Models of adaptation to climate change for complex life cycles

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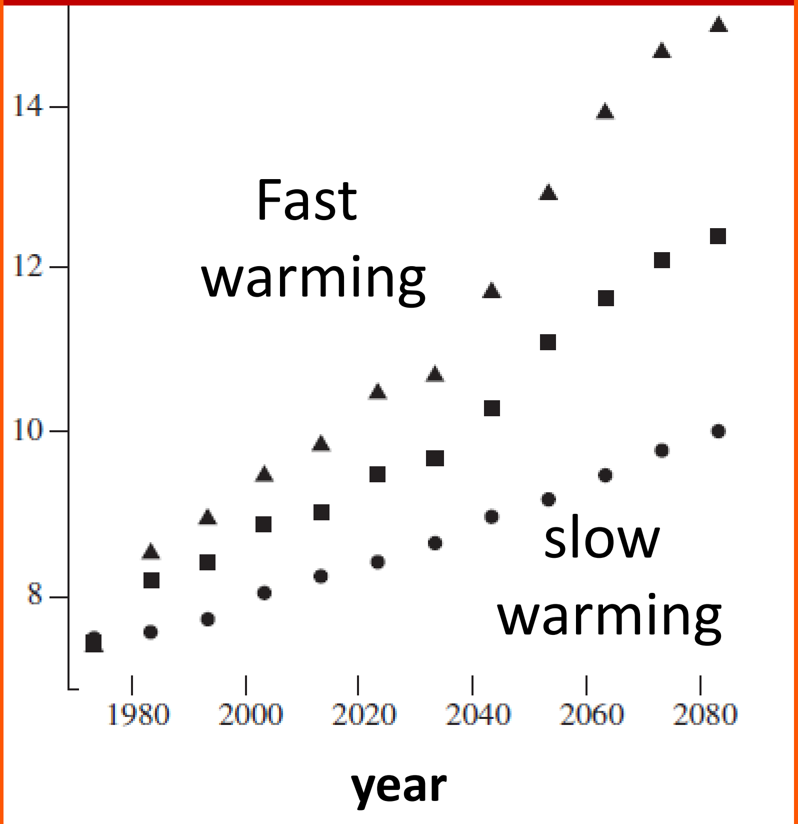
ADAPTIVE CHALLENGES ASSOCIATED WITH CLIMATE CHANGE: ATTEMPTS TO FORMALIZE THEM

