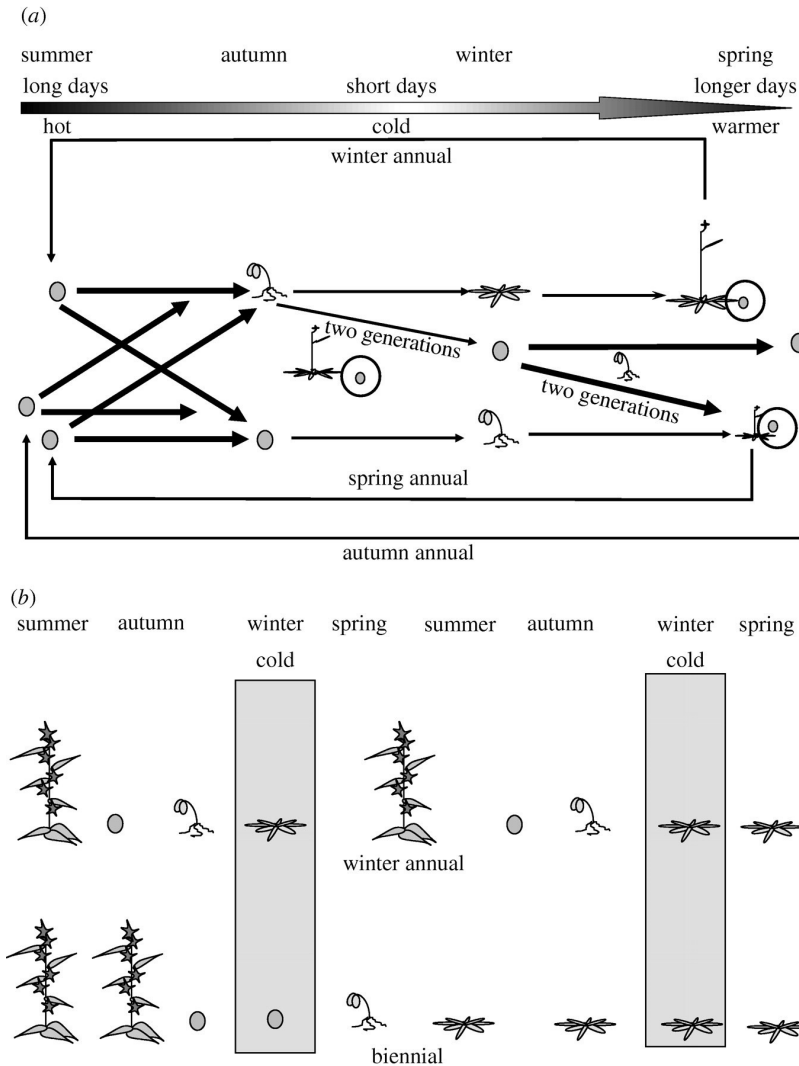# Complex life cycles and eco-evolutionary dynamics in changing environments

Module 5

Winterschool "Forward-time individual-based simulations in Ecology and Evolutionary Biology" Mar 20-24 Tvärminne
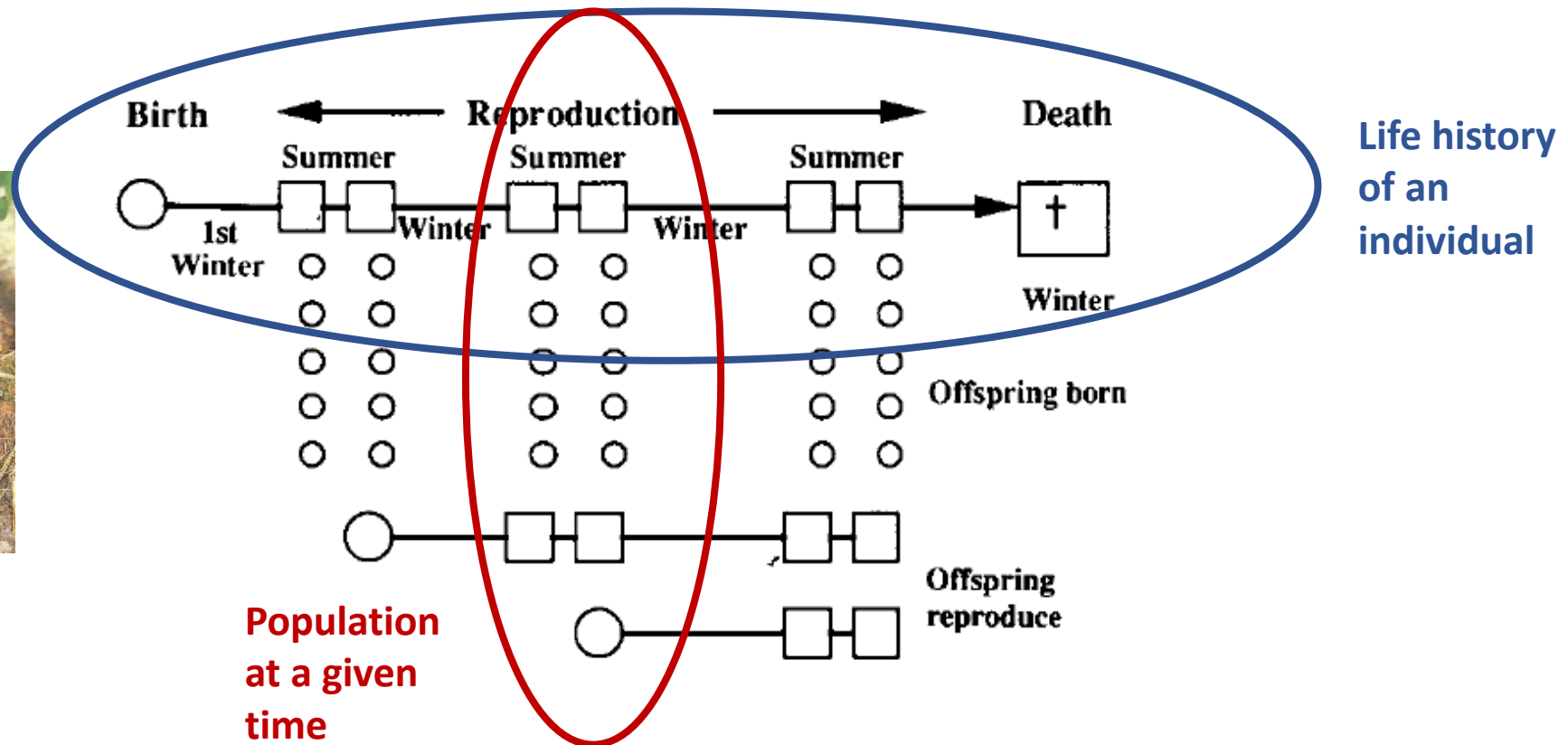
Complex life cycle

- Life history

©Scott Namestnik

Donohue 2009

Structured populations

- What is it?
    - Population heterogeneous regarding the (st)age of individuals
    - Several (st)age co-occur in the population

Life history of an individual

Population at a given time

Structured populations

« ...to understand the mechanistic basis of population fluctuations, we also generally need to allow for the demographic structure of the population. Animals of different age and sex often expend different amounts of energy at different times of the year, associated with behavior, the costs and timing of reproductive effort, growth, and maintenance. These differences can lead to variation in the strength and form of the association between vital rates, density, and extrinsic factors across age and sex classes. Fluctuations in the structure of the population, independent of the total population size, may then lead to interactions between density, weather, and the population structure to introduce heterogeneities that have an important impact on the population dynamics.» Coulson et al. 2001

Demography in structured populations

- ## How to describe changes in population structure and size with time?

