Ecology and evolution in randomly fluctuating environments

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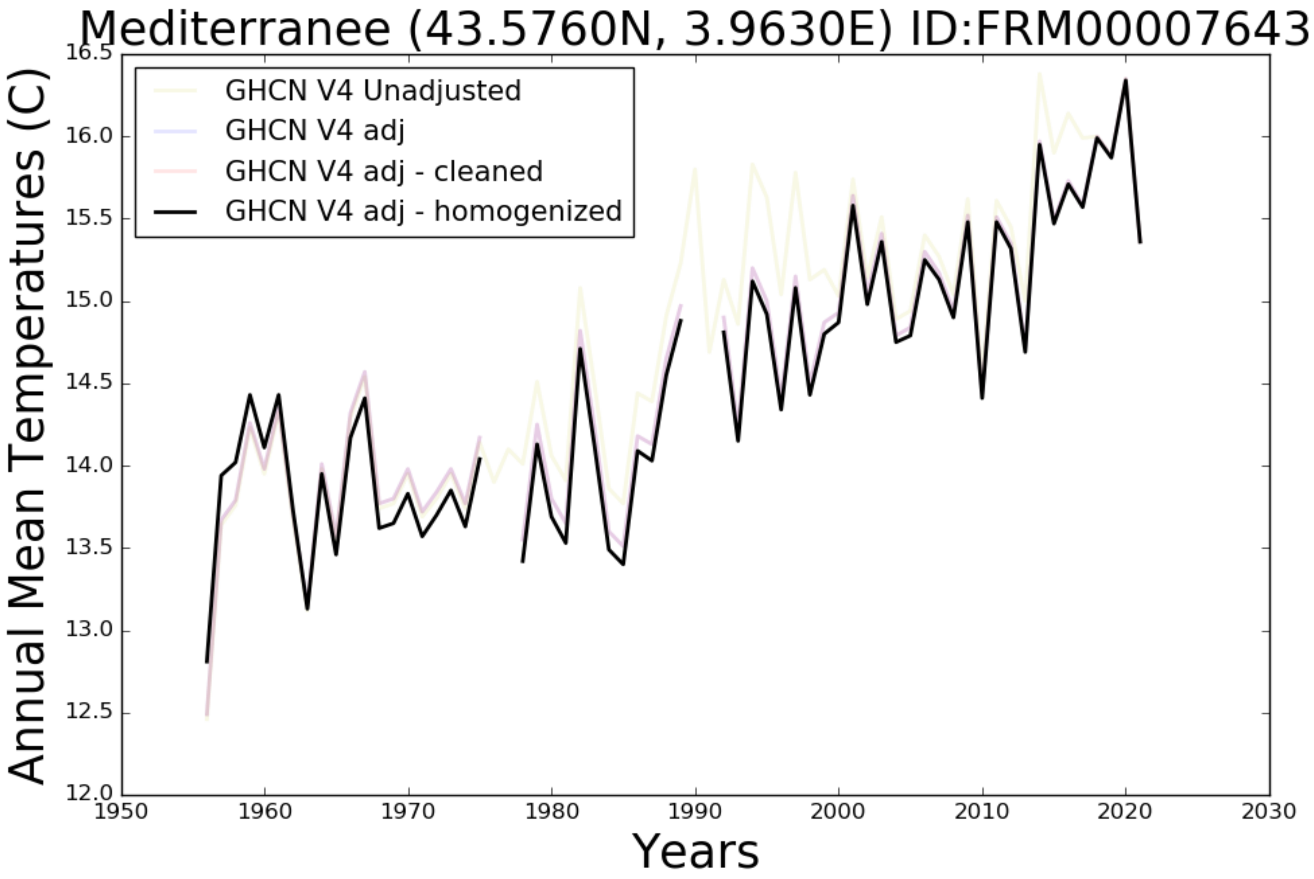
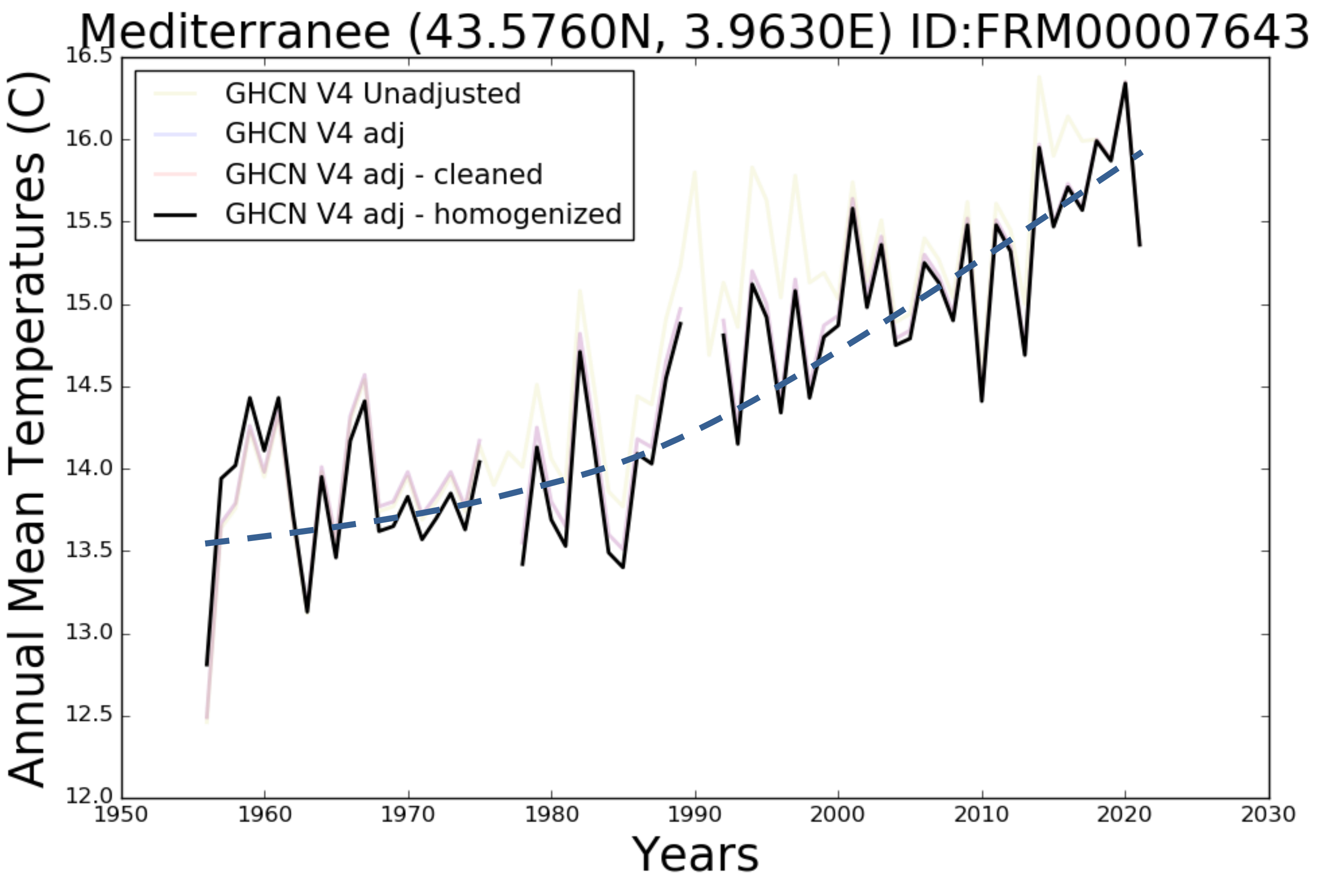
Environments fluctuate randomly