Climate warming will favor different phenotypes

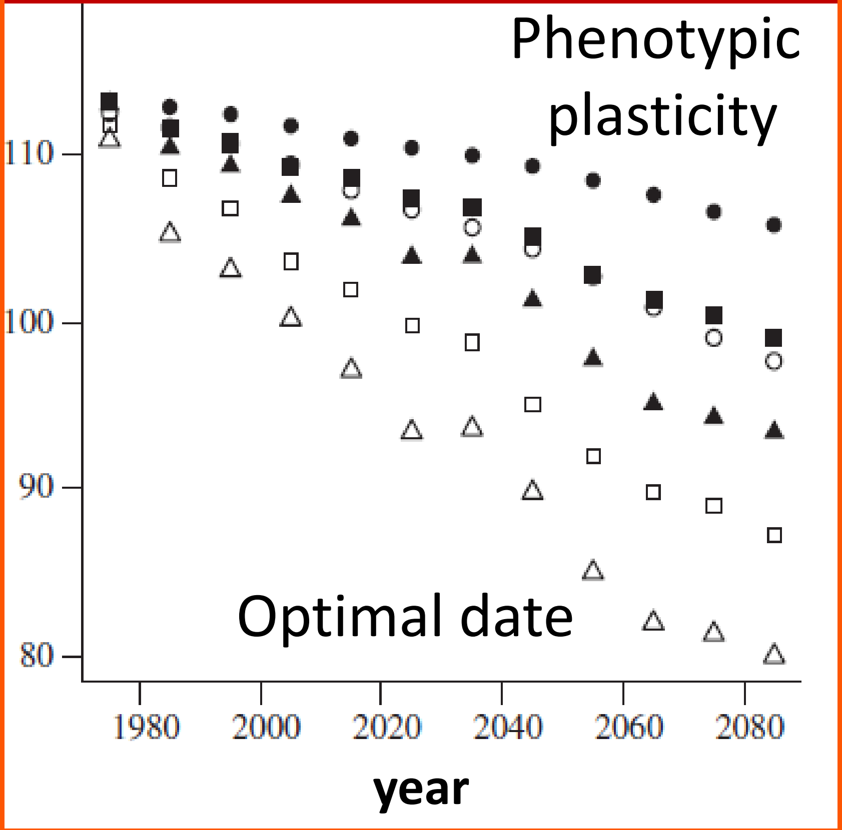
Parus major

Gienapp et al. 2013

Temperature



Laying date

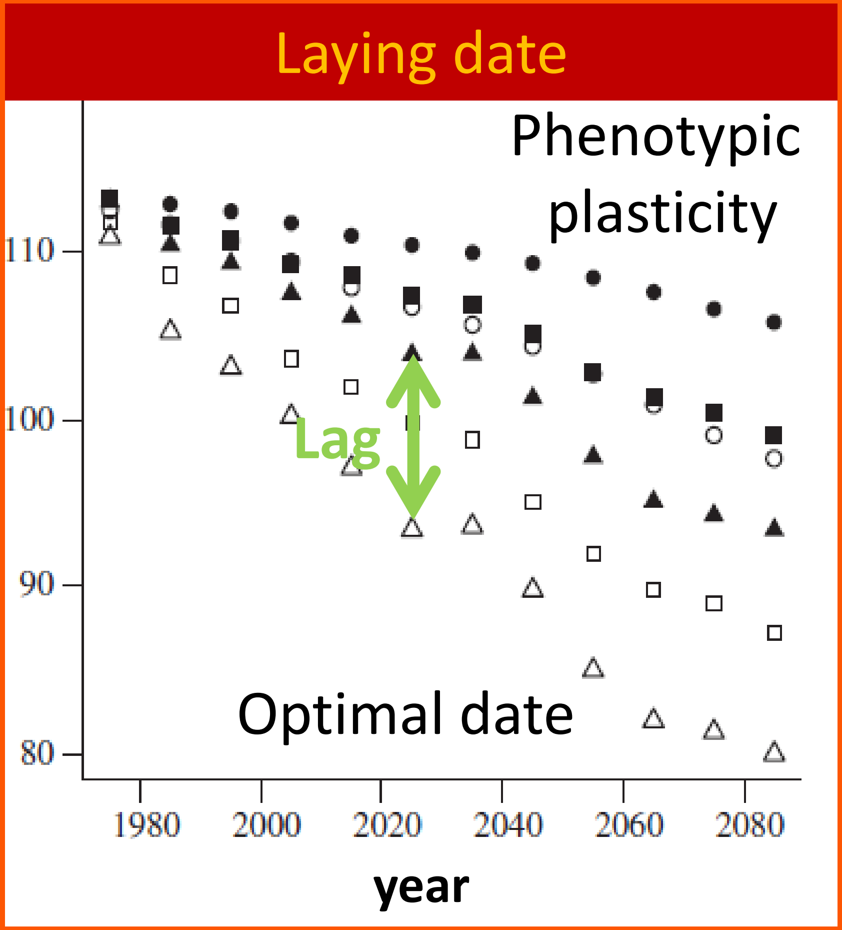


Climate warming will favor different phenotypes

Parus major

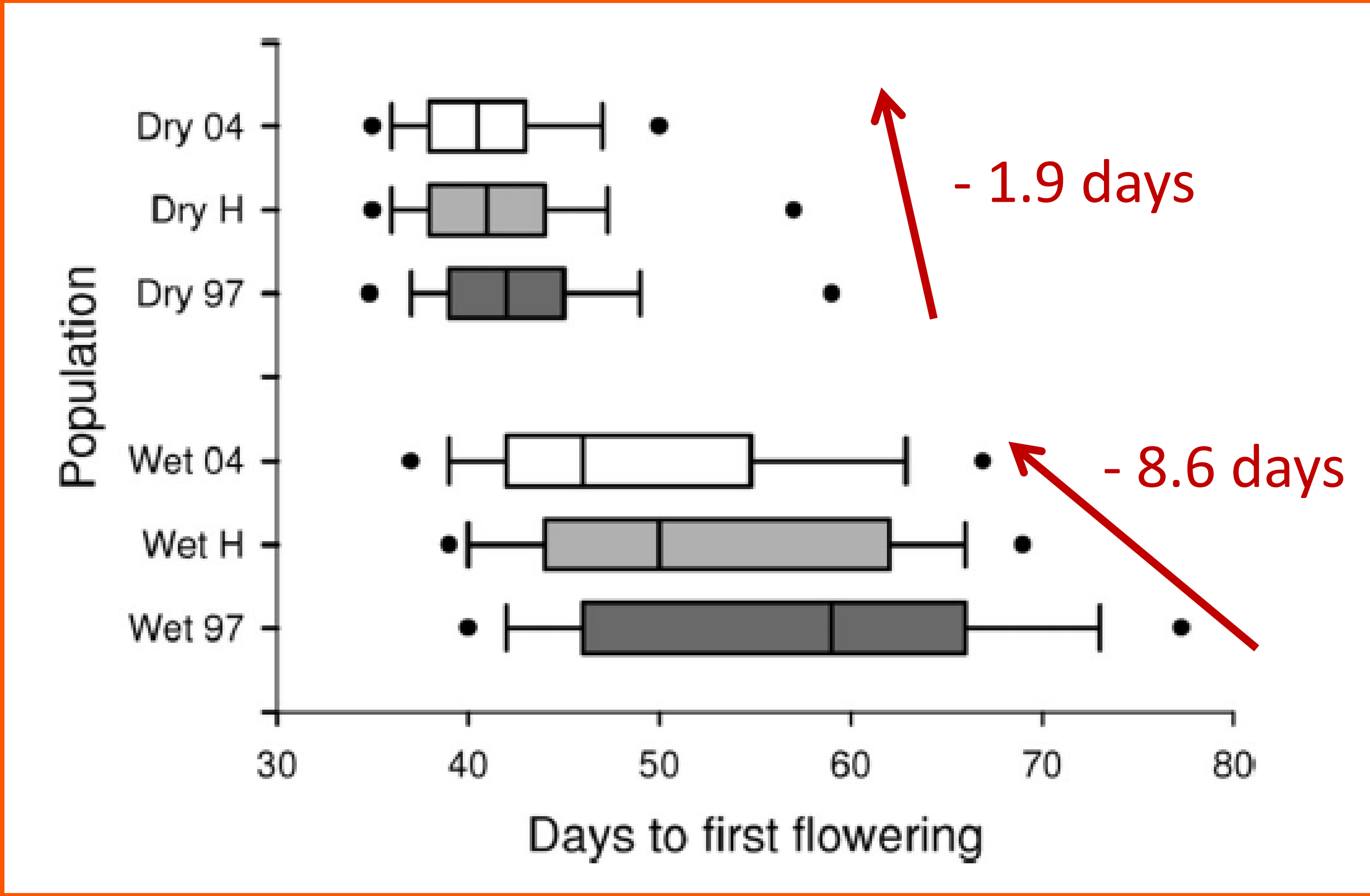
Gienapp et al. 2013

Selection for genotypes with earlier laying date



Climate change has already triggered evolutionary change

Franks et al. 2007



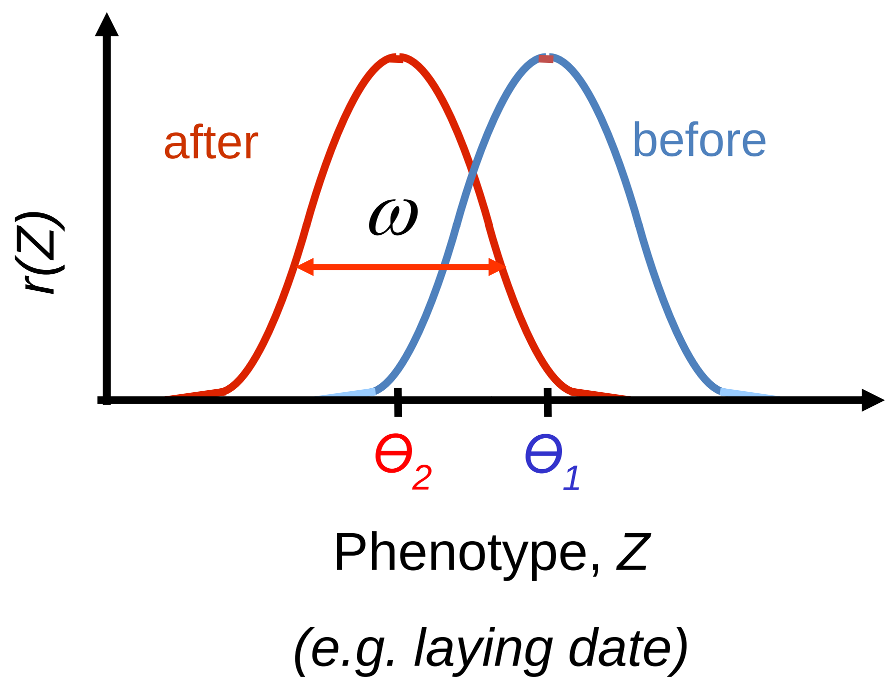
Brassica rapa

Is this fast enough?

