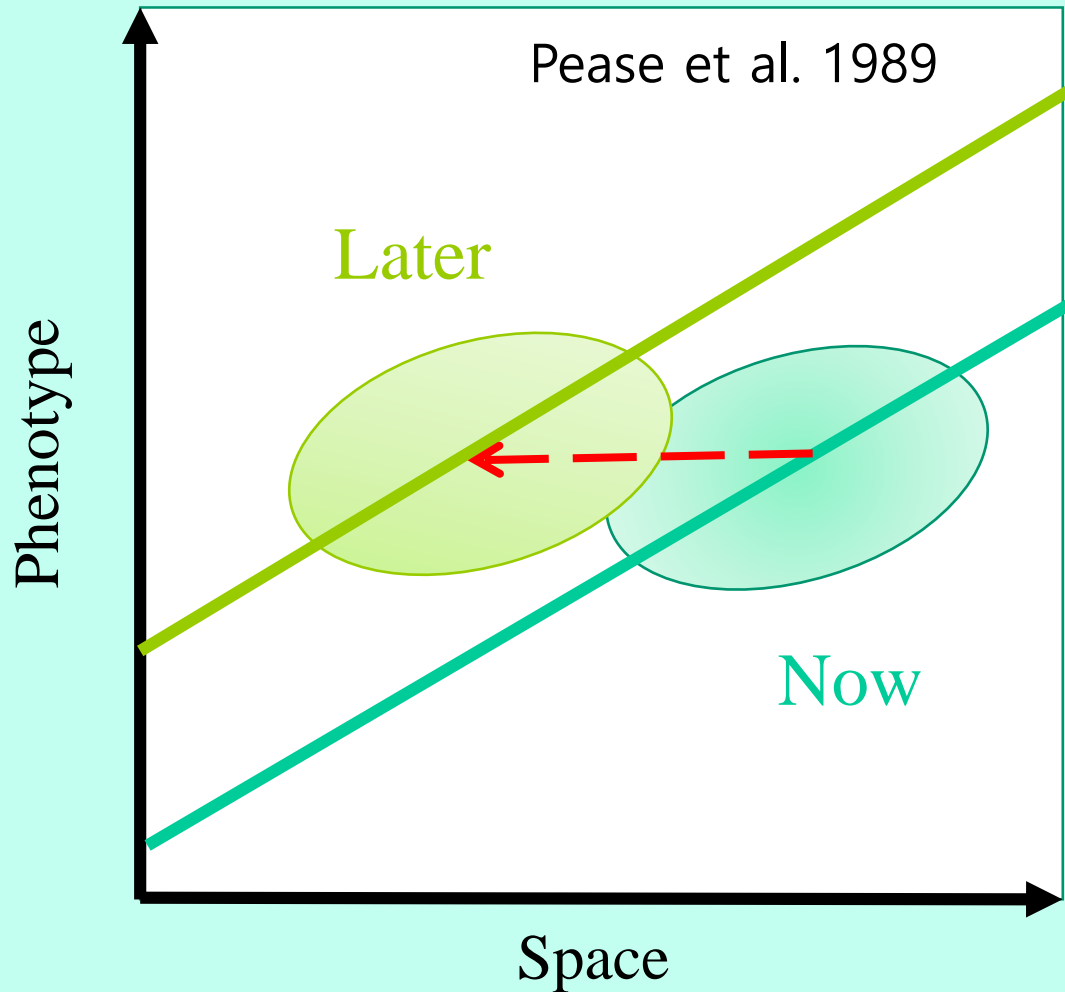


← N Latitude S →

Migration and adaptation can help tracking the climate



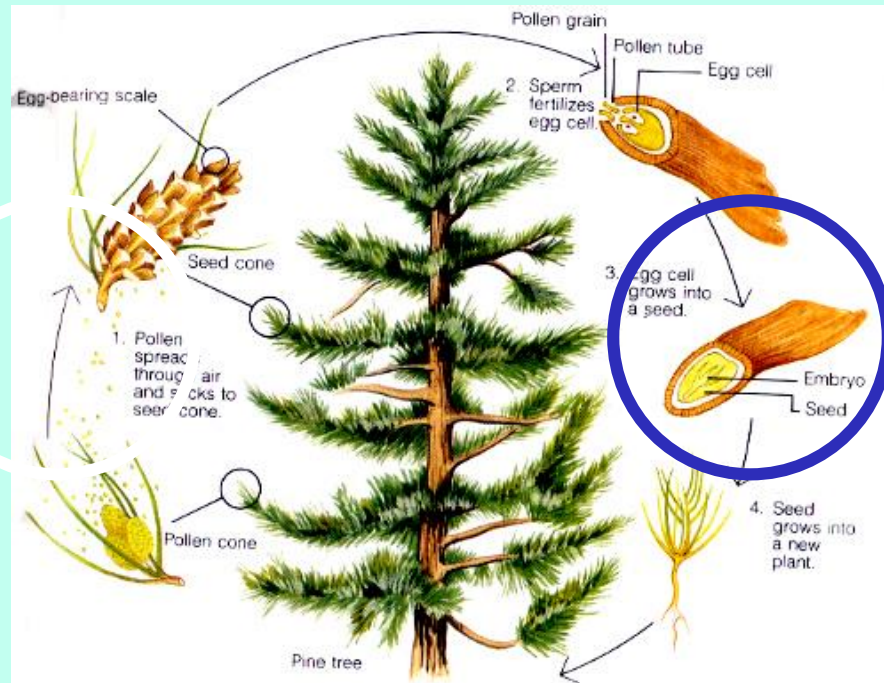
Migration and adaptation can help tracking the climate



Surviving species
move at the
same speed as
climate

Niche
conservatism!

Seed and pollen dispersal in a changing climate

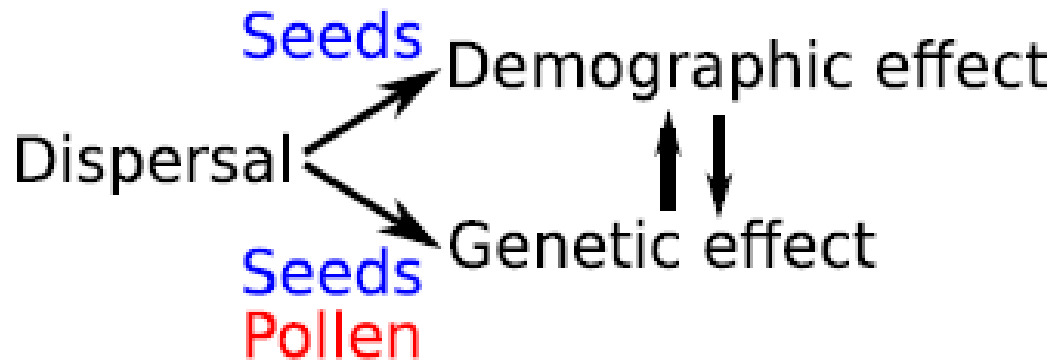


Kremer et al.
2013 Eco. Let.