Life stages

- Embryos
- Yearlings
- Juveniles
- Mature females
- Post reproductive females

Life history events

Census at t	Reproduction	Survival	Growth	Census at t+1
$N_0(t)$	$N_2 f_2 + N_3 f_3 + N_0$	$(N_2 f_2 + N_3 f_3 + N_0)s_0$	$(N_2 f_2 + N_3 f_3 + N_0)s_0(1 - g_0)$	$N_0(t+1)$
$N_1(t)$	N_1	$N_1 s_1$	$(N_2 f_2 + N_3 f_3 + N_0)s_0(1 - g_0) + N_1 s_1(1 - g_1)$	$N_1(t+1)$
$N_2(t)$	N_2	$N_2 s_2$	$N_2 s_2(1 - g_2) + N_1 s_1 g_1$	$N_2(t+1)$
$N_3(t)$	N_3	$N_3 s_3$	$N_3 s_3(1 - g_3) + N_2 s_2 g_2$	$N_3(t+1)$
$N_4(t)$	N_4	$N_4 s_4$	$N_4 s_4 + N_3 s_3 g_3$	$N_4(t+1)$

Number of females
If fecundities account for both males and females: account for the sex ratio

Demography in structured populations

- How to describe changes in population structure and size with time?
  - Notion of transition
  - Stage and age structure
  - Discrete / continuous structure and time

Census at t	Reproduction	Survival	Growth	Census at t+1
0	$N_2 f_2 + N_3 f_3$	$(N_2 f_2 + N_3 f_3)s_0$		
$N_1(t)$	N_1	$N_1 s_1$	$(N_2 f_2 + N_3 f_3)s_0$	$N_1(t+1)$
$N_2(t)$	N_2	$N_2 s_2$	$N_2 s_2 (1 - g_2) + N_1 s_1$	$N_2(t+1)$
$N_3(t)$	N_3	$N_3 s_3$	$N_3 s_3 (1 - g_3) + N_2 s_2 g_2$	$N_3(t+1)$
$N_4(t)$	N_4	$N_4 s_4$	$N_4 s_4 + N_3 s_3 g_3$	$N_4(t+1)$

g0 = 1
g1 = 1
-> Embryo embedded in yearling stage ; yearling last only one year
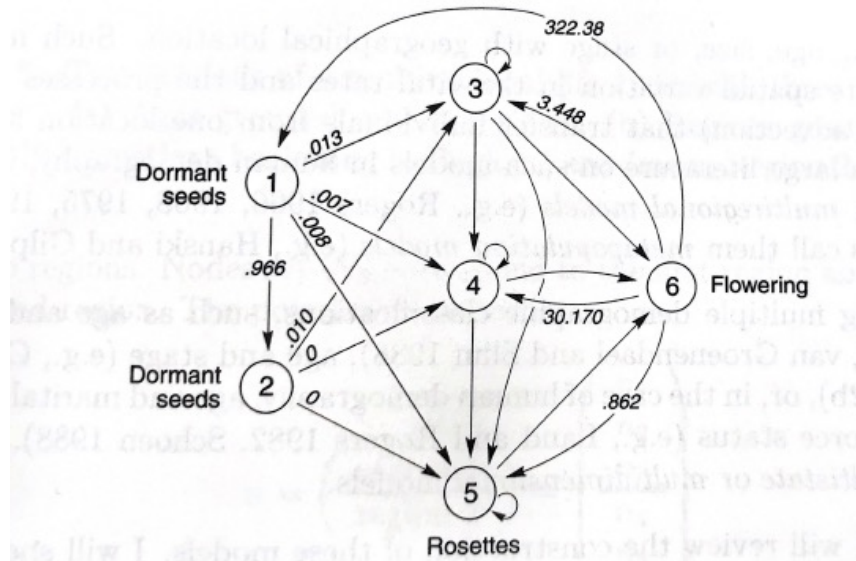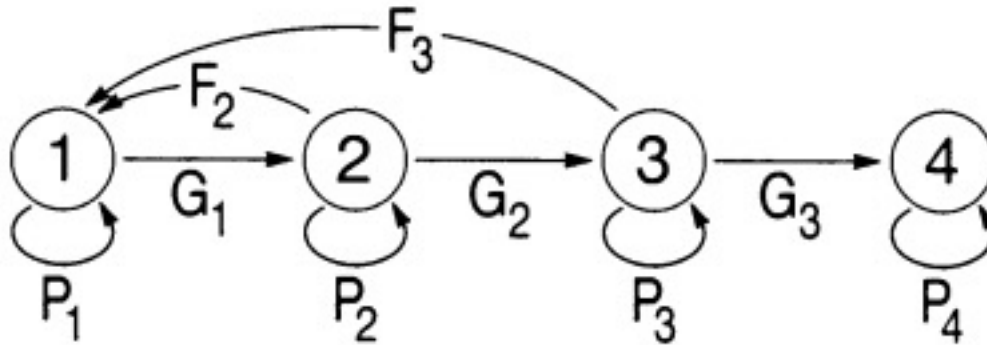
! SEEDS

Demography in structured populations

- Matrix representation

$$
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{pmatrix}_t =
\begin{pmatrix}
0 & f_2 s_0 & f_3 s_0 & 0 \\
s_1 & s_2(1 - g_2) & 0 & 0 \\
0 & s_2 g_2 & s_3(1 - g_3) & 0 \\
0 & 0 & s_3 g_3 & N_4 s_4
\end{pmatrix}
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{pmatrix}_{t+1}
$$

$\mathbf{N}(t + 1) = \mathbf{A}\,\mathbf{N}(t)$

The elements of **A** (i.e. the a_{ij}) are the **demographic transitions**

Age structure and stage structure

Continuous vs Discrete

- Continuous time

$$\frac{d\,N_x(t)}{dt} = \sum_y N_y(t) b_{y \to x}(t) - N_x(t) \sum_y g_{x \to y} - d_x N_x(t)$$