Modelling adaptation in a changing environment

Lynch et al. 1991

Malthusian fitness *r* of individual with phenotype z

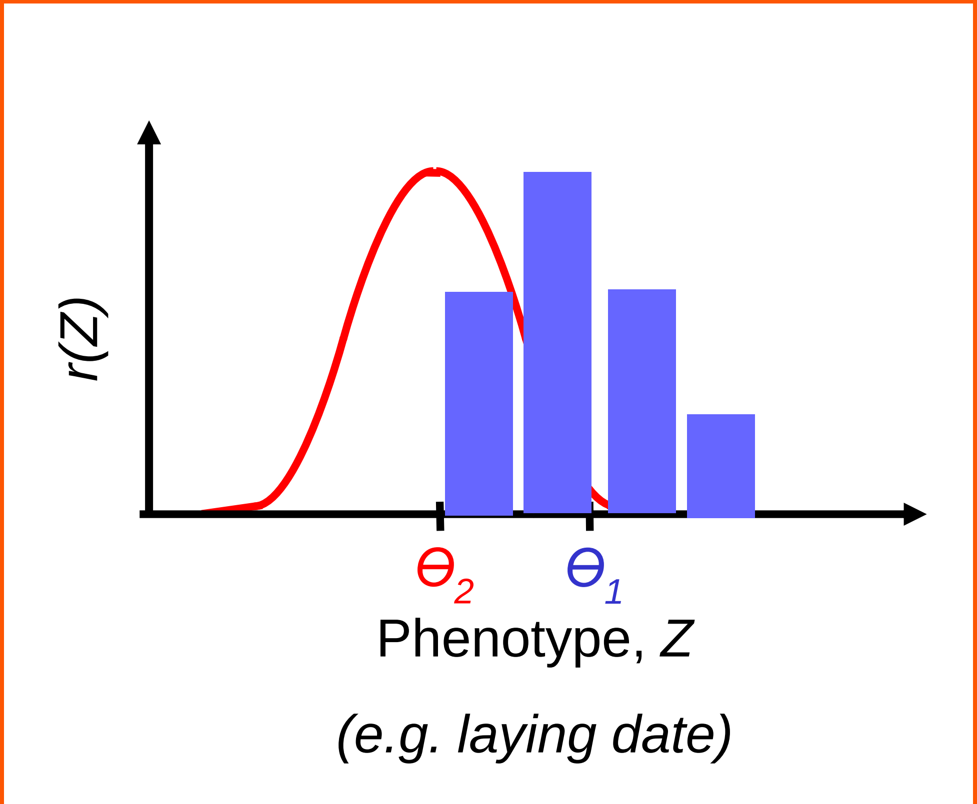


Gaussian selection

Optimal phenotype changes linearily through time with speed *k*

Modelling adaptation in a changing environment

Lynch et al. 1991



Gaussian distribution of phenotypes

↓

Mean population growth rate

$\bar{r}$

Modelling adaptation in a changing environment

Lynch et al. 1991

Mean population growth rate

Maximal growth rate

Phenotypic variance

Lag between mean phenotype and optimum

$$\bar{r} = r_0 - \frac{P}{2V_s} - \frac{(\bar{z} - \theta)^2}{2V_s}$$

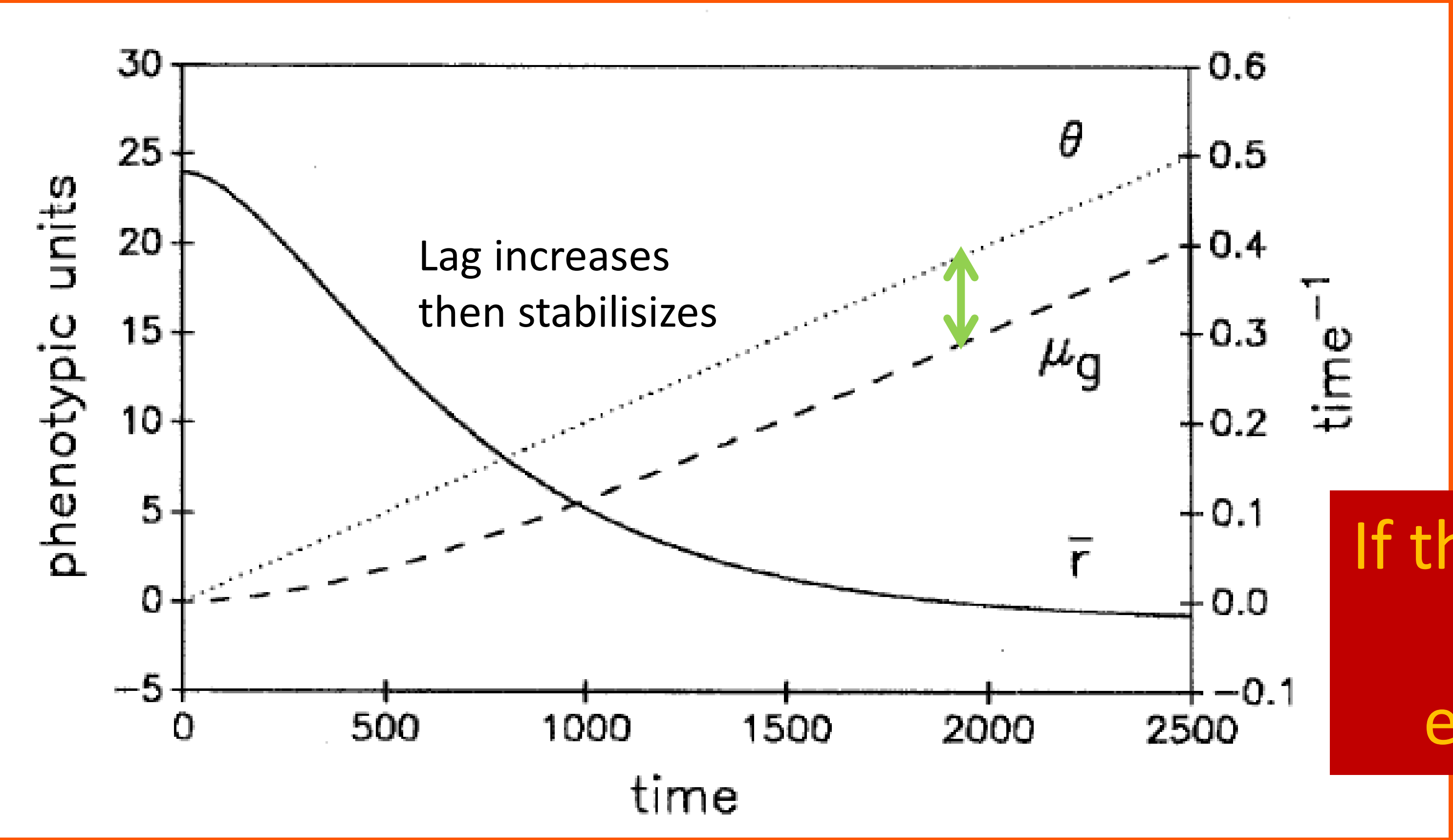
Variance load

Lag load

Modelling adaptation in a changing environment

Lynch et al. 1991

Mean phenotype evolves to track the shifting optimum with a constant lag



If the lag is too large: extinction

Modelling adaptation in a changing environment

Lynch et al. 1991

Mean phenotype evolves to track the shifting optimum with a constant lag

Lag is larger when

$$\frac{\theta(t)-\bar{z}(t)}{V_s}=\frac{k}{G}$$

Speed of climate change is greater

Genetic variance is smaller

Critical speed of climate change

$k > k_c$

$\bar{r} < 0$

ADAPTIVE CHALLENGES IN HETEROGENEOUS POPULATIONS: THE TOOL-KIT

Adaptation in structured populations

Heterogeneity in many populations

Climate change may have differential effects on individuals in different stages

The same trait may be under different selection pressures in different stages

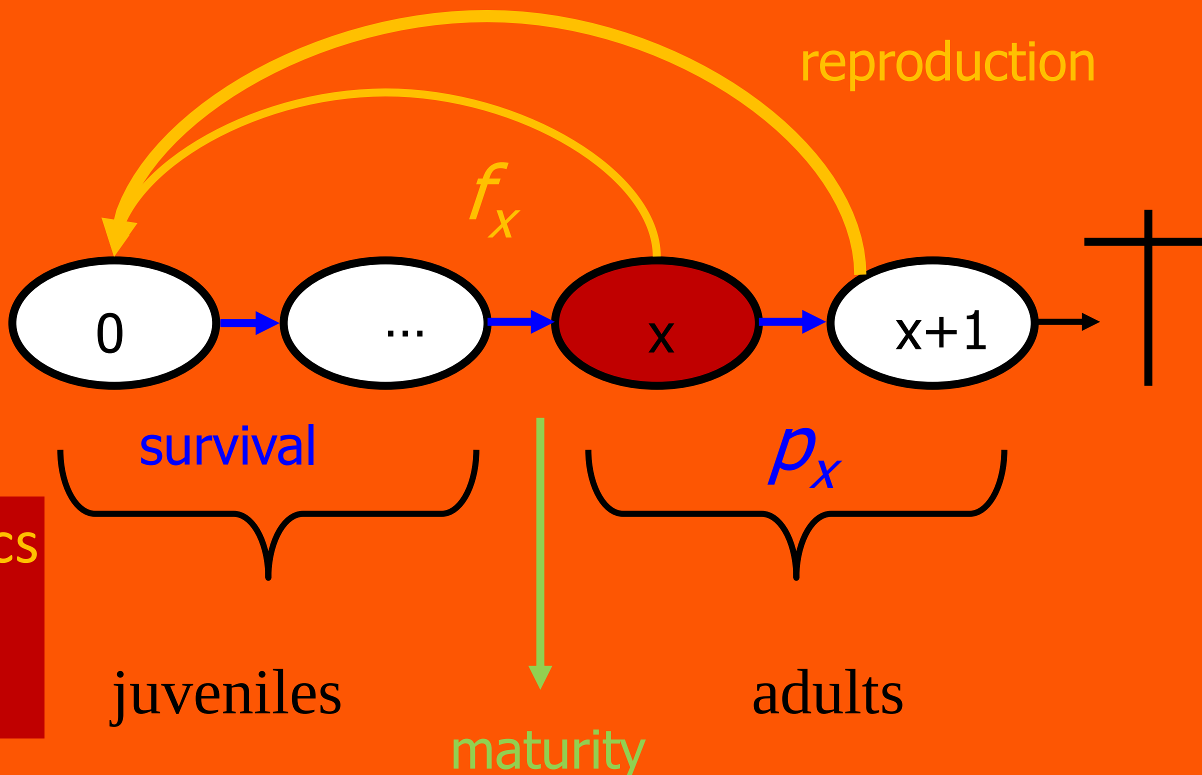
Marschall et al. 2016

Evolutionary changes in an age-structured population

A sophisticated tool-kit

Lande 1982

Engen et al. 2011



Quantitative genetics in age structured populations

see also Barfield et al. 2011 for stage-structured populations

A model for adaptation in a staged-structured population

- Stage-structured demographic model

$$\mathbf{N}[t+1] = \mathbf{A}[t]\mathbf{N}[t]$$

Stage = age (+ location)