1: Boer, G. J. (2009. *J. Clim.*)

Environments fluctuate randomly



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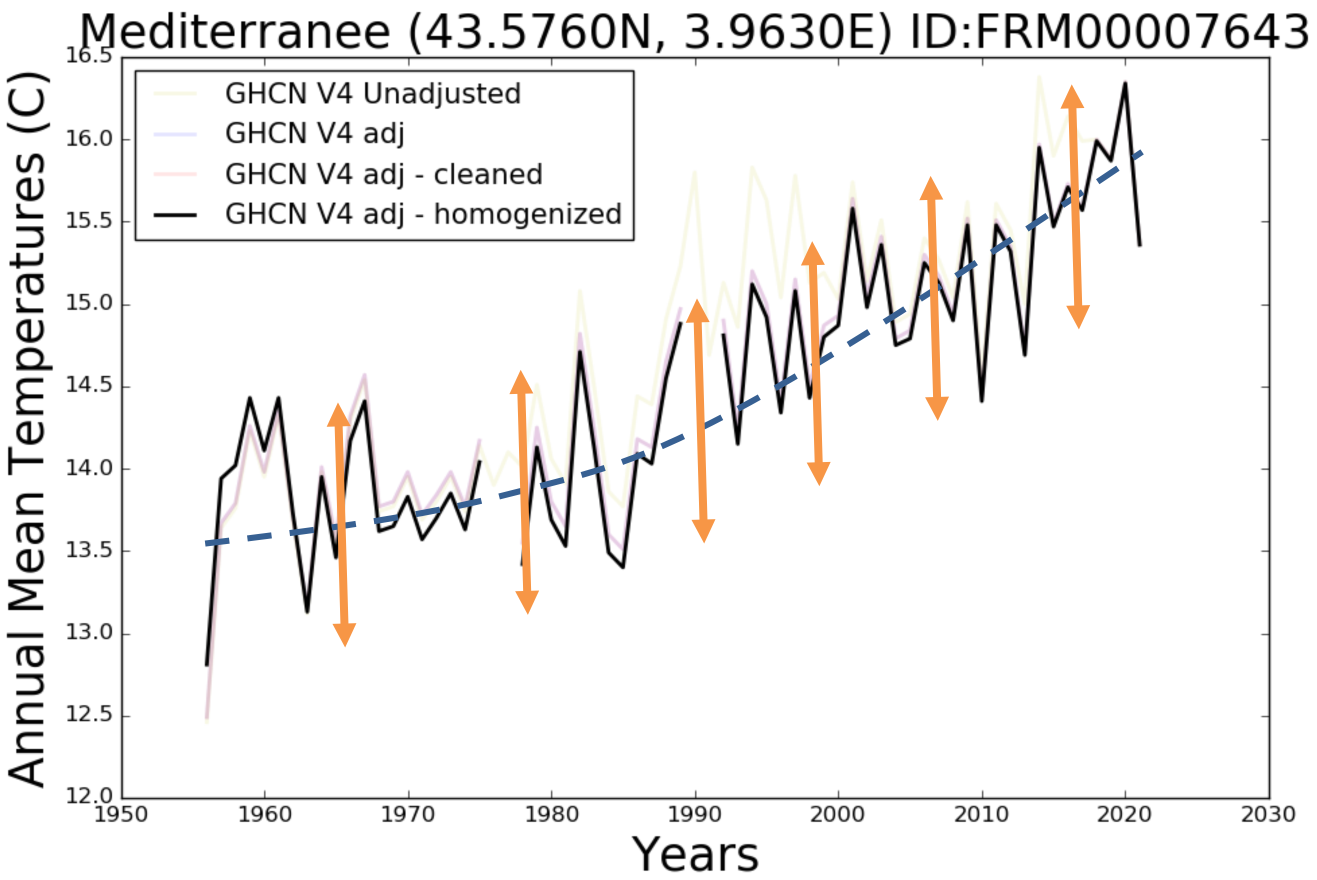
Environments fluctuate randomly