- Age/Other continuous trait

$$N_0(t+1) = \int_0^\infty N_x(t) f_x(t) dx$$

In practice,
- Wild populations are observed at discrete time intervals
- Continuous characters can structure the population (e.g. size) but can always be discretized into stages (see IPM framework)

Simulations with NEMOAGE

- Simulate the demography of the killerwhale (Caswell and Brault 1993)

Leslie matrix for the female population

$$
\mathbf{A} = \begin{pmatrix}
0 & 0.0043 & 0.1132 & 0 \\
0.9775 & 0.9111 & 0 & 0 \\
0 & 0.0736 & 0.9534 & 0 \\
0 & 0 & 0.0452 & 0.9804
\end{pmatrix}
$$

➤ No density regulation
➤ 300 generations
➤ Vary initial stage structure
➤ Pay attention to the mating system

Simulations with NEMOAGE
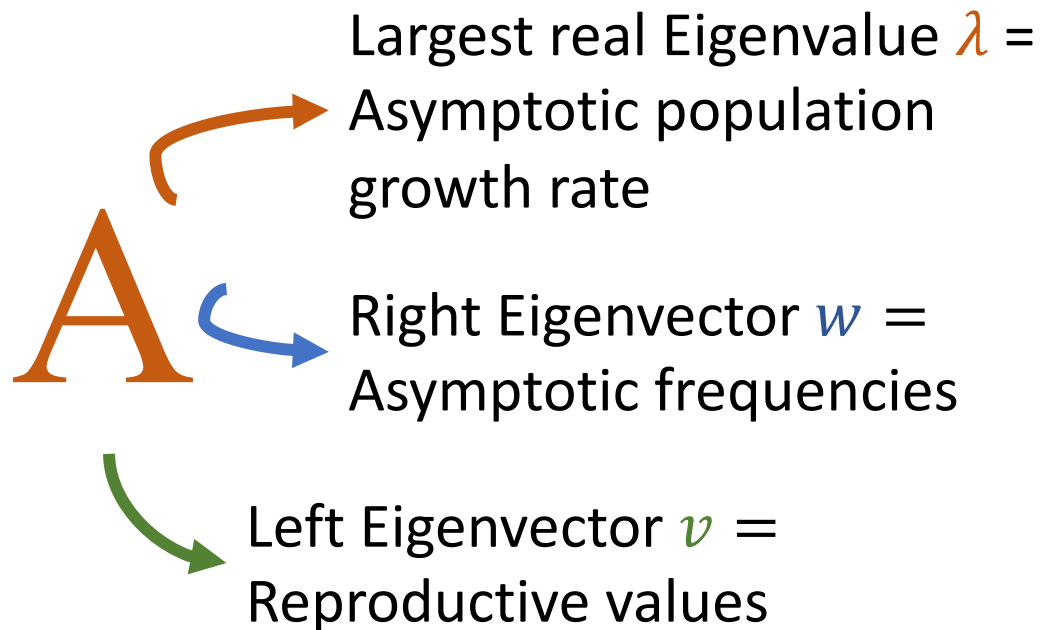
- Simulate the demography of the killerwhale (Caswell and Brault 1993)

$$A = \begin{pmatrix} 0 & 0.0043 & 0.1132 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{pmatrix}$$

- Observe that the population reaches a constant (st)age structure corresponding to a constant exponential growth rate (log representation) after a transient period

Demography in structured populations

- Exponential growth rate and equilibrium population size
  - Asymptotic behavior
  - Directly obtained from the Eigen properties of the transition matrix
    $$\mathbf{N}(t+1) = \mathbf{A}\,\mathbf{N}(t)$$

Largest real Eigenvalue λ =
Asymptotic population
growth rate

$\mathbf{A}$

Right Eigenvector $w =$
Asymptotic frequencies

Left Eigenvector $v =$
Reproductive values

Simulations with NEMOAGE

- Compare simulation result with deterministic expectation

➢ Use R

Demography in structured populations

- ## Sources of stochasticity in population dynamics

The fitness of individual i in a given year is

$$w_i = \mu_w + \delta_i, \text{ with } E[\delta_i] = 0$$

The rate of population increase in a given year is

$$\lambda = \bar{W} = \frac{1}{N}\sum_{i=1}^{N} w_i = \mu_w + \frac{1}{N}\sum_{i=1}^{N} \delta_i$$

Stochasticity in population dynamics results from yearly variation in population growth rate

$$\sigma_w^2 = \text{Var}[\mu_w] + \frac{1}{N^2}\sum_{i=1}^{N}\text{Var}[\delta_i] = \sigma_e^2 + \frac{1}{n}\sigma_d^2$$

Environmental
stochasticity

Demographic
stochasticity
F(population size)

Also true in structured populations (Lande et al. 2003)

Demography in structured population

- Density-dependence: $a_{ij}(N(t))$

  - Beverton-Holt: $a_{ij}(N(t)) = \dfrac{a_{ij}(t)}{1 + b\,N(t)}$

  - Ricker: $a_{ij}(N(t)) = a_{ij}(t)\exp(-b\,N(t))$
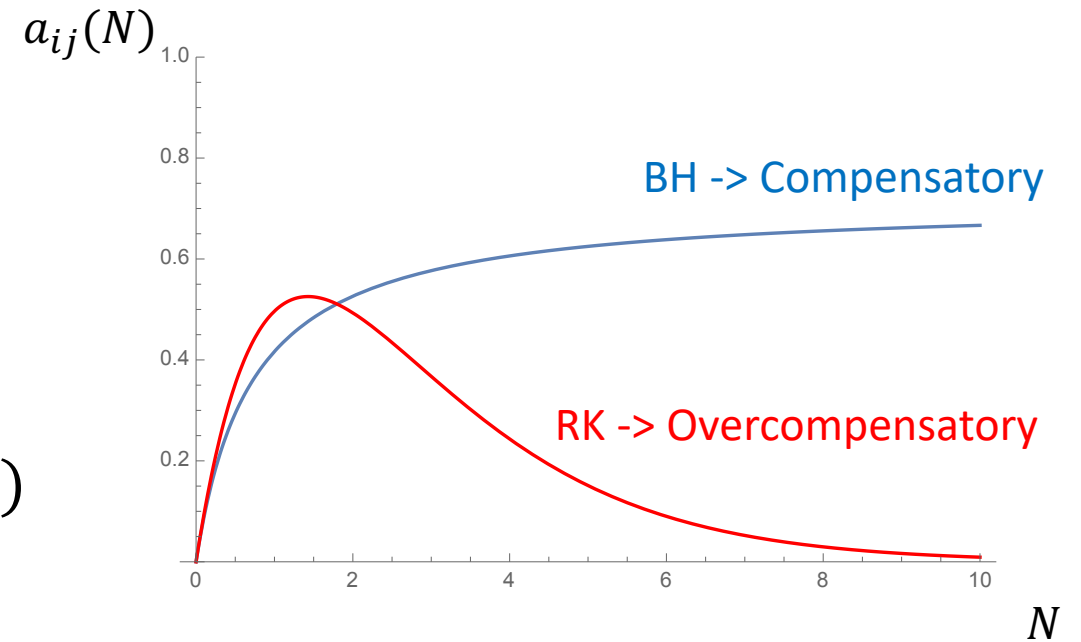
- Simulations with NEMOAGE