$$a_{ij} = \left| \begin{array}{l} t_{ij} \\ f_{ij} \end{array} \right.$$

Change in stage for the same individual: survival, dispersal

Production of new individuals: fecondity

A model for adaptation in a staged-structured population

- Connecting demographic rates to phenotypes

$$a_{ij}(\mathbf{z},t) = A_{ij} \exp\left[-\frac{1}{2}\left(\mathbf{z} - \boldsymbol{\theta}_{ij}[t]\right)^{\mathrm{T}} \mathbf{W}_{ij}^{-1}\left(\mathbf{z} - \boldsymbol{\theta}_{ij}[t]\right) \right]$$

Vector of phenotypic values

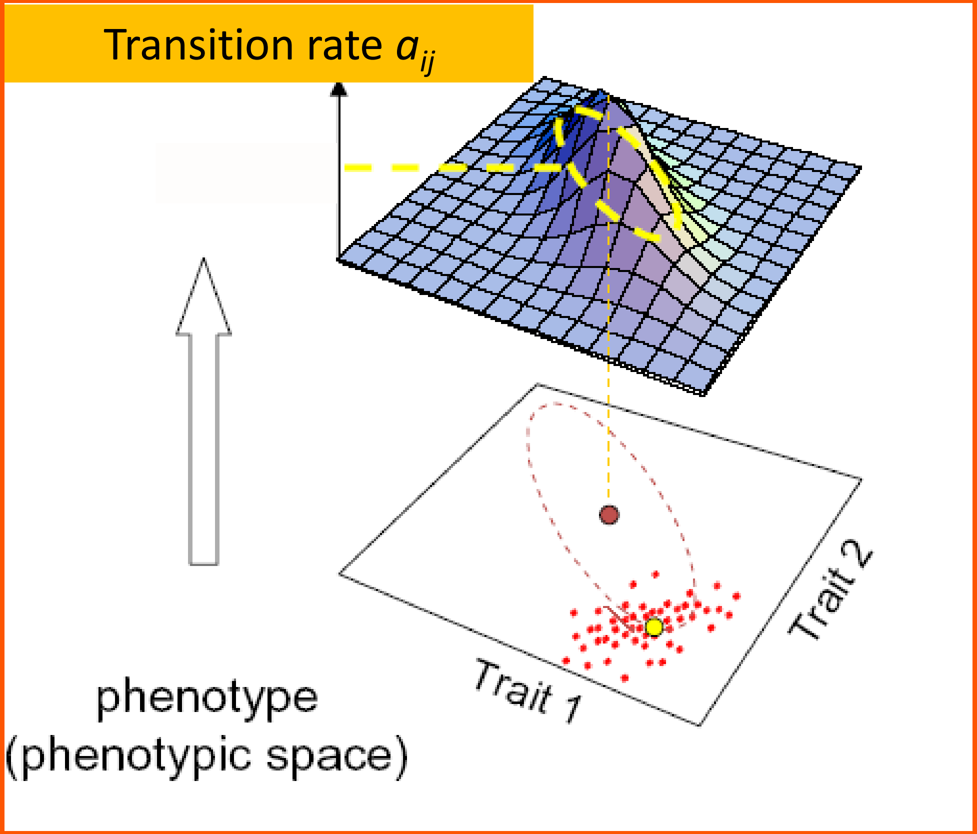
Optimal phenotypic values maximizing the transition rate between stage i and j

Selection matrix measuring the consequences of deviating from the optimal phenotype

A model for adaptation in a staged-structured population

- Connecting demographic rates to phenotypes

Optimal phenotypes can vary in time and depending on stage



A model for adaptation in a staged-structured population

- Change in phenotypic distribution

$$\mathbf{z} = \mathbf{g} + \mathbf{e}$$

Random environmental deviations

$$\mathcal{N}(\mathbf{0}, \mathbf{V}_E)$$

Vector of breeding values

$$\rho_i(\mathbf{z}, \mathbf{g})$$

Joint distribution of phenotype and breeding value among stage i individuals

A model for adaptation in a staged-structured population

- Change in phenotypic distribution

Barfield et al. 2011

$$\rho_i^*(\mathbf{z},\mathbf{g}) = \sum_j \frac{N_j t_{ij}(\mathbf{z}) \rho_j(\mathbf{z},\mathbf{g})}{N_i^*}$$

individuals changing stage from j to i

A model for adaptation in a staged-structured population

- Change in phenotypic distribution

New individuals in stage i

$$\rho_i^*(\mathbf{z},\mathbf{g}) = \omega_i(\mathbf{z}\,|\,\mathbf{g}) \iint R(\mathbf{g}\,|\,\mathbf{g}',\mathbf{g}'')\Phi_i(\mathbf{g}')\Phi_i(\mathbf{g}'')\,\mathrm{d}\mathbf{g}'\,\mathrm{d}\mathbf{g}''$$

Distribution of breeding value in the offspring knowing that of its parents

Distribution of breeding value among parents of stage i individuals

$$\Phi_i(\mathbf{g}) = \sum_j \frac{N_j \int f_{ij}(\mathbf{z})\rho_j(\mathbf{z},\mathbf{g})\mathrm{d}\mathbf{z}}{N_i^*}$$

Distribution of phenotypic value knowing the breeding value

$$\mathcal{N}(\mathbf{g},\mathbf{V}_E)$$

A model for adaptation in a staged-structured population

- Assumption 1: Infinitesimal model of trait inheritance

$$R(\mathbf{g} \mid \mathbf{g}', \mathbf{g}'') = \frac{1}{\sqrt{(2\pi)^m \det(\mathbf{V}_{LE})}} \exp\left(-\frac{1}{2} (\frac{\mathbf{g}' + \mathbf{g}''}{2})^{\mathrm{T}} \mathbf{V}_{LE} (\frac{\mathbf{g}' + \mathbf{g}''}{2}) \right)$$

Breeding value of offspring = mean of its parents + random normal deviate of constant variance

Large number of loci of small effects

A model for adaptation in a staged-structured population

- Assumption 2: Joint gaussian distribution of breeding and phenotypic values

Mean breeding (phenotypic) value in stage i

$\bar{\mathbf{g}}_i$ $\bar{\mathbf{z}}_i$

Genetic (phenotypic) variances-covariances in stage i

$\mathbf{G}_i$ $\mathbf{P}_i$

Assumed constant across time

A model for adaptation in a staged-structured population

- Assumption 2: Joint gaussian distribution of breeding and phenotypic values

$$\bar{\mathbf{g}}_i\left[t+1\right]=\sum_j \frac{N_j\left[t\right]}{N_i\left[t+1\right]}\bar{a}_{ij}\left[t\right]\left(\bar{\mathbf{g}}_j\left[t\right]+\mathbf{G}_j\nabla\ln\bar{a}_{ij}\right)$$

$$\bar{\mathbf{z}}_i\left[t+1\right]=\sum_j \frac{N_j\left[t\right]}{N_i\left[t+1\right]}(\bar{\mathbf{z}}_j\left[t\right]\bar{t}_{ij}+\bar{\mathbf{g}}_j\left[t\right]\bar{f}_{ij}+\mathbf{P}_j\nabla\bar{t}_{ij}+\mathbf{G}_j\nabla\bar{f}_{ij})$$

Selection gradients

$$\nabla=\left\{\partial/\partial\bar{z}_1,\partial/\partial\bar{z}_2\ldots\partial/\partial\bar{z}_n\right\}$$