Maximal pollen dispersal
distance up to
thousands of km

Maximal seed
dispersal distance up
to tens km

Effect of pollen on niche and range evolution under a changing climate



Robin Aguilée

A model of range and niche evolution with pollen dispersal

Aguilée et al. 2016 PNAS

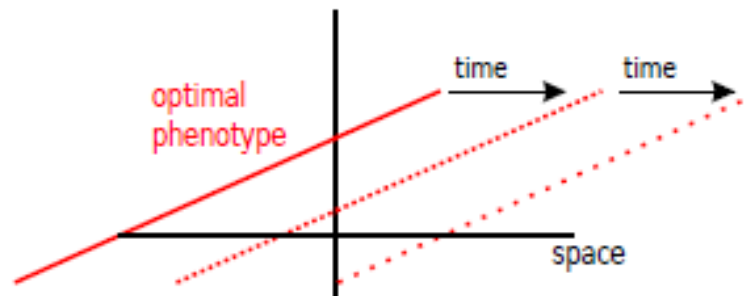


Gaël Raoul François Rousset

Models of range evolution with pollen

A quantitative genetic model for population size $n(x, t)$ and mean phenotype $\bar{z}(x, t)$ with:

- A linear spatial gradient shifting in time at constant speed



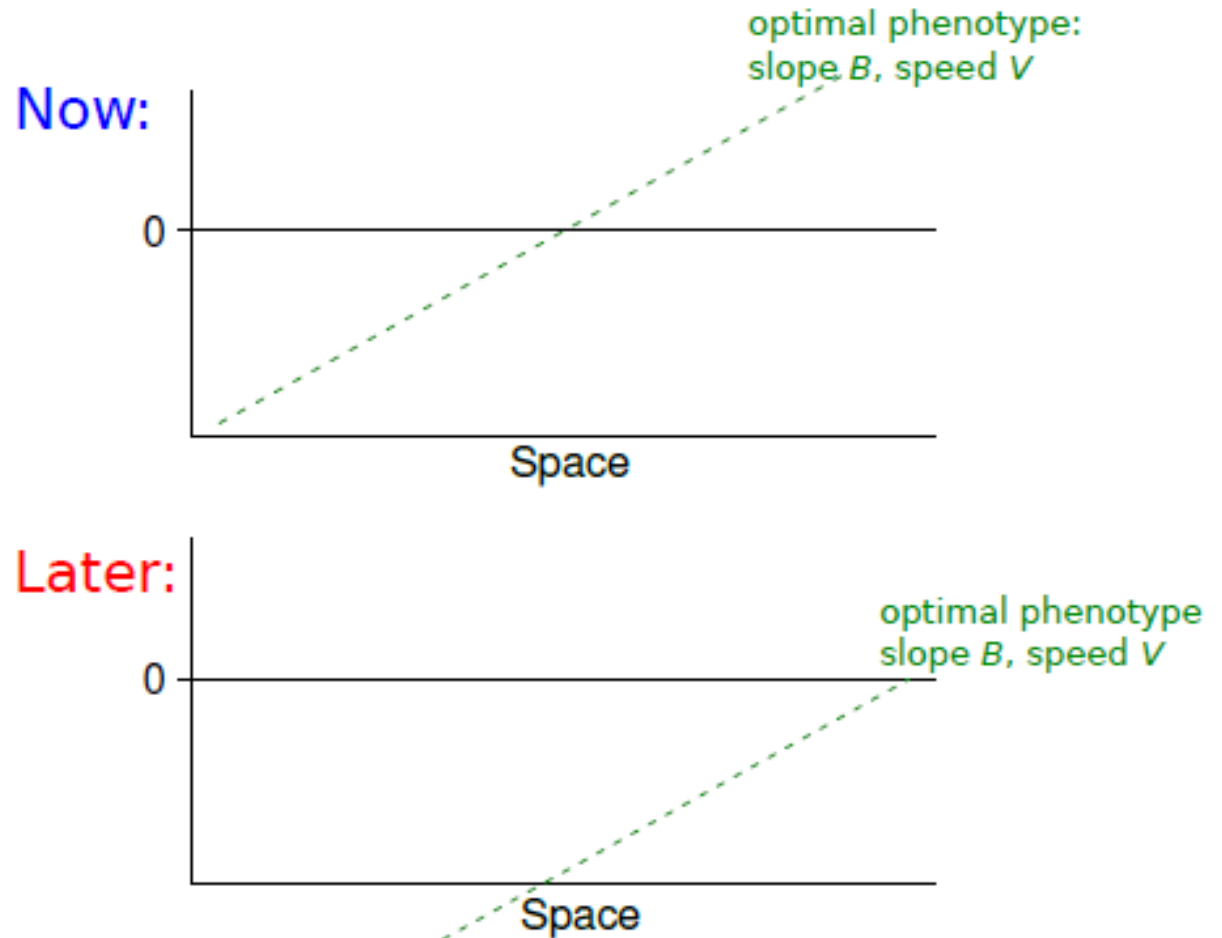
- Seed and pollen dispersal (diffusion, Gaussian dispersal kernel)
- Feedbacks between demography and adaptation

Two strong assumptions:

- Global density dependence
- Constant genetic variance

Relaxed without altering
qualitative conclusions about the
effect of pollen dispersal