Simulations with NEMOAGE

- Compare Beverton-Holt and Ricker regulation

$$A = \begin{pmatrix} 0 & 0 & f_3 \\ 0.45c(N) & 0 & 0 \\ 0 & 0.05 & 0.1 \end{pmatrix}$$

$c(N)$ measures the effect of density-dependent competition on survival

➤ Vary f_3
➤ Vary the mode of regulation

From demography to fitness

- Asexual case with two genotypes

$$\mathbf{A}_i = E[\mathbf{A}|i]$$

Projection matrix given that the individual has genotype i

$$\lambda_i$$

Largest Eigenvalue of A
-> Asymptotic growth rate of genotype i

$$\bar{\lambda} = p\lambda_1 + q\lambda_2$$

Mean asymptotic growth rate

Change in genotypic frequencies

$$\Delta q = \frac{pq(\lambda_2 - \lambda_1)}{\bar{\lambda}}$$

The asymptotic growth rate can be used as a measure of fitness

If each genotype has reached the stable stage structure

Evolution in structured population

- Sexual case for a quantitative trait

$$z = g + e$$

Quantitative trait with value given by an additive genetic component and an environmental component

Distribution given by $p(g, z)$

Evolution in structured population

- Sexual case for a quantitative trait

$$z = g + e$$

$$a_{ij}(z) = t_{ij}(z) + f_{ij}(z)$$

- Transitions between stages depend on the trait (selection)
- We need to separate transitions of individuals (e.g. survival) from production of newly produced individuals (e.g. reproduction)

Evolution in structured population

- Sexual case for a quantitative trait

$$z = g + e$$

$$a_{ij}(z) = t_{ij}(z) + f_{ij}(z)$$

$$N_j(t + 1) = \sum_i \bar{a}_{ij} N_i(t)$$

$$\mathbf{N}(t + 1) = \mathbf{A}\,\mathbf{N}(t)$$

Demography depends on the mean transitions

Evolution in structured populations

- Joint distribution of phenotype and genetic value at t + 1

$$p_i'(g,z) = \theta_i(g,z)\frac{\sum_j N_j(t)\bar{t}_{ij}}{N_i(t+1)} + \varphi_i(g,z)\frac{\sum_j N_j(t)\bar{f}_{ij}}{N_i(t+1)}$$

Evolution in structured populations

- Joint distribution of phenotype and genetic value at t + 1

$$p_i'(g,z) = \theta_i(g,z)\frac{\sum_j N_j(t)\bar{t}_{ij}}{N_i(t+1)} + \varphi_i(g,z)\frac{\sum_j N_j(t)\bar{f}_{ij}}{N_i(t+1)}$$

Bookkeeping…

How to be predictive ?

      - Further assumptions for analytical tractability

      - Simulations

Evolution in structured populations

- Normal approximation: The joint distribution of genotypic values

- Weak selection: the ecological processes occur much faster than the evolutionary processes

- Lande's theorem

$$\bar{z}(t+1) - \bar{z}(t) = G \frac{\partial \ln \bar{\lambda}}{\partial \bar{z}}$$

Classical breeder's equation

Change in the mean trait value between two censuses (including all life history events)

Heritable genetic variance

Selection gradient = Effect of the trait on fitness

Evolution in structured populations

Decomposition
by stage

$$\bar{z}(t+1) - \bar{z}(t) = \frac{1}{\bar{\bar{\lambda}}} \sum_{ij} G_i \frac{\partial \bar{\lambda}}{\partial \bar{a}_{ij}} \frac{\partial \bar{a}_{ij}}{\partial \bar{z}}$$

Evolutionary
change

Additive genetic variance in stage i

Sensitivity of fitness to a change in $\bar{a}_{ij}$

Effect of the trait on $\bar{a}_{ij}$

Evolution in structured populations

- Demographic sensitivity
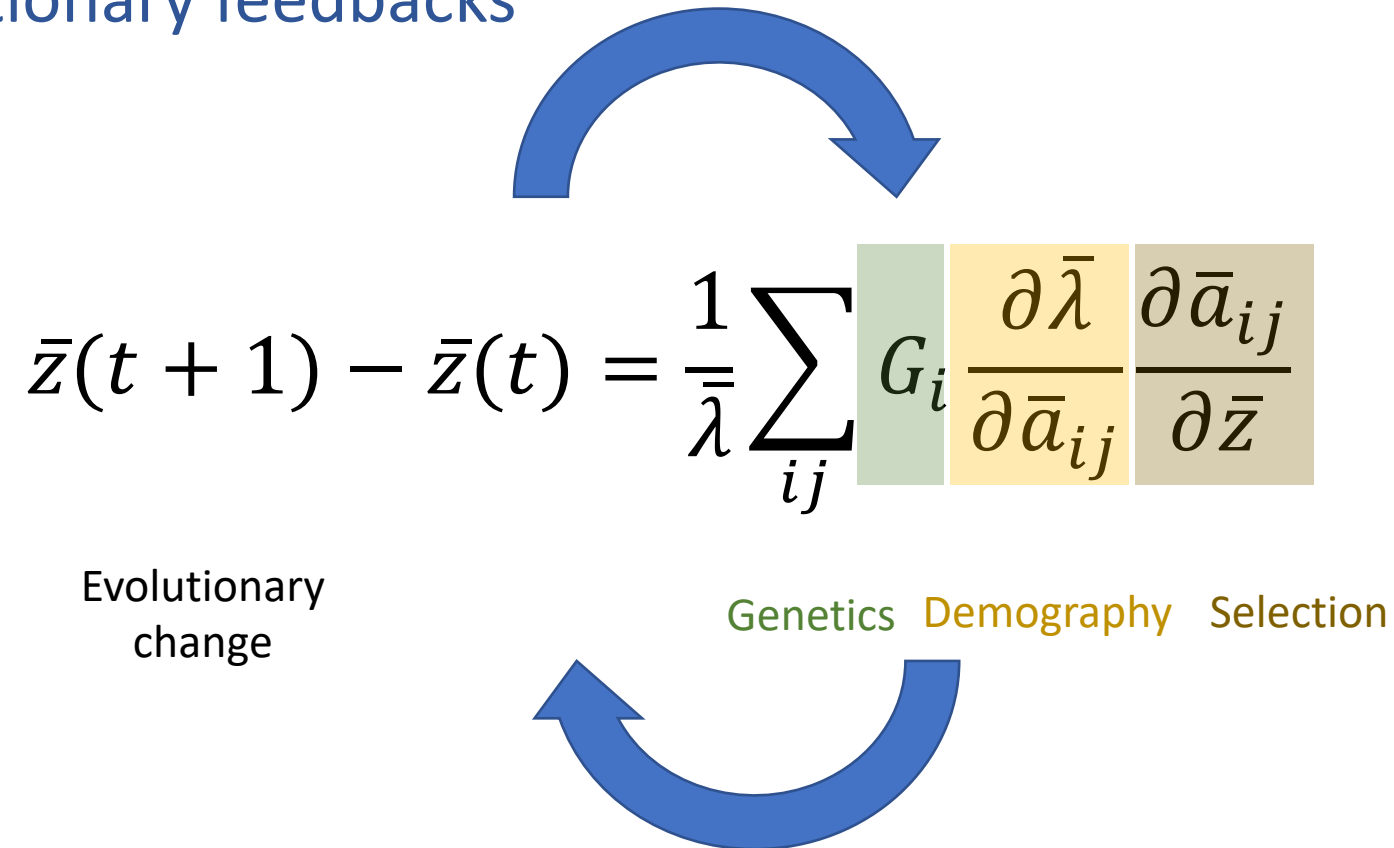
$$\bar{z}(t+1) - \bar{z}(t) = \frac{1}{\bar{\bar{\lambda}}} \sum_{ij} G_i \frac{\partial \bar{\lambda}}{\partial \bar{a}_{ij}} \frac{\partial \bar{a}_{ij}}{\partial \bar{z}}$$