A model for adaptation in a staged-structured population

- Joint gaussian distribution of breeding and phenotypic values

$$\ln\left(\bar{a}_{ij}[t]\right) = \ln A_{ij} + \frac{1}{2}\ln\left(\left|\mathbf{V}_{ij}{}^{-1}\mathbf{W}_{ij}\right|\right) - \frac{1}{2}\left(\bar{\mathbf{z}}_j[t] - \boldsymbol{\theta}_{ij}[t]\right)'\mathbf{V}_{ij}{}^{-1}\left(\bar{\mathbf{z}}_j[t] - \boldsymbol{\theta}_{ij}[t]\right)$$

$$\mathbf{V_{ij} = W_{ij} + P_j}$$

Variance load

Evolutionary (lag) load

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

All stages share the same rate of evolution

Weak selection

$$\Delta\bar{\mathbf{z}} = \bar{\mathbf{z}}_k[t+1] - \bar{\mathbf{z}}_k[t] = \Delta\bar{\mathbf{g}}$$

$$= \sum_{i,j} \mathbf{G}_j \frac{\partial \ln(\bar{\lambda})}{\partial \ln(\bar{a}_{ij})} \nabla \ln(\bar{a}_{ij})$$

$\bar{\lambda}$ Largest eigenvalue of $\bar{\mathbf{A}}$

Lande 1982

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

All stages share the same rate of evolution

$$\Delta \bar{\mathbf{z}} = \sum_{i,j} \mathbf{G}_j e_{ij} \nabla \ln(\bar{a}_{ij})$$

Demographic elasticities

$$e_{ij} = \frac{\partial \ln(\bar{\lambda})}{\partial \ln(\bar{a}_{ij})}$$

Effect of perturbations of the transitions in the life cycle on the exponential population growth rate

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

All stages share the same rate of evolution

$$\Delta \bar{\mathbf{z}} = \sum_{i,j} \mathbf{G}_j e_{ij} \mathbf{V}_{ij}^{-1} \left(\boldsymbol{\theta}_{ij}[t] - \bar{\mathbf{z}}_j[t] \right)$$

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

$$if\ \forall k\ \bar{\mathbf{z}}_k[t] = \bar{\mathbf{z}}[t]$$

Weak selection

$$\forall k\ \mathbf{G}_k = \mathbf{G}$$

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{V}_\nu^{-1}\left(\boldsymbol{\theta}_\nu[t] - \bar{\mathbf{z}}[t]\right)$$

Same form as in unstructured population

Engen et al. 2011

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

$$\boldsymbol{\theta}_{\nu}[t] = \sum_{i,j} e_{ij} \mathbf{V}_{\nu} \mathbf{V}_{ij}^{-1} \boldsymbol{\theta}_{ij}[t]$$

Integrative phenotypic optima

$$\mathbf{V}_{\nu}^{-1} = \sum_{i,j} e_{ij} \mathbf{V}_{ij}^{-1}$$

Overall strength of stabilizing selection

ADAPTIVE CHALLENGES IN HETEROGENEOUS POPULATIONS: COULD CLIMATE CHANGE AFFECT LIFE HISTORY TRADE-OFFS?

Antagonistic pleiotropy and adaptation to climate

Ehrlen & Munzbergova 2009

Lathyrus vernus

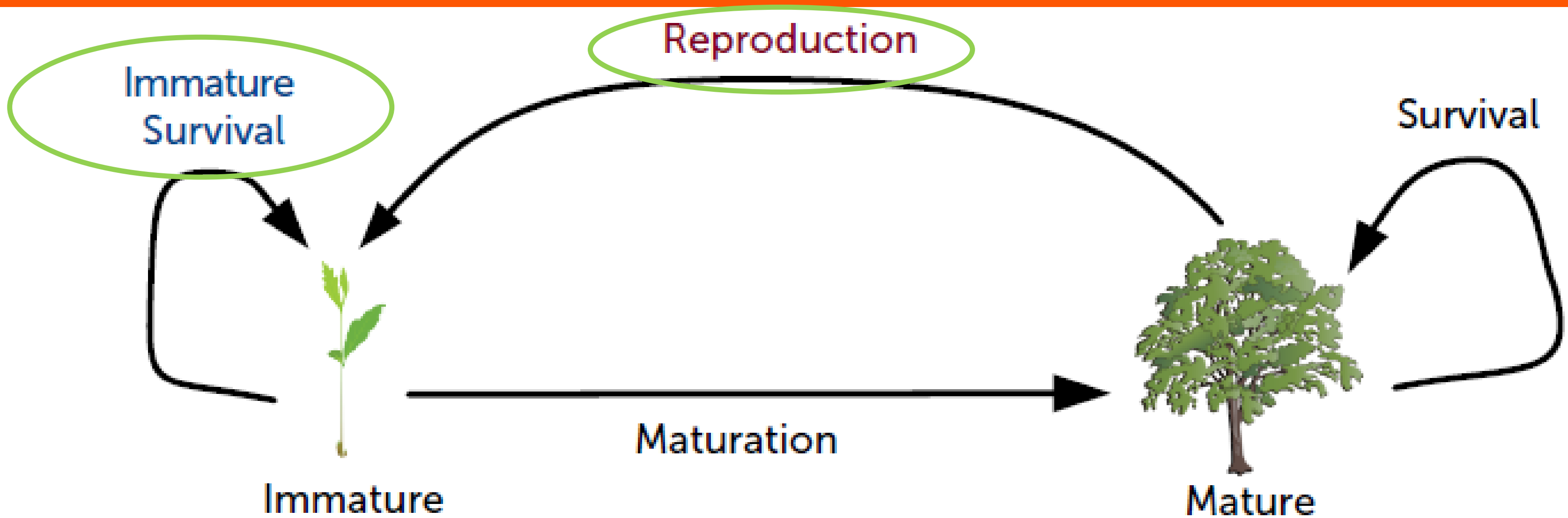
Earlier flowering favored by climate change

→ Increases seed set

→ Increases risk of grazing → Decreases survival probability

Antagonistic pleiotropy and adaptation to climate

- Evolution of leafing date in a structured population

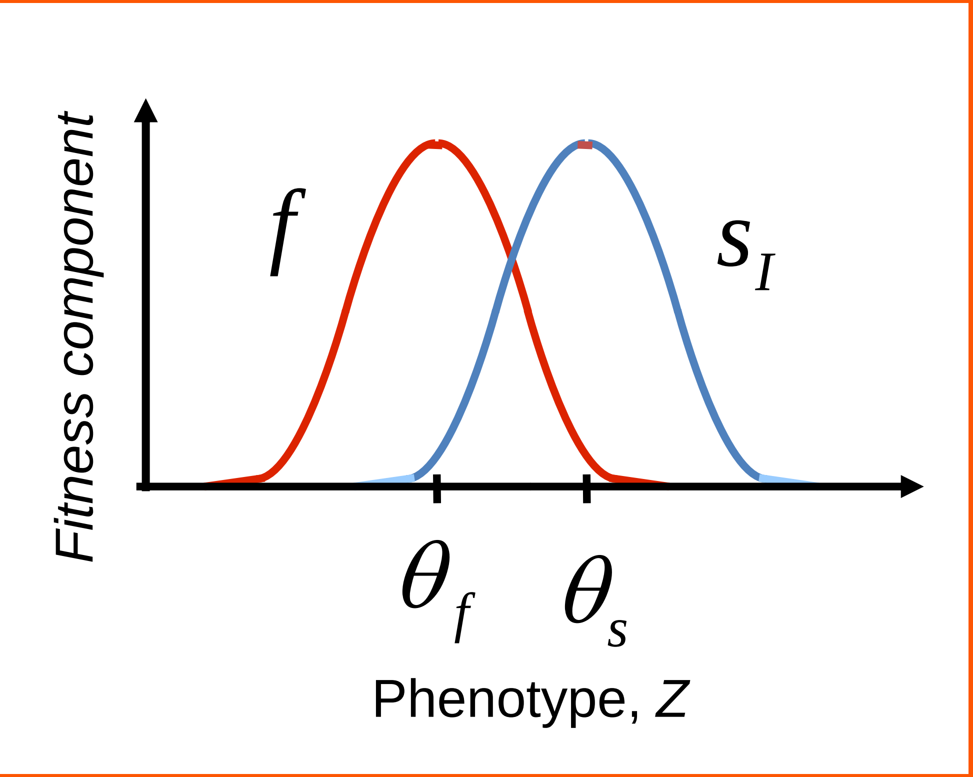


Stage-structured population

Hypotheses

Same leafing date during the whole life

Antagonistic pleiotropy and adaptation to climate



Optimal leafing date maximizing fecundity may differ from the date maximizing immature survival