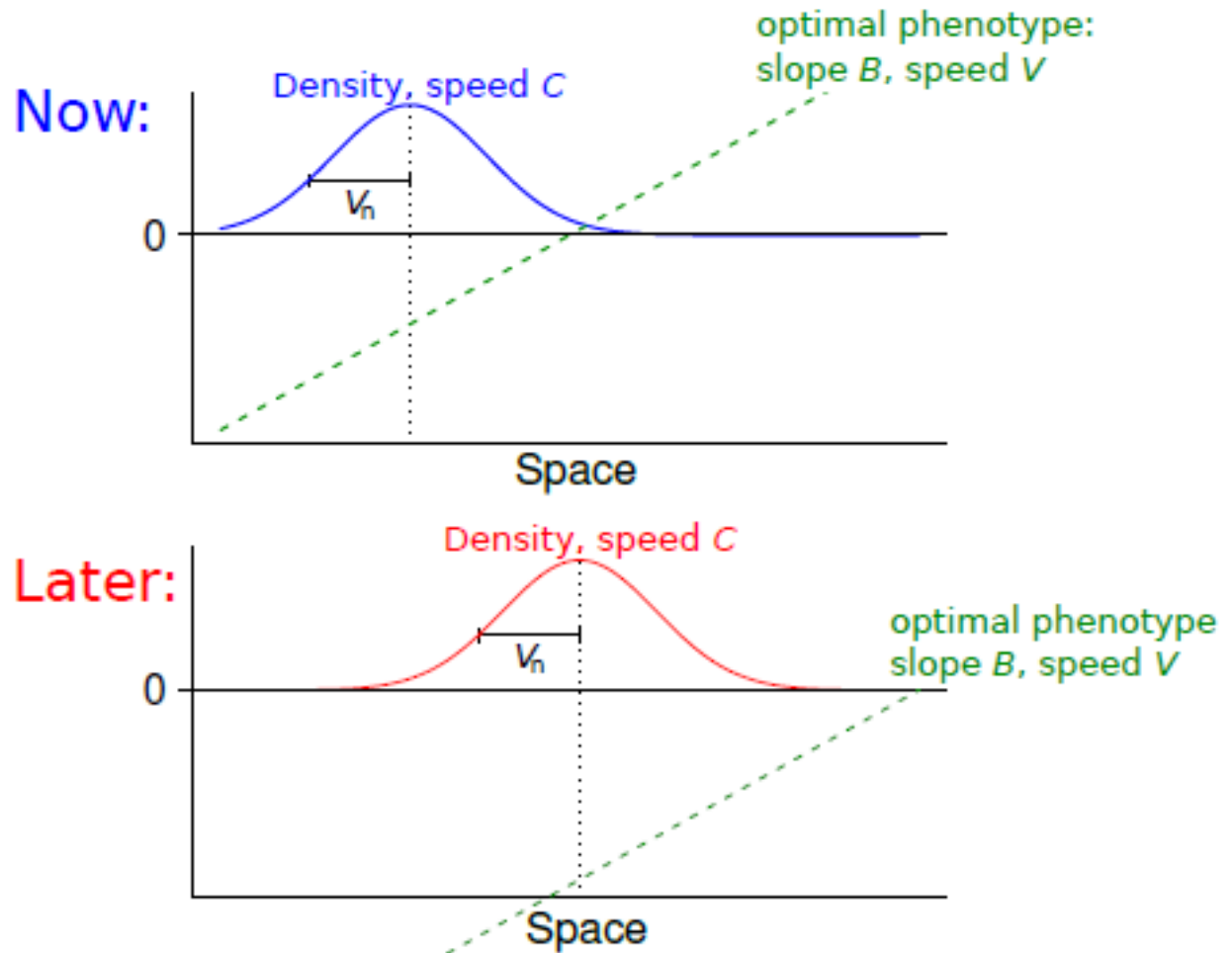
Models of range evolution with pollen



With pollen dispersal: spatial range shift and climatic niche shift

V_n = size of the range

C = speed of spatial range shift:
slower than climate

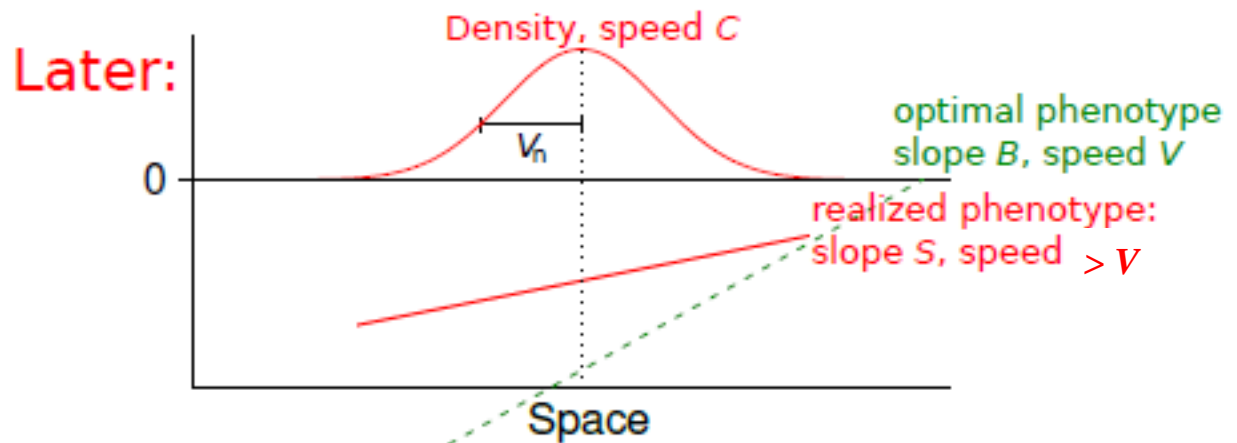
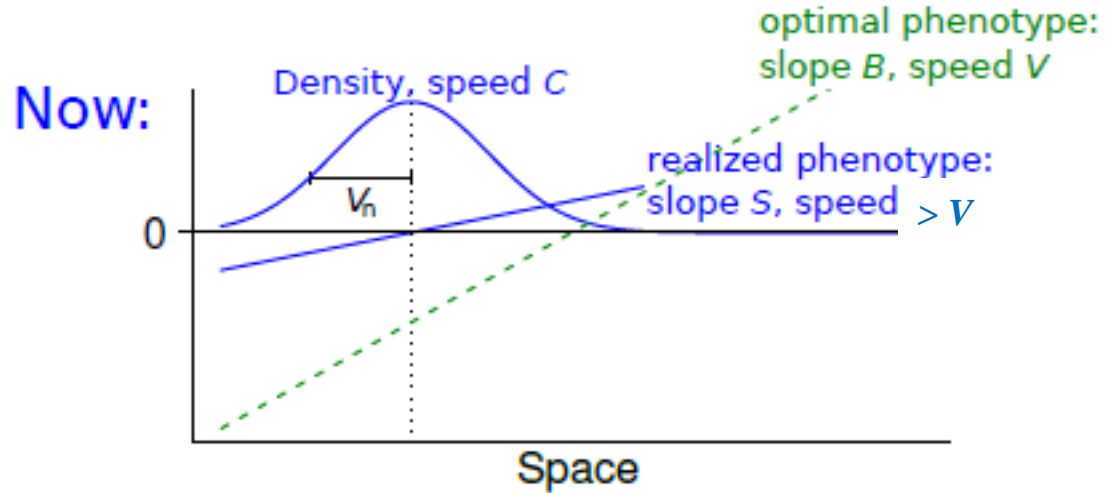