Evolutionary
change

Genetics   Demography   Selection

Evolution in structured populations

- Demographic sensitivity
- Eco-evolutionary feedbacks

$$\bar{z}(t+1) - \bar{z}(t) = \frac{1}{\bar{\lambda}} \sum_{ij} G_i \frac{\partial \bar{\lambda}}{\partial \bar{a}_{ij}} \frac{\partial \bar{a}_{ij}}{\partial \bar{z}}$$

Evolutionary
change

Genetics   Demography   Selection

Evolution of a structured population in a changing environment

We need to specify how the transitions depend on the environment

Depends on knowledge on the case study ⚠️

A general model: Moving optimum

Evolution of a structured population in a changing environment

- Gaussian selection
- Moving optimum model (in space or time)

$$p_i(z)$$

$$\textcolor{red}{a_{ij}}$$

The optimum phenotype depends on the environment

Evolution of a structured population in a changing environment

- Gaussian selection
- Moving optimum model (in space or time)

$p_i(z)$

$\color{red}{a_{ij}}$

$\bar{z}_i$

Phenotypic variance

θ_{ij} Variance of the selection -> 1/strength of selection

z

The optimum phenotype depends on the environment

Evolution of a structured population in a changing environment

- Gaussian selection
- Moving optimum model (in space or time)

$$p_i(z)$$

$$a_{ij}$$
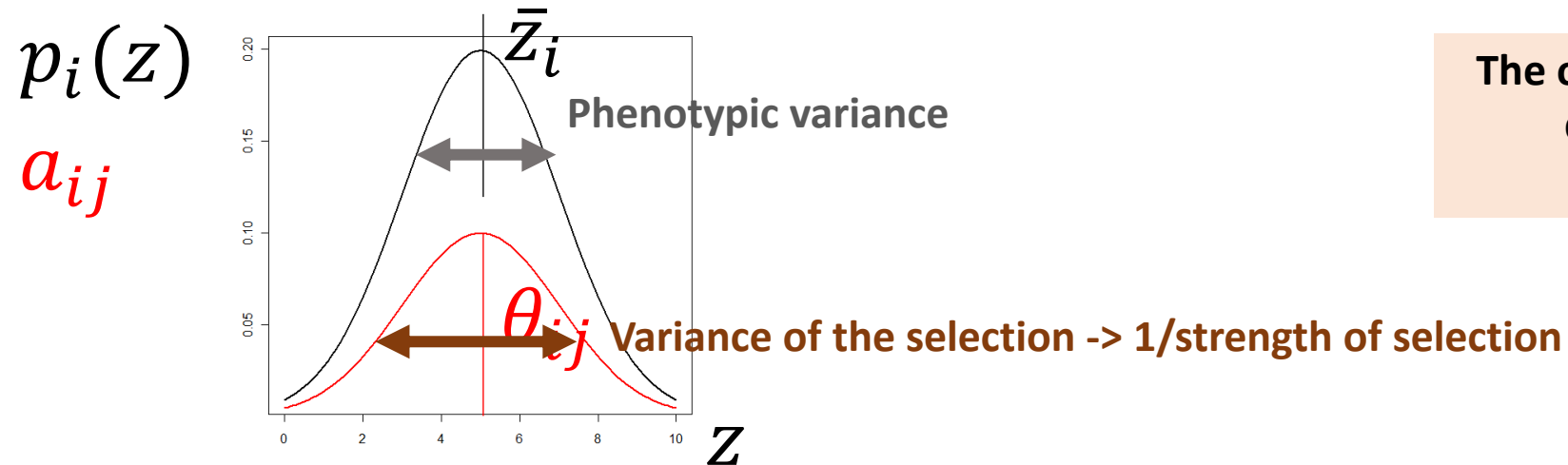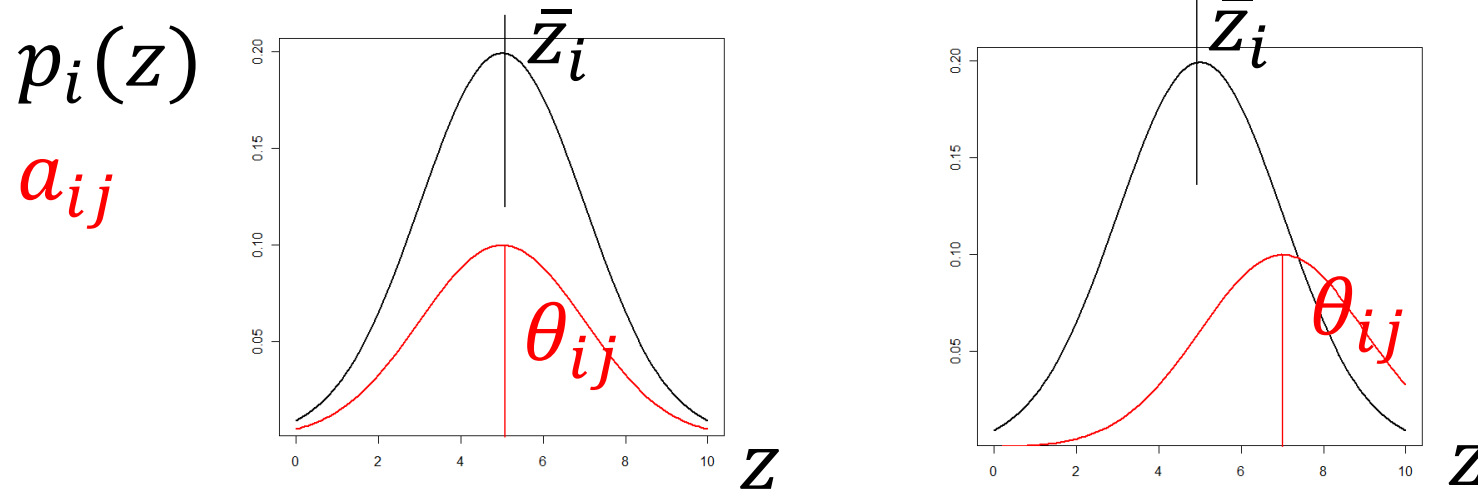
The optimum phenotype depends on the environment