Both optima change with climate warming

Antagonistic pleiotropy and adaptation to climate

- In a constant environment, at equilibrium the mean phenotype lies between the two optima

$$\bar{z}_{eq} = \theta_v = \frac{\gamma_f \theta_f + \gamma_s \theta_s}{\gamma_f + \gamma_s}$$

Engen et al. 2011

Weights depending on demographic elasticities

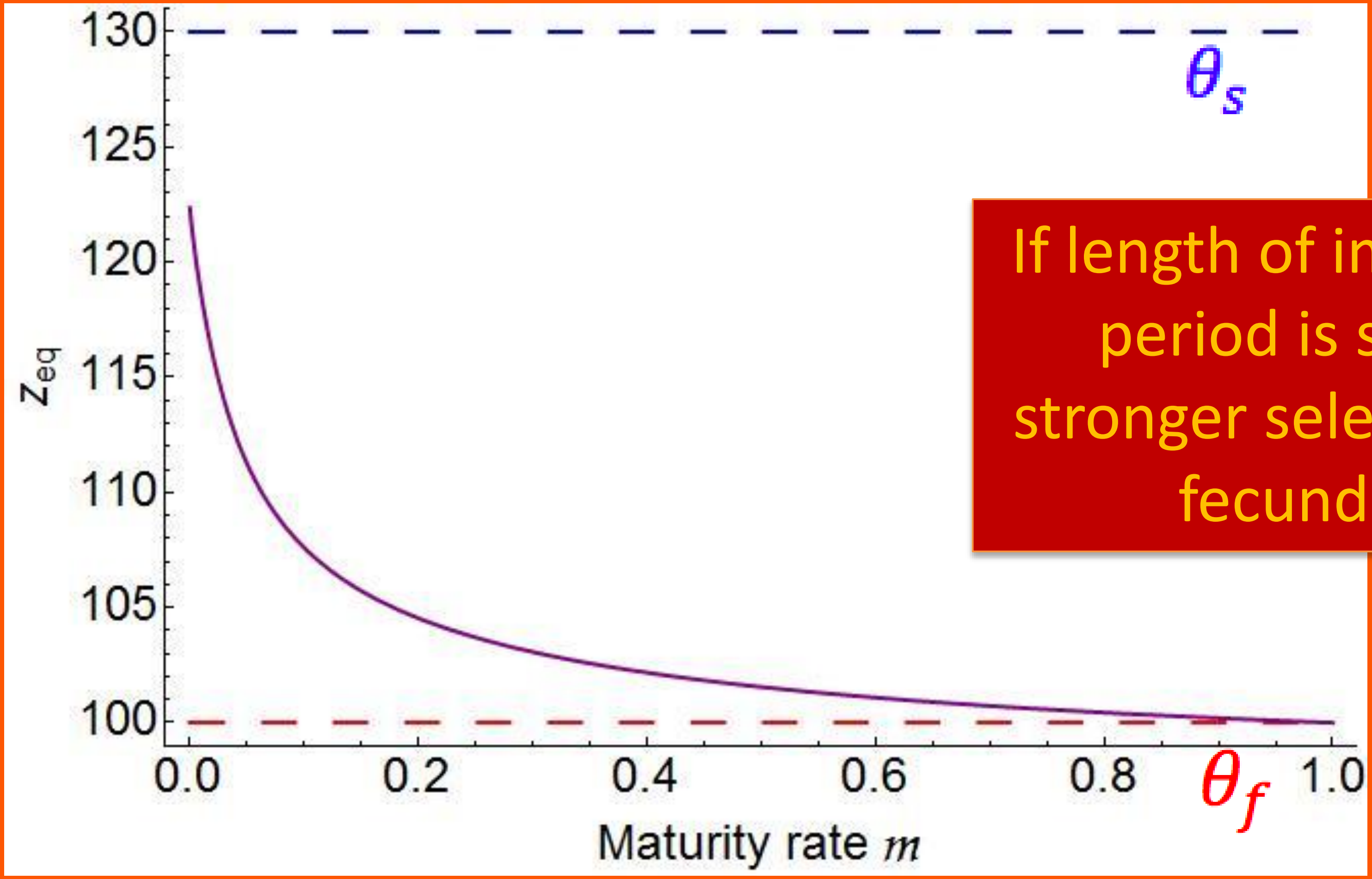
Antagonistic pleiotropy and adaptation to climate

- Phenotypic mismatch vary among life history traits

$$\theta_f - \bar{z}_{eq} = \theta_f - \theta_v = \frac{\gamma_s\left(\theta_f - \theta_s\right)}{\gamma_f + \gamma_s}$$