With pollen dispersal: spatial range shift and climatic niche shift

V_n = size of the range

C = speed of spatial range shift:
slower than climate

S = slope of the realized phenotype



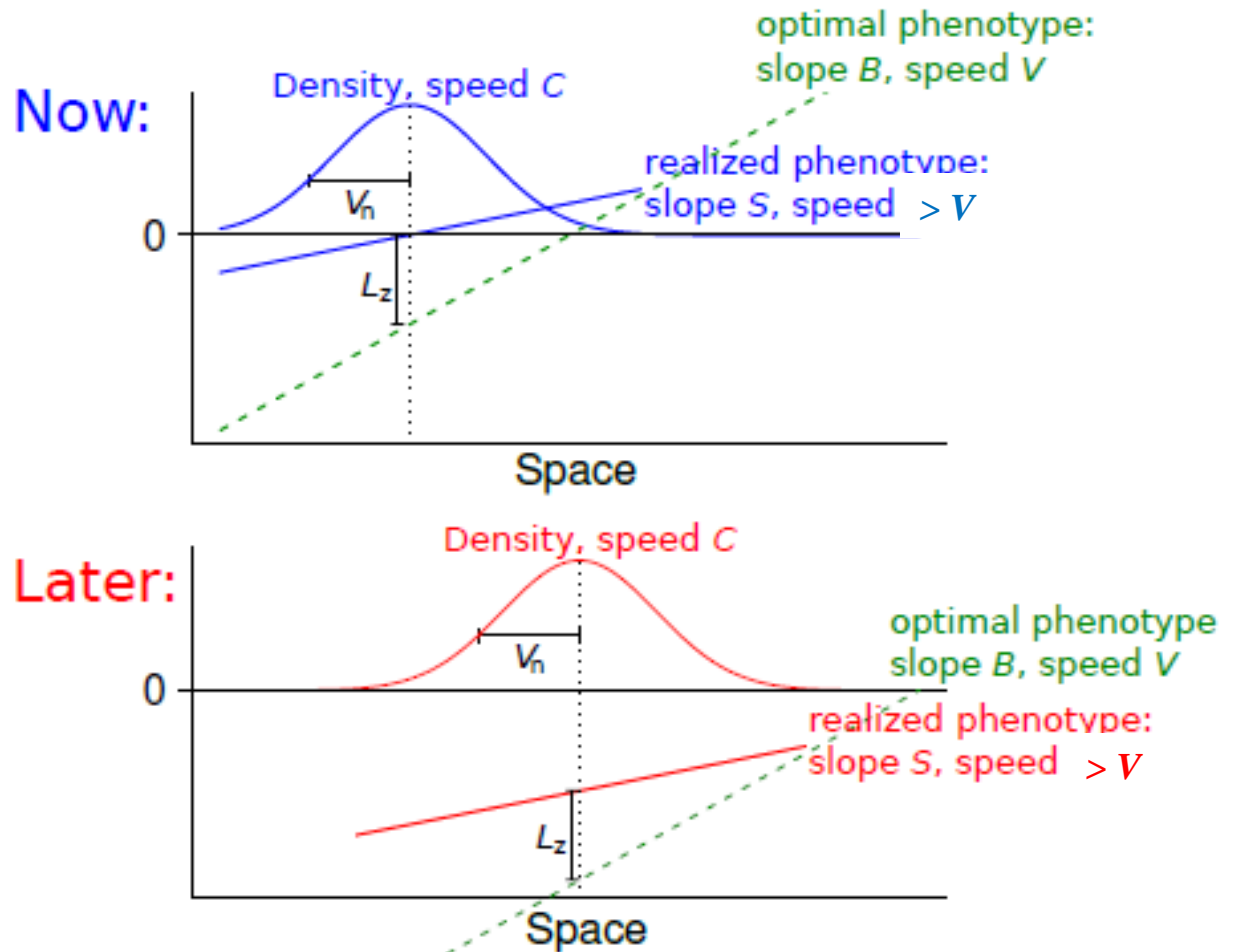
With pollen dispersal: spatial range shift and climatic niche shift

V_n = size of the range

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L_z = maladaptation at the core of the range



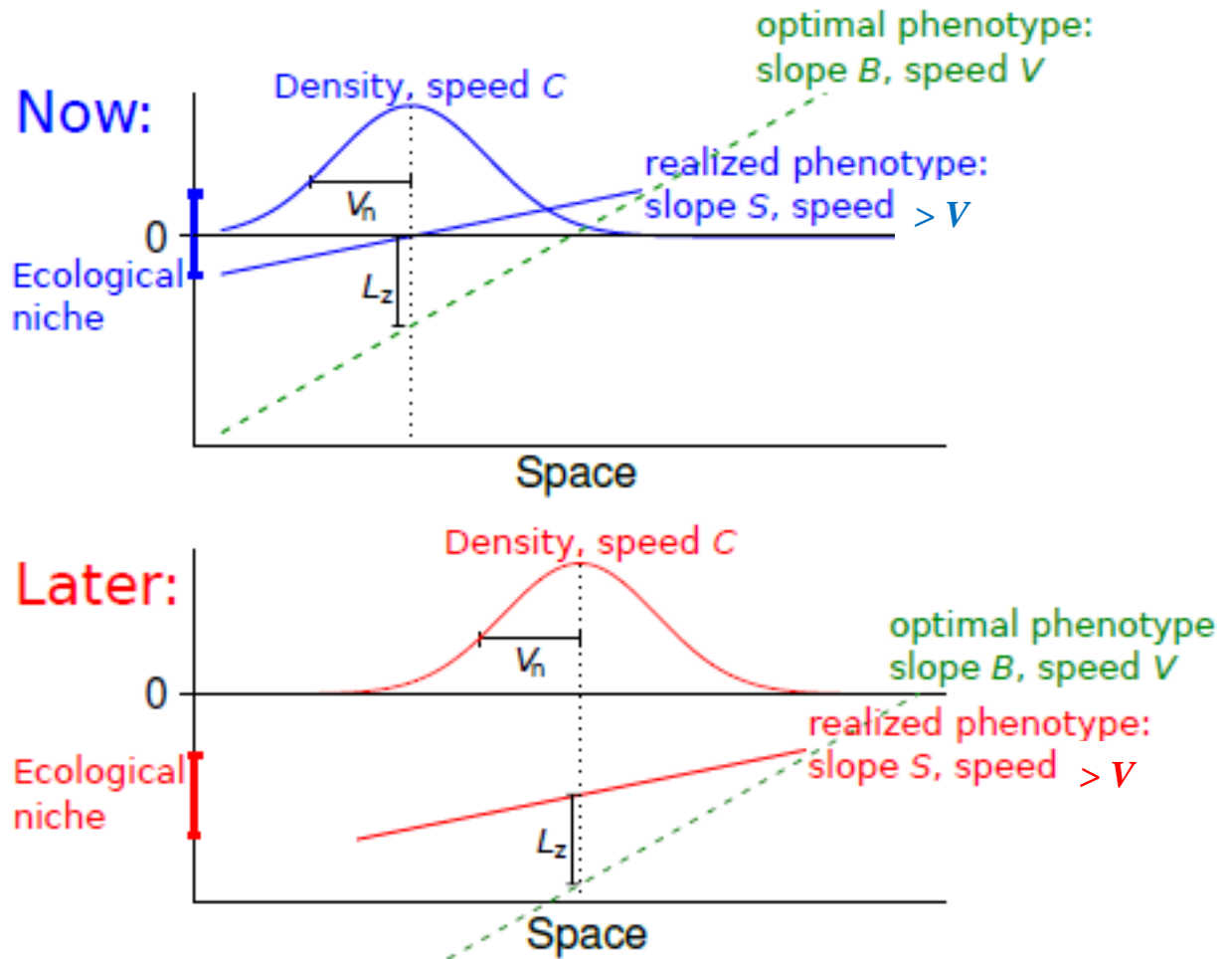
With pollen dispersal: spatial range shift and climatic niche shift