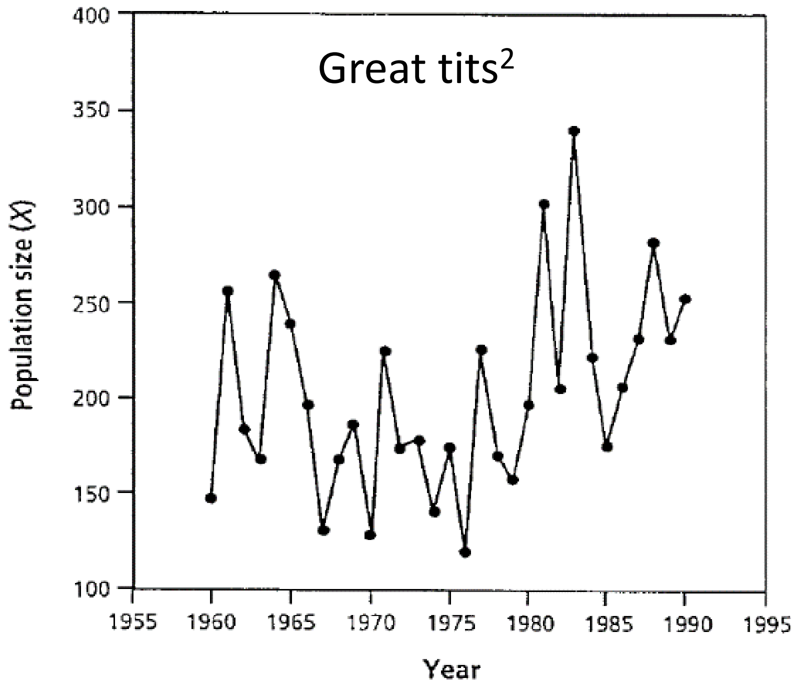


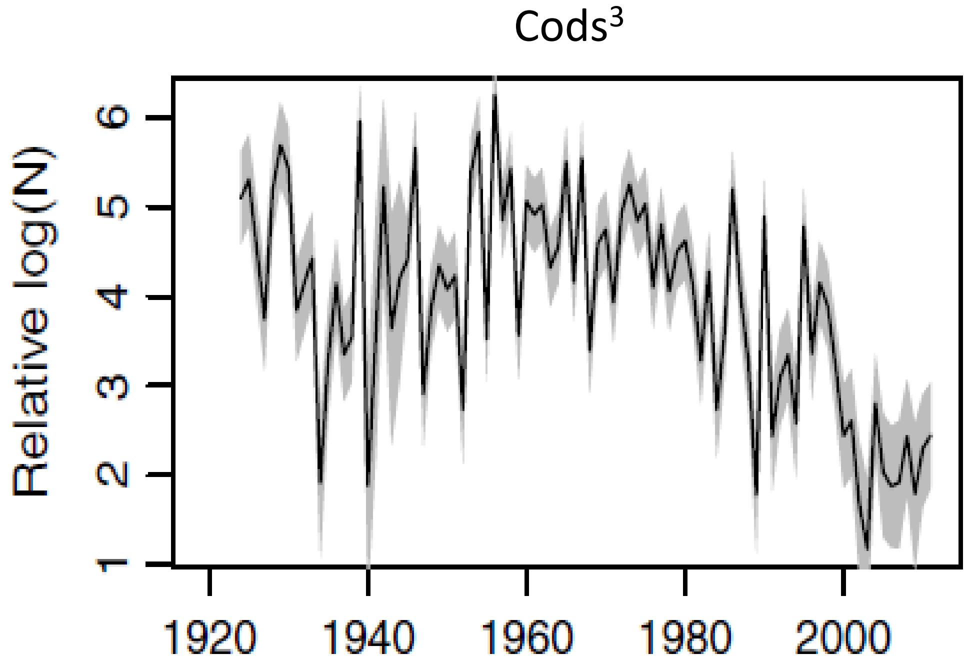
- Faster than trends → Major cause of stress for living organisms
- Global change alters **magnitude and predictability of fluctuations**[1]

1: Boer, G. J. (2009. *J. Clim.*)

Random environments make <u>demography</u> stochastic

- Cause fluctuations in vital rates (survival/fecundity), affecting **population size/density**[1]





- Strong source of stochasticity → **Extinction risk** even for initially large populations[1]