Simulations with NEMOAGE

- Evolutionary rescue

$$A = \begin{pmatrix} 0.4 & 0 & 2.89 \\ 0.4 & 0 & 0 \\ 0 & 0.8c(N) & 0.5 \end{pmatrix}$$

> ➢ Quanti trait
> ➢ Choose a number of loci, the effect of mutation and the mutation rate
> ➢ Gaussian selection with $\theta(t = 0) = 0$
> ➢ Compare expected genetic variance with the strength of selection
> ➢ Perform burn-in simulations for different life histories (e.g. vary s_3) and a constant optimum (verify that genetic variance has reached equilibirum)

Simulations with NEMOAGE

- Evolutionary rescue

$$A = \begin{pmatrix} 0.4 & 0 & 2.89 \\ 0.4 & 0 & 0 \\ 0 & 0.8c(N) & 0.5 \end{pmatrix}$$

➤ Implement environmental change
`selection_rate_environmental_change (@g0 0, @g250 0.05, @g500 0)`
➤ Characterize the evolutionary and demographic dynamics
➤ How does the life history trait that you varied affect the evolutionary and demography dynamics?
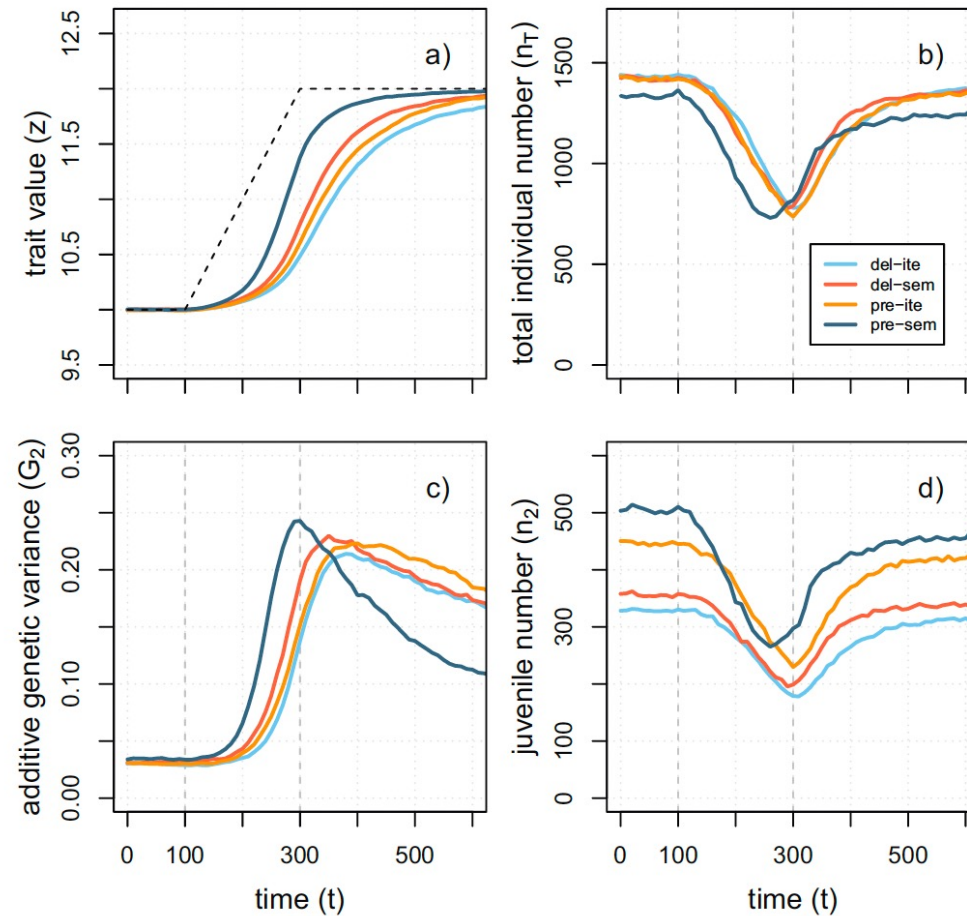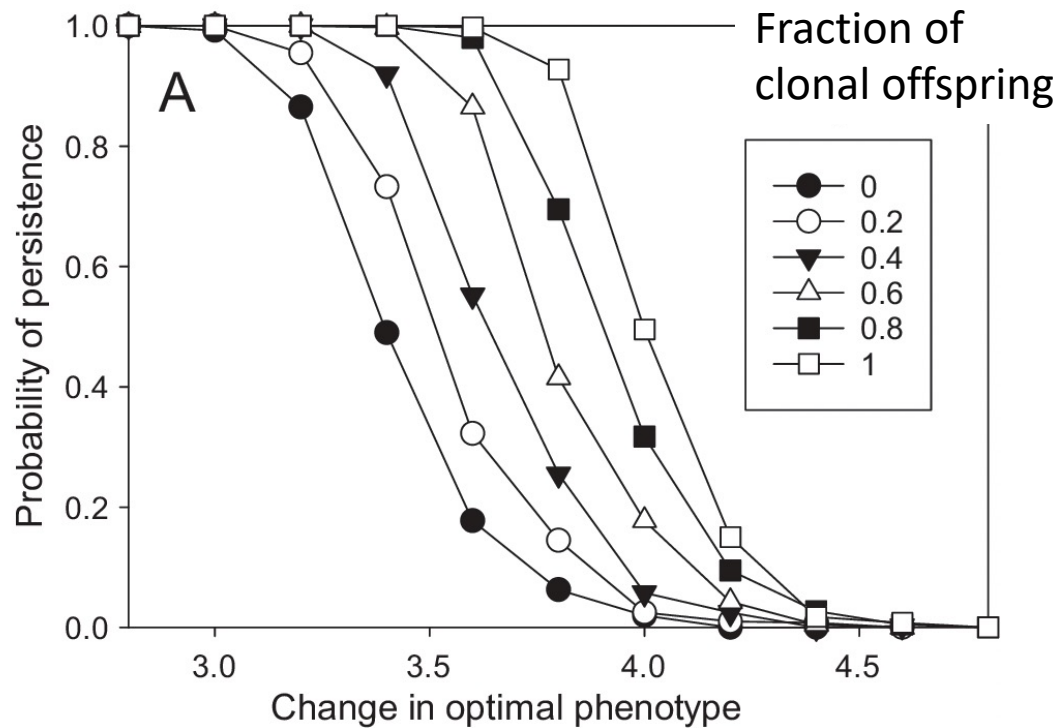➤ Add some cloning – How does it affect the dynamics