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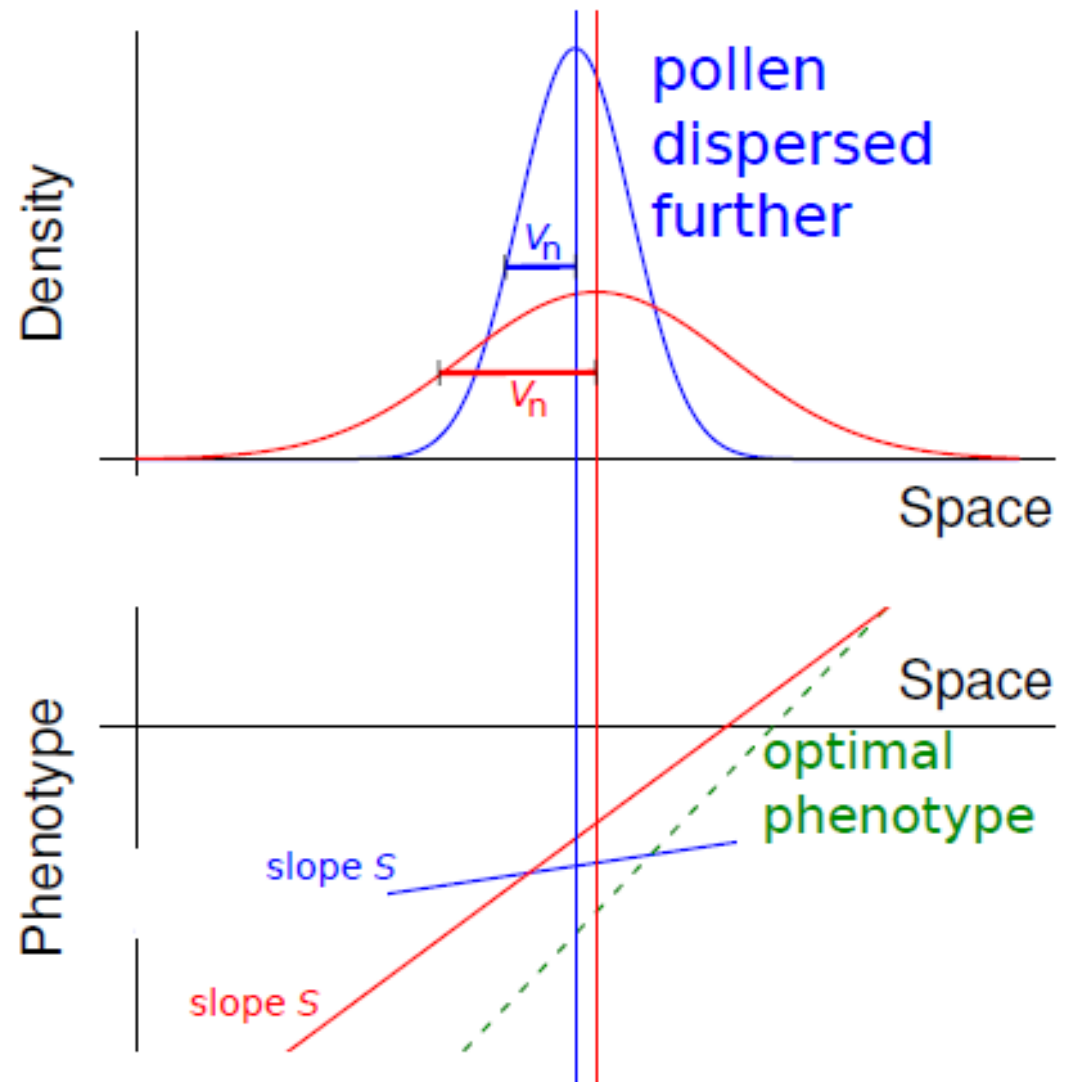
L_z = maladaptation at the core of the range



Models of range evolution with pollen

Blue = pollen dispersed further

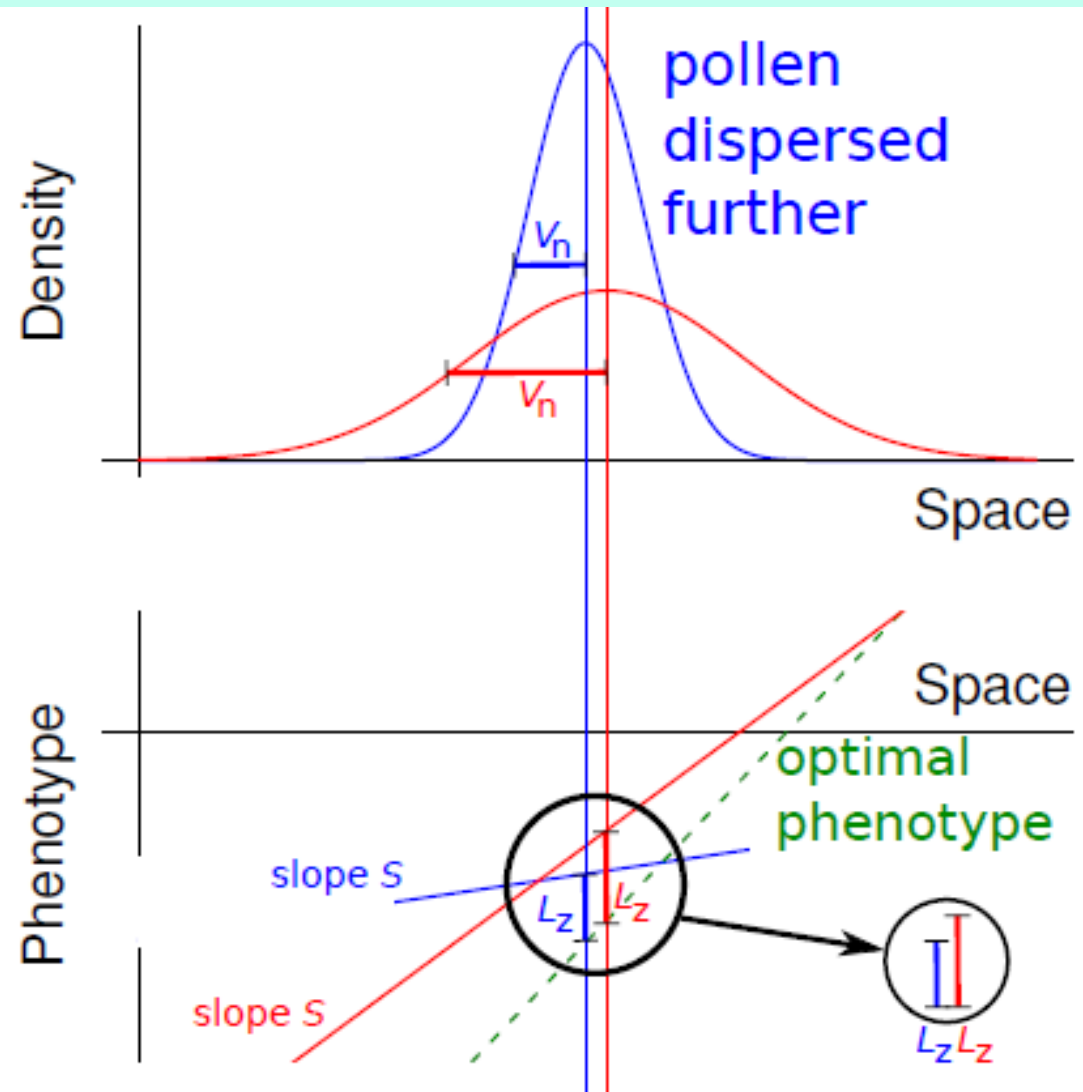
- Flatter phenotypic cline ($|S|$)
- Narrower range (V_n)