Weights depending on demographic elasticities

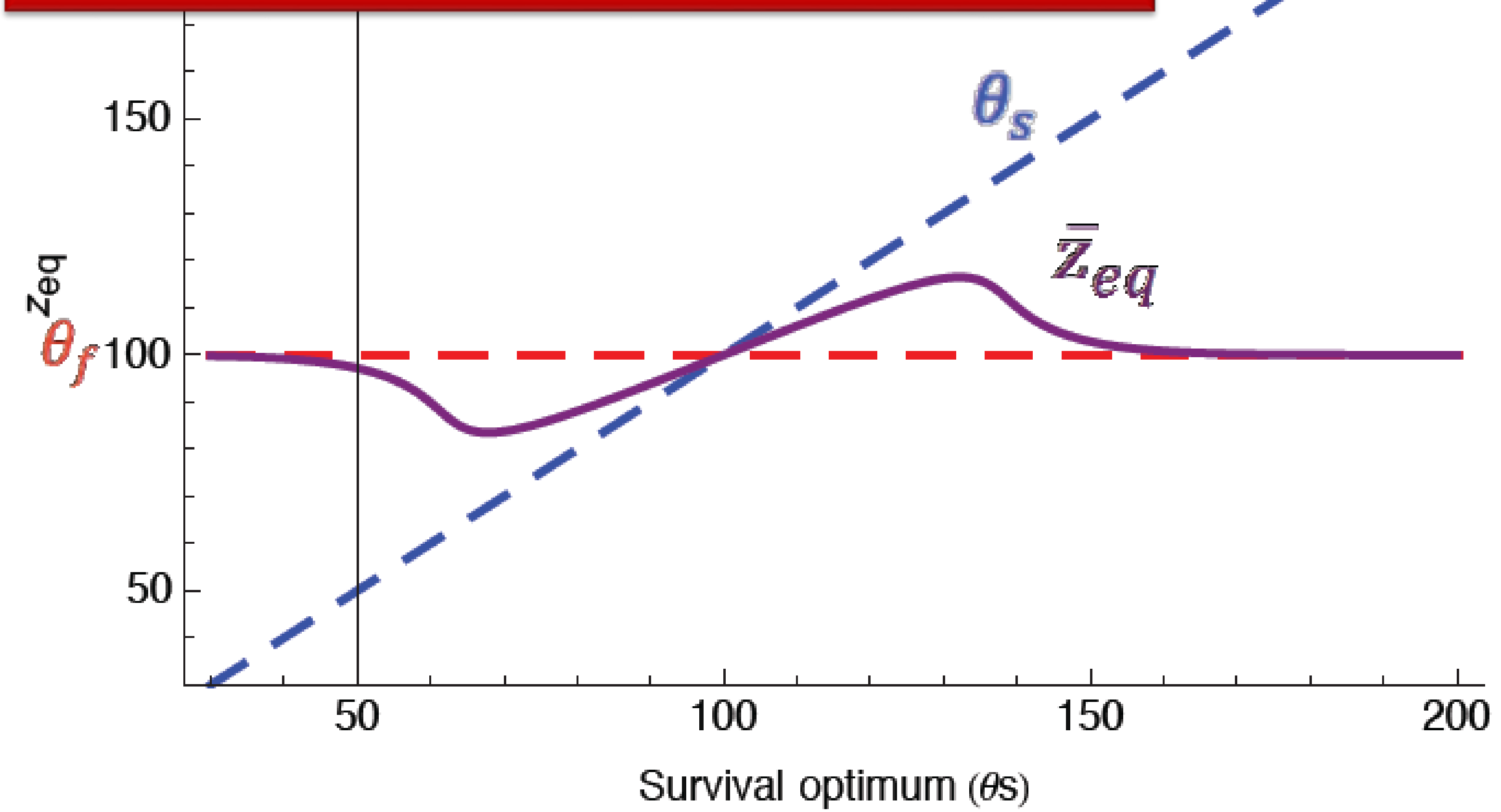
Predictions in a stable climate



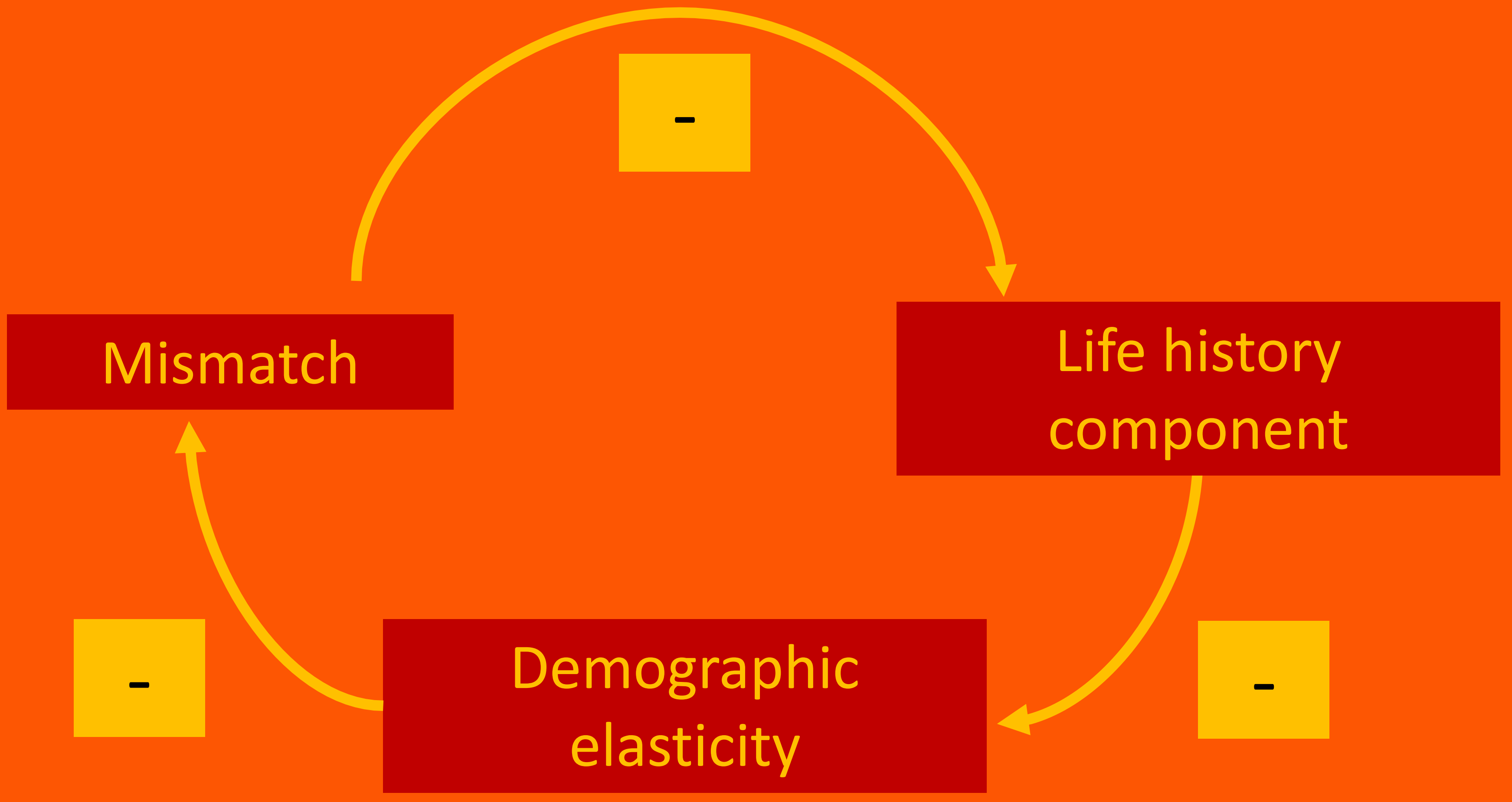
If length of immature period is short, stronger selection on fecundity

Predictions in a stable climate

The weights evolve together with the trait through its effect on life history traits



Meltdown of life history



Predictions in a warming environment

Optimal date maximizing fecundity

$$\theta_f(t) = \theta_f(0) + k_f t$$

Optimal date maximizing juvenile survival

$$\theta_s(t) = \theta_s(0) + k_s t$$

Predictions in a warming environment

$$if\ k_s = k_f = k$$

Conjecture

Lag in adaptation at equilibrium

$$\theta_v(t) - \bar{z}(t) = \frac{k}{\left(\gamma_f + \gamma_s\right) G_I}$$

Rate of climate change

Integrative optimal date

Genetic variance

Strength of selection

Antagonistic pleiotropy and adaptation to climate

- Phenotypic mismatch vary among life history traits

$$\theta_f(t) - \bar{z}(t) = \theta_f(0) - \theta_v(0) + \frac{k}{(\gamma_f + \gamma_s)G}$$