Evolutionary Lag and effect on life history

Two life-history gradient
- Precocious – delayed maturity
- Semelparous – Iteroparous

Evolvability-persistence trade-off
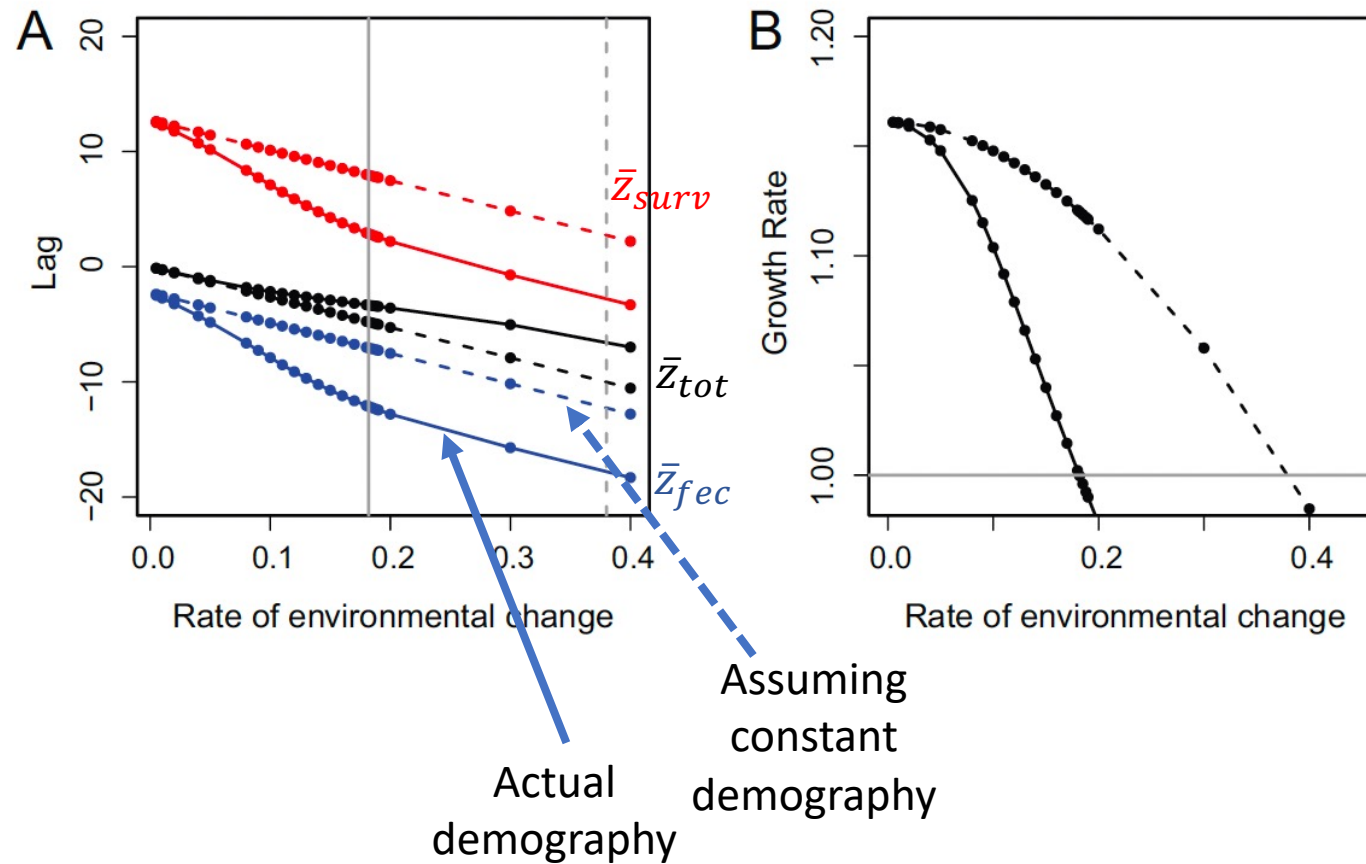

Schmid et al. 2022 AmNat

Cloning

One-step environmental change
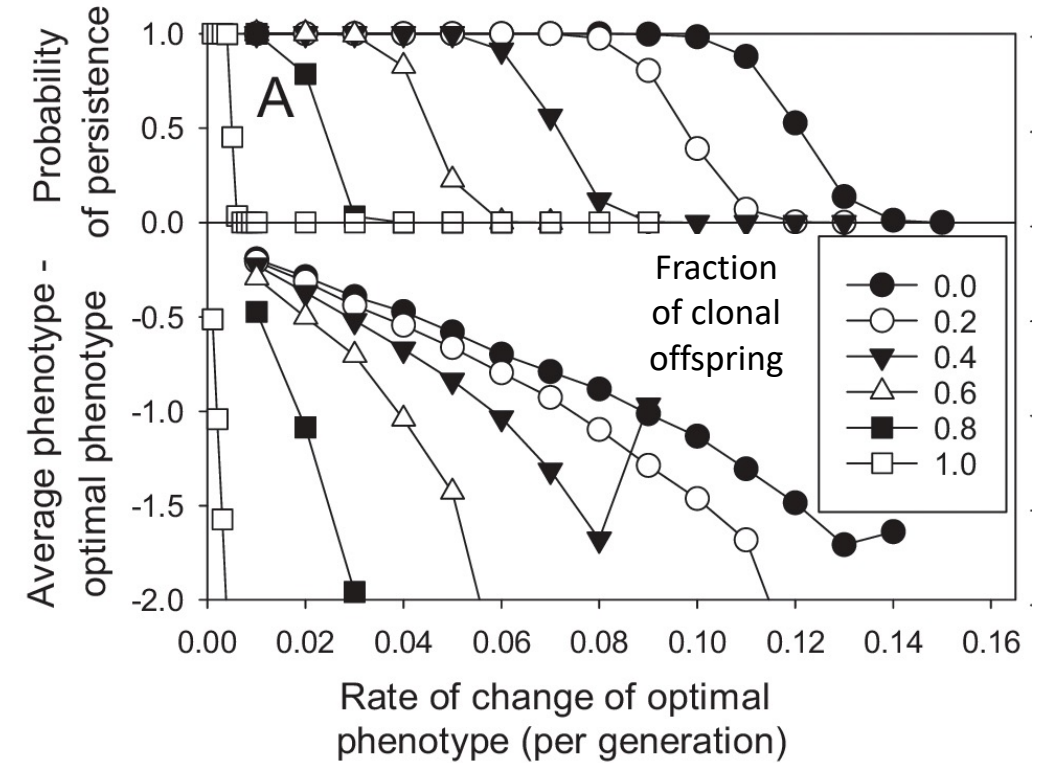
Linear environmental change

Effect of cloning depends on the type of environmental change

Eco-evolutionary feedback

Cotto et al. 2019 AmNat
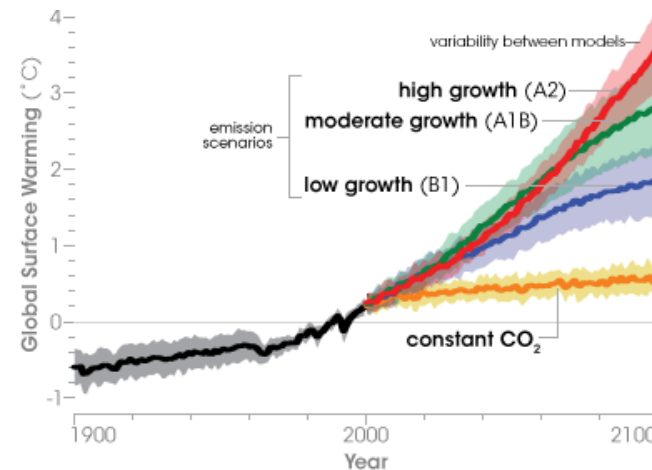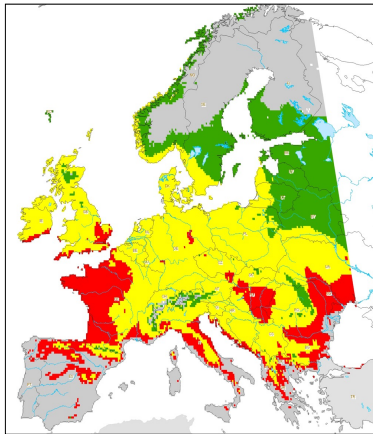
Individual based simulations

- Account for stochastic processes (demographic stochasticity and drift)
- Account for demography-genetics-evolution feedback loops
- Allow to make predictions in complex scenarios (e.g. spatiotemporal variation of the environment)

Predicting species range
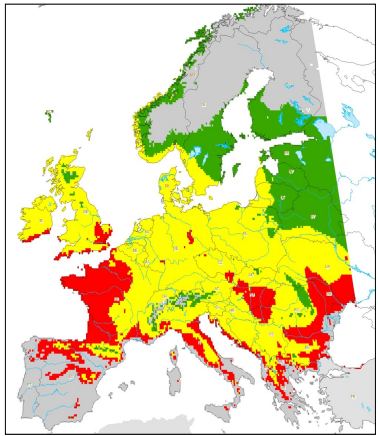
Niche Modelling

\+

Climate Modelling