Models of range evolution with pollen

Blue = pollen dispersed further

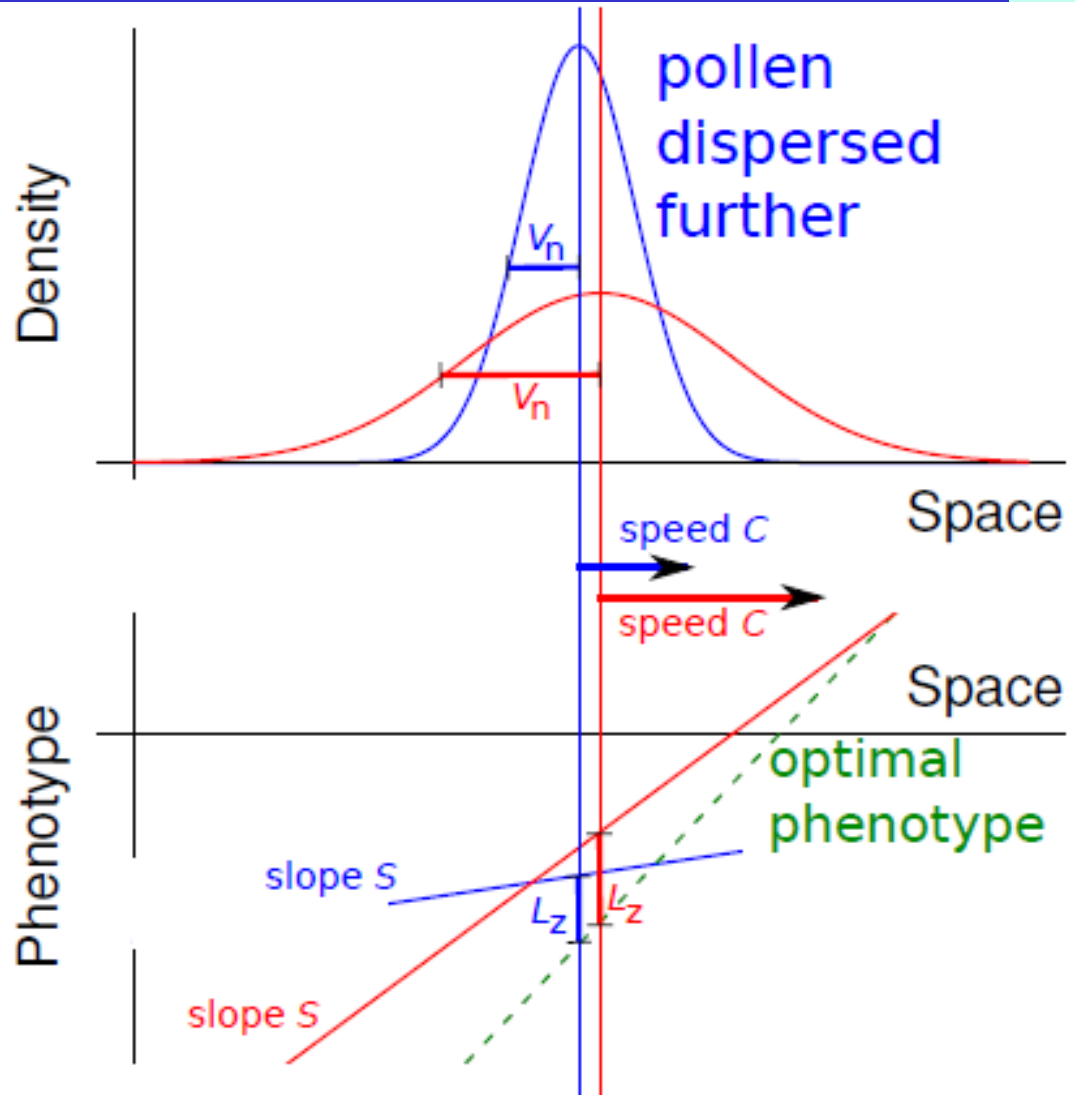
- Flatter phenotypic cline ($|S|$)
- Narrower range (V_n)
- Better adaptation at the core ($|L_z|$)