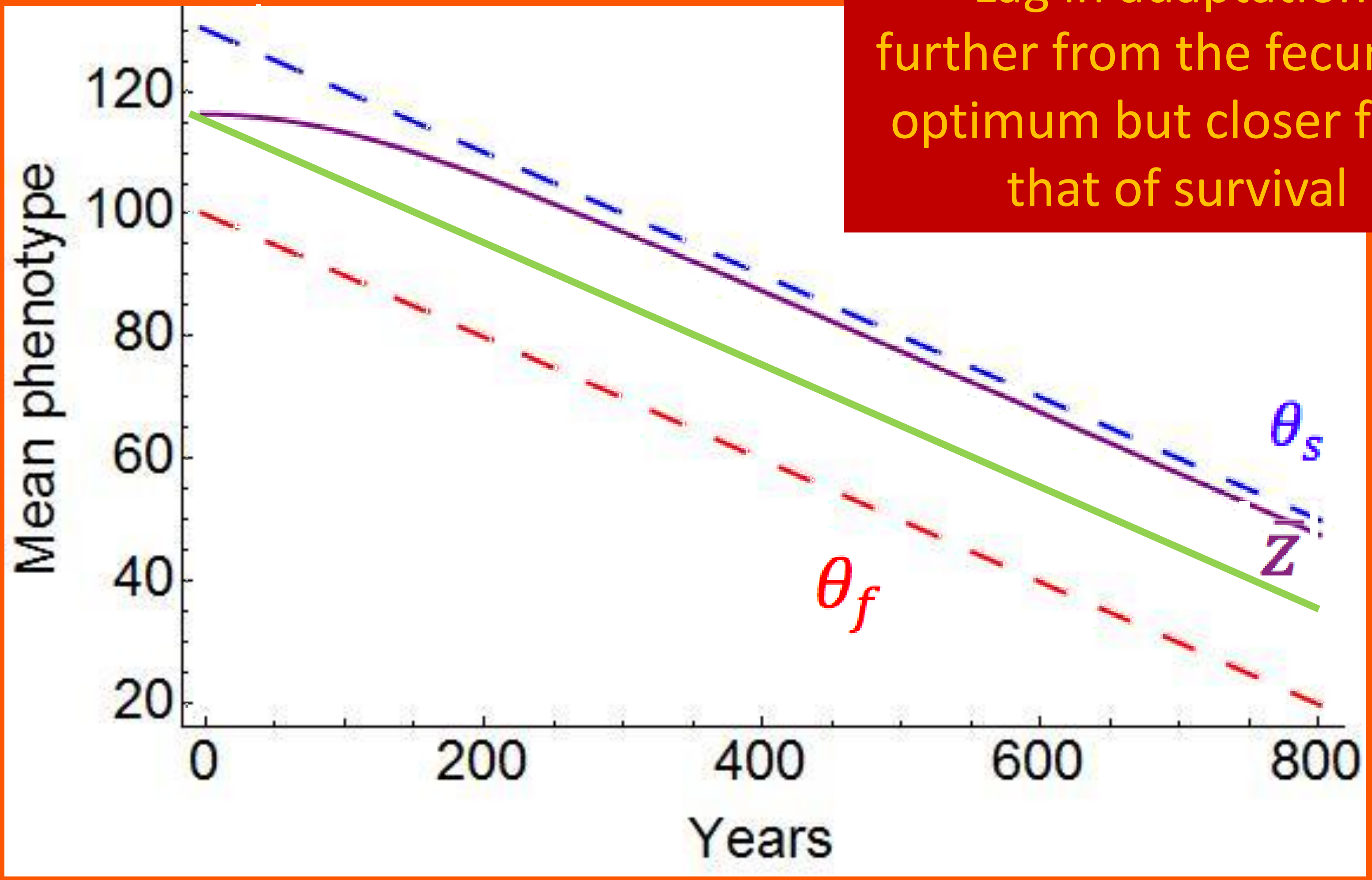
Initial mismatch

Mismatch due to lag in adaptation

Same or opposite sign

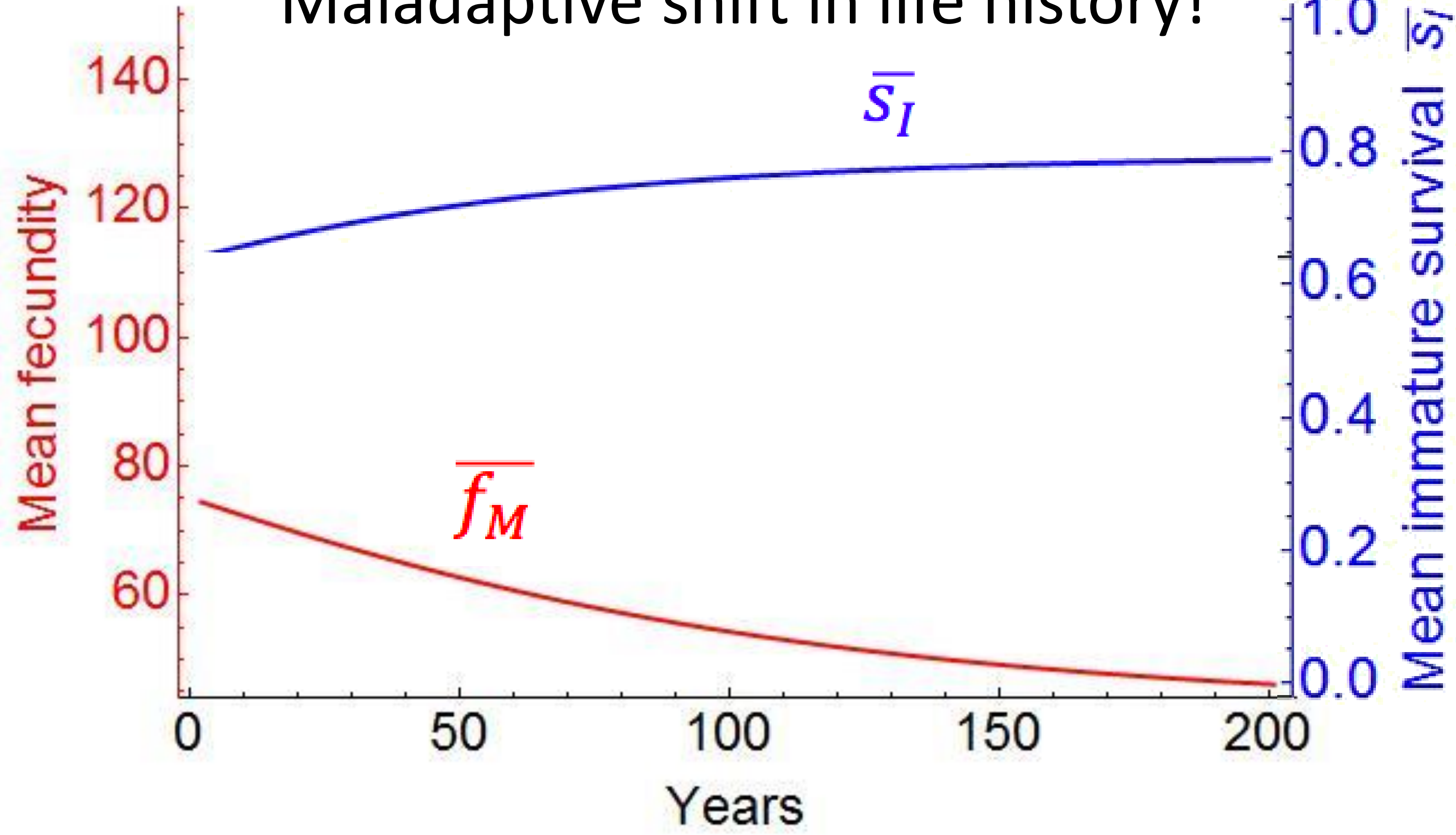
Predictions in a warming environment

Lag in adaptation: further from the fecundity optimum but closer from that of survival



Predictions in a warming environment

Maladaptive shift in life history!



Antagonistic pleiotropy and adaptation to climate

- Lag in adaptation results in mean phenotype shifting along the trade-off between survival and fecundity
- Improvement in some fitness component following climate change may actually correspond to maladaptive response, reflecting slow evolution!

Predictions in a warming environment

$$if\ k_s \neq k_f$$

Conjecture

Lag in adaptation at equilibrium

Integrative rate of climate change

$$\theta_v(t) - \bar{z}(t) = \frac{k_v \nearrow}{(\gamma_f + \gamma_s) G_I}$$

↓

Integrative optimal date

$$k_v = \frac{\gamma_f k_f + \gamma_s k_s}{\gamma_f + \gamma_s}$$

Antagonistic pleiotropy and adaptation to climate

- Phenotypic mismatch vary among life history traits

$$\theta_f(t) - \bar{z}(t) = \theta_f(0) - \theta_v(0) + (k_f - k_v)t + \frac{k_v}{(\gamma_f + \gamma_s)G}$$

Initial mismatch

Mismatch diverges!

Mismatch due to lag in adaptation

Antagonistic pleiotropy and adaptation to climate

- Divergence of mismatch-> extinction?
- Stationary lag with respect to the integrative optimum?
- Non linear change in integrative optimum

Thanks

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AGENCE NATIONALE DE LA RECHERCHE ANR

EVORANGE

MECC

Luis-Miguel Chevin

Matthias Grenié

A model for adaptation in a staged-structured population

- Assumption 3: stable stage distribution

$$if\ \forall k\ \bar{\mathbf{z}}_k[t] = \bar{\mathbf{z}}[t]$$

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{V}_\nu^{-1}\left(\boldsymbol{\theta}_\nu[t] - \bar{\mathbf{z}}[t]\right)$$

$$\boldsymbol{\theta}_\nu[t] = \sum_{i,j} e_{ij}\mathbf{V}_\nu\mathbf{G}^{-1}\mathbf{G}_j\mathbf{V}_{ij}^{-1}\boldsymbol{\theta}_{ij}[t]$$

Integrative phenotypic optima

$$\mathbf{V}_\nu^{-1} = \sum_{i,j} e_{ij}\mathbf{G}^{-1}\mathbf{G}_j\mathbf{V}_{ij}^{-1}$$

Overall strength of stabilizing selection