"Today's scientists are facing the enormous challenge of predicting how climate change will affect species distributions and species assemblages. To do so, ecologists are widely using phenomenological models of species distributions that mainly rely on the concept of species niche and **generally ignore species' demography, species' adaptive potential, and biotic interactions**."
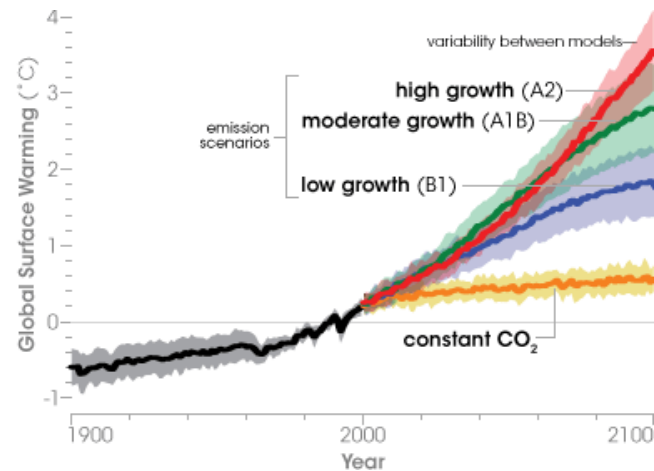Lavergne et al. 2010 Annu. Rev. Ecol. Evol. Syst.
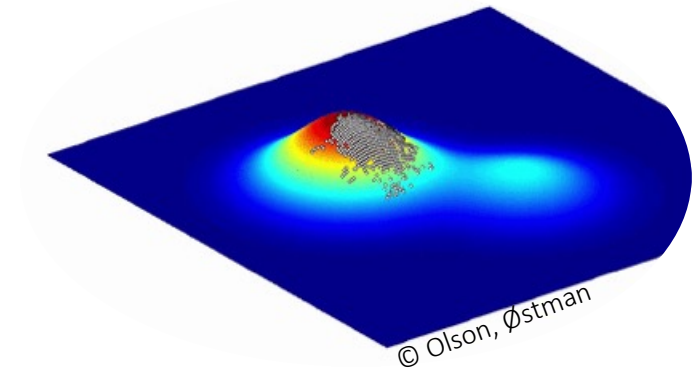
Predicting species range

Niche Modelling

+

Climate Modelling

+

Eco-Evolutionary Modelling

© Olson, Østman

- Complex life history
- Demography
- Dispersal capacity
- Evolution

Simulations with NEMOAGE

- Evolution of a species range

➢ Simulate a species distribution model (R-script)
➢ Define a life history of your choice (see Compadre or Comadre databases if needed)
➢ Predict future species distribution (build-on previous simulations)
➢ How are the predictions sensitive to unknown parameters?
➢ How does evolution play out? And demography?