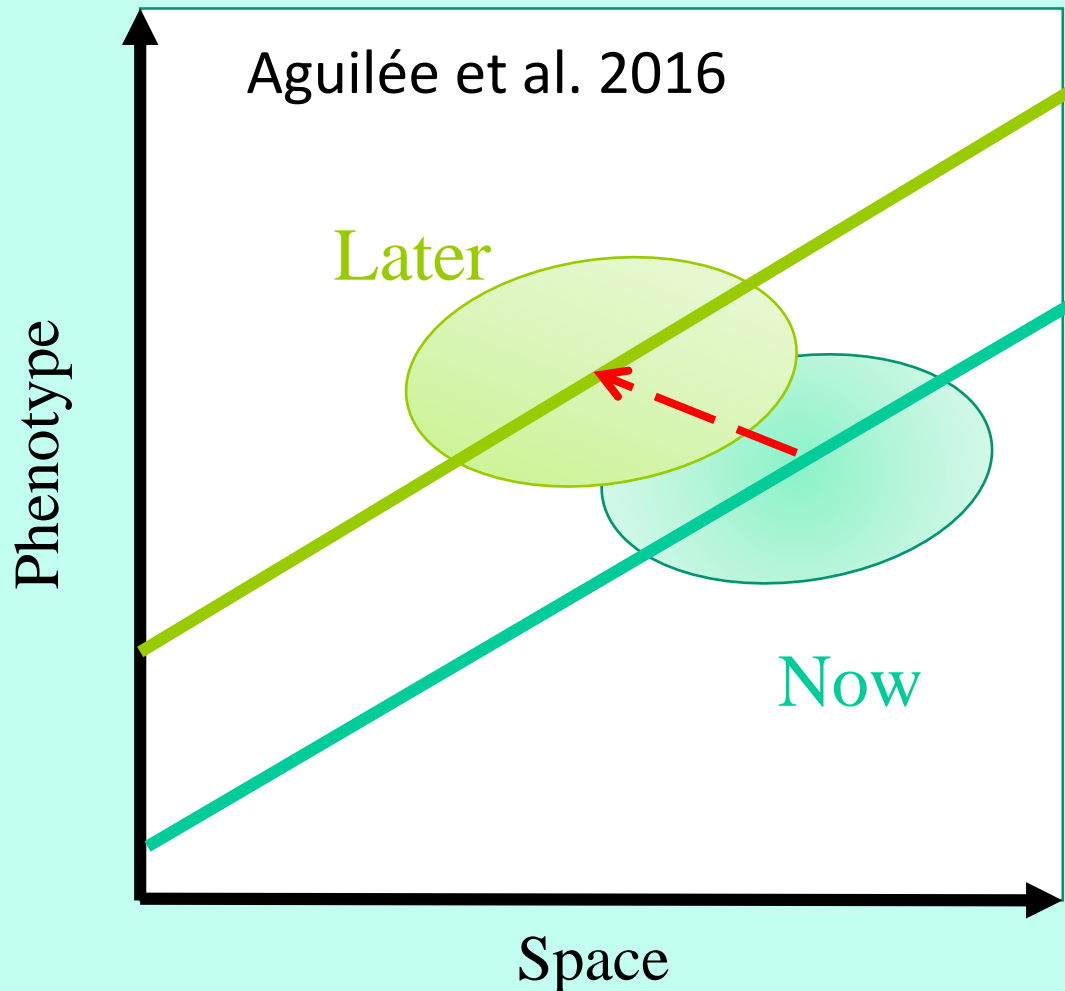
Models of range evolution with pollen

Blue = pollen dispersed further

- Flatter phenotypic cline ($|S|$)
- Narrower range (V_n)
- Better adaptation at the core ($|L_z|$)
- Slower wave (C)



Migration and adaptation can help tracking the climate



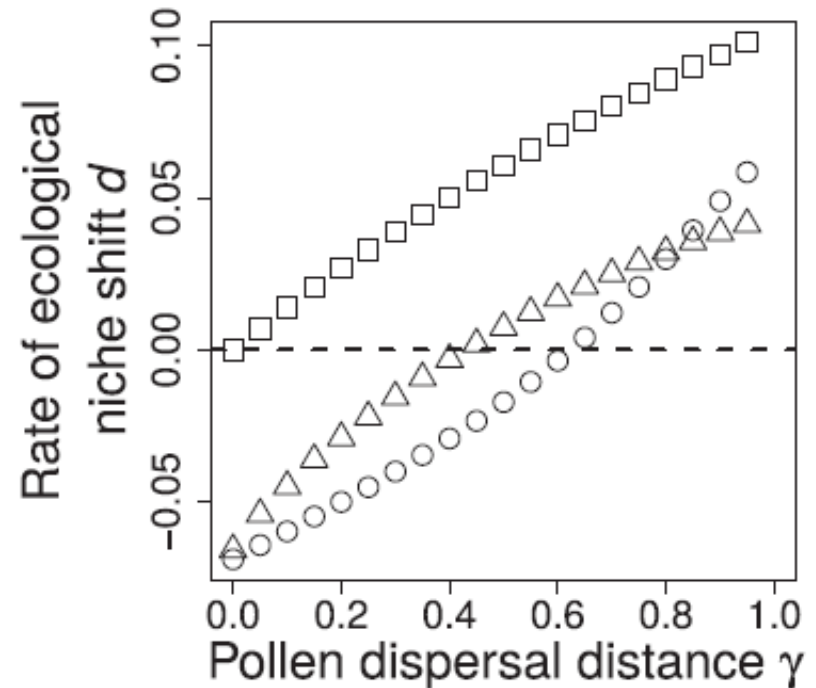
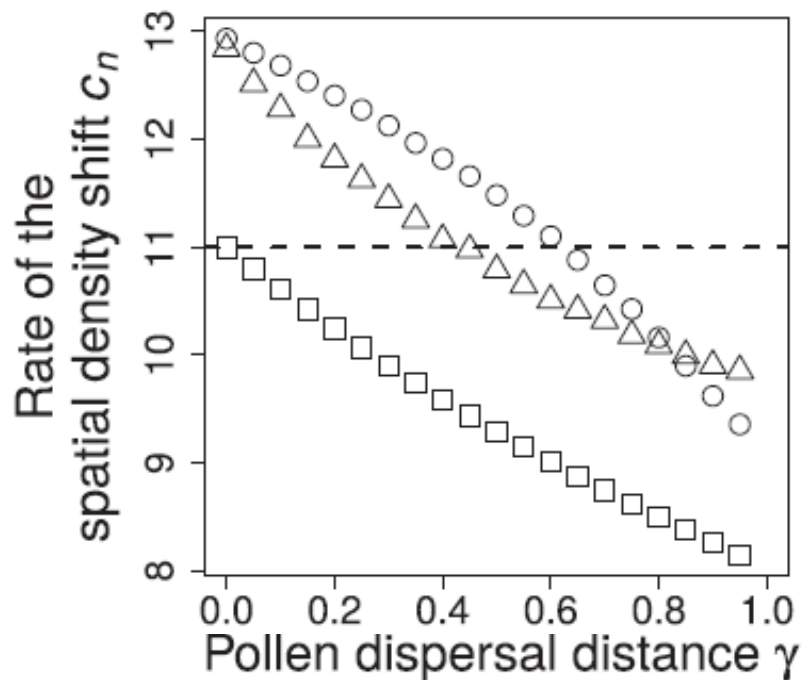
Long distance pollen dispersal slows down climate tracking through space

Long distance pollen dispersal results in niche shift and adaptation to warmer climate!

Effect of pollen on niche and range evolution under a changing climate



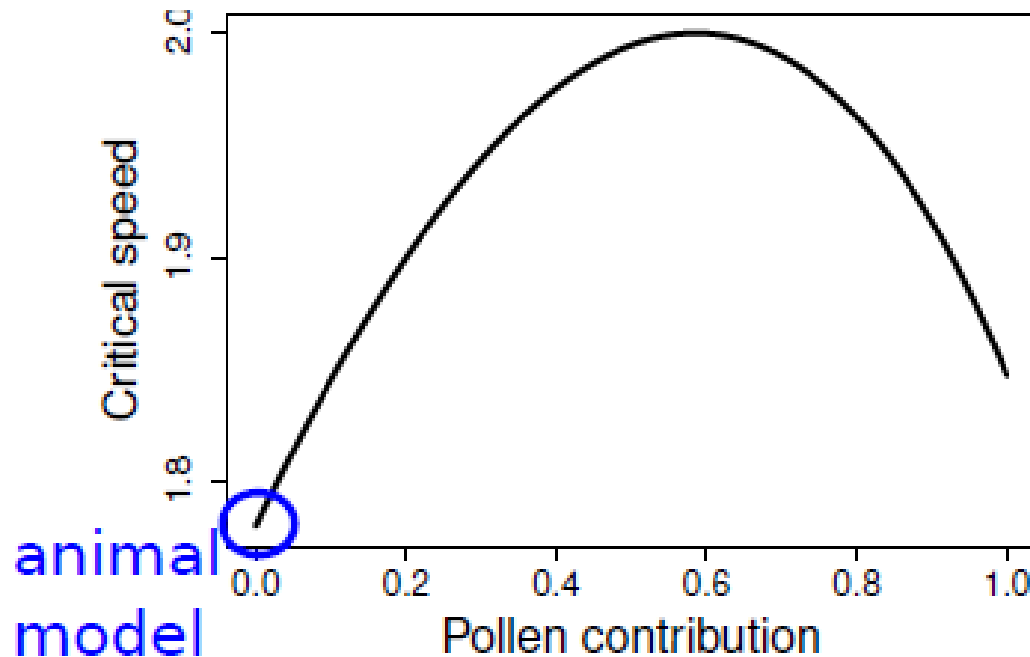
Parametrizing the model for Sitka Spruce and relaxing strong assumptions



Pollen dispersal can help persisting under faster climate change

Extinction of the species will occur if climate change is too fast

Aguilée et al. 2016

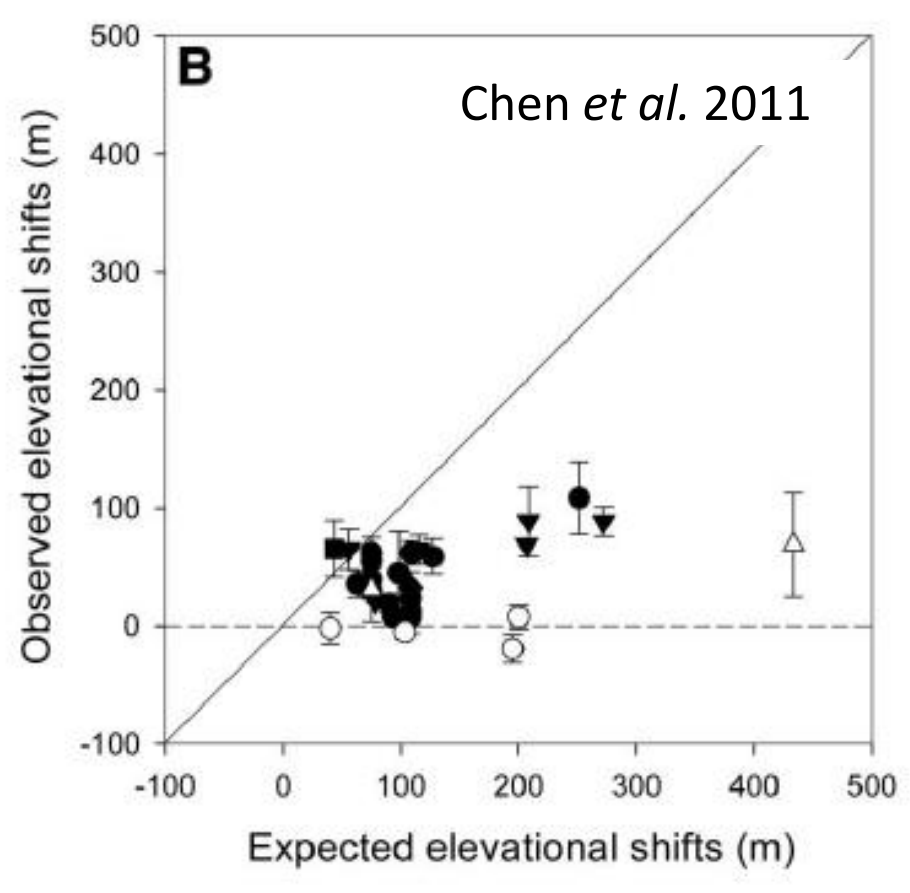
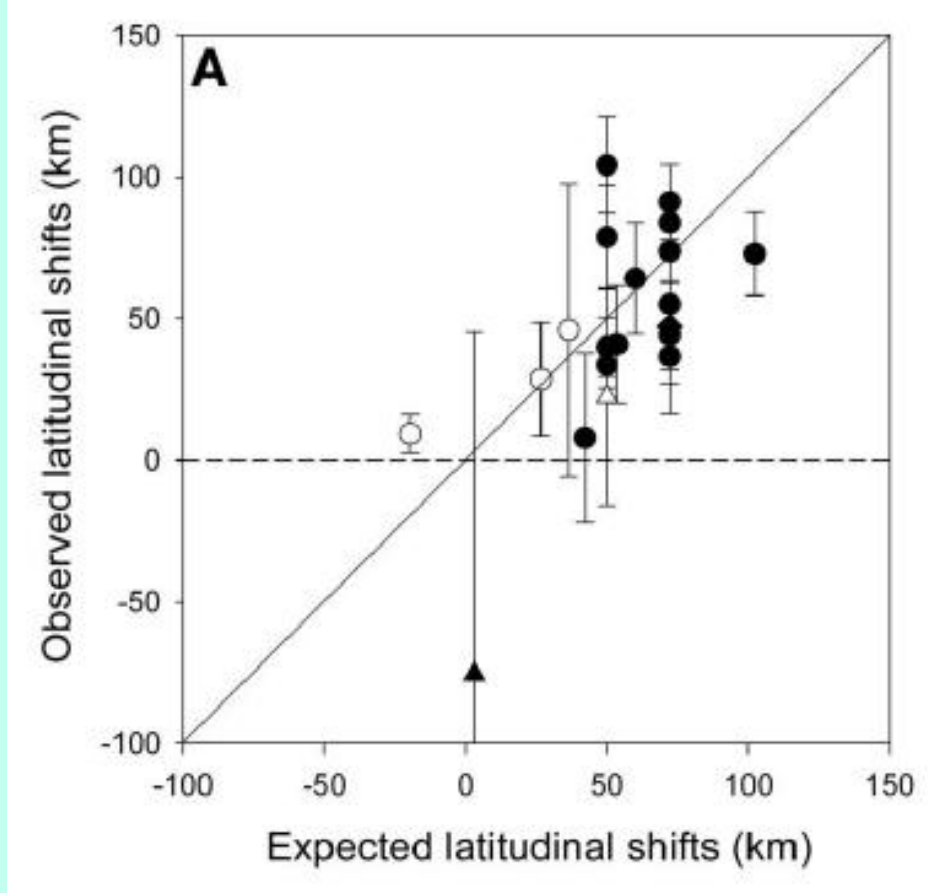


Long distance pollen dispersal can allow persistence under faster climate change

Conclusions

- Pollen dispersal worsens maladaptation at the margins but improves adaptation at the core
- Pollen dispersal slows spatial range shifts, which is compensated by climatic niche shift
- For shallow/moderate gradients: pollen dispersal allows tracking faster climate changes

Species have shifted on average by 11m in altitude and 17km in latitude per decade



Interested in models of adaptation to changing
environment?

PhD position available in our lab, Montpellier,
starting **September 2018**

Co-supervized by Ophélie Ronce (biology) and
Matthieu Alfaro (mathematics)