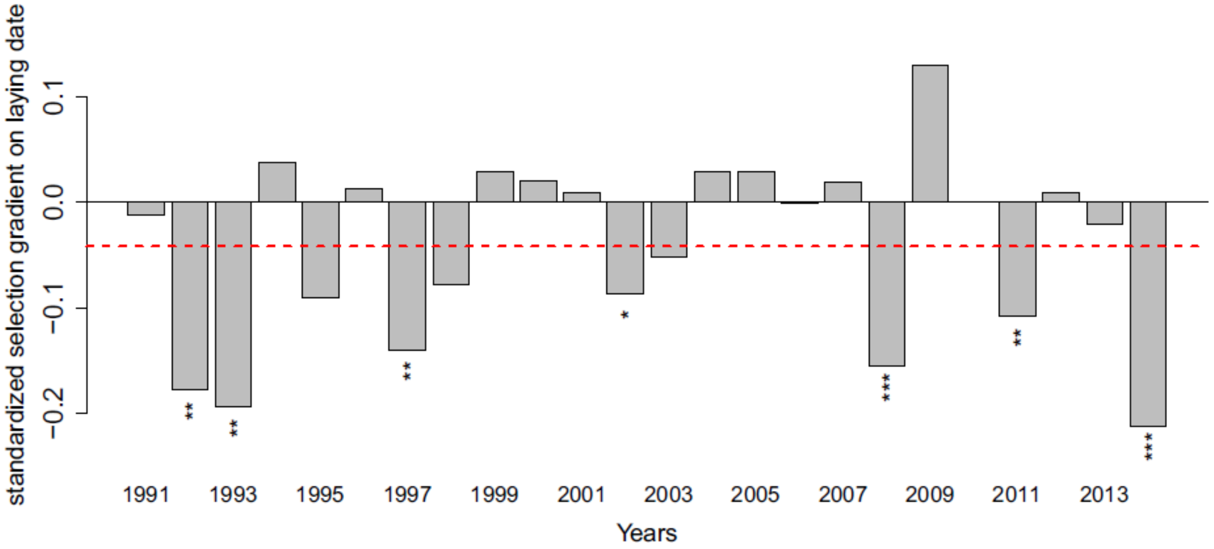
1: reviewed by Lande et al (2003 OUP)
2: Saether et al (1998, Am Nat)
3: Rogers et al (2017 J Anim Ecol)

Random environments make evolution stochastic

- Source of **fluctuating selection**:
  Different phenotypes/genotypes are favored by natural selection at different times

Laying date of blue tits in Mediterranean forests
(near Montpellier and Corsica)

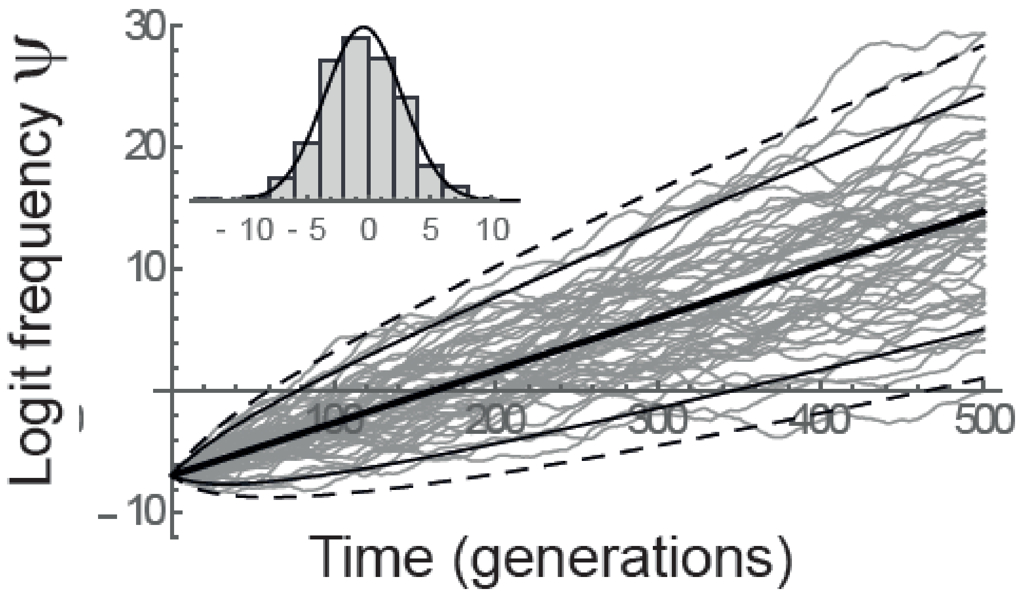
Charmantier et al (2015 Evol Appl)



Marrot et al (2018)

Random environments make evolution stochastic

- Source of **fluctuating selection**:
  Different phenotypes/genotypes are favored by natural selection at different times
- Major **source of chance** in evolution:
  Increases variance among replicate instances of evolution, as drift does
  (causing fixations, etc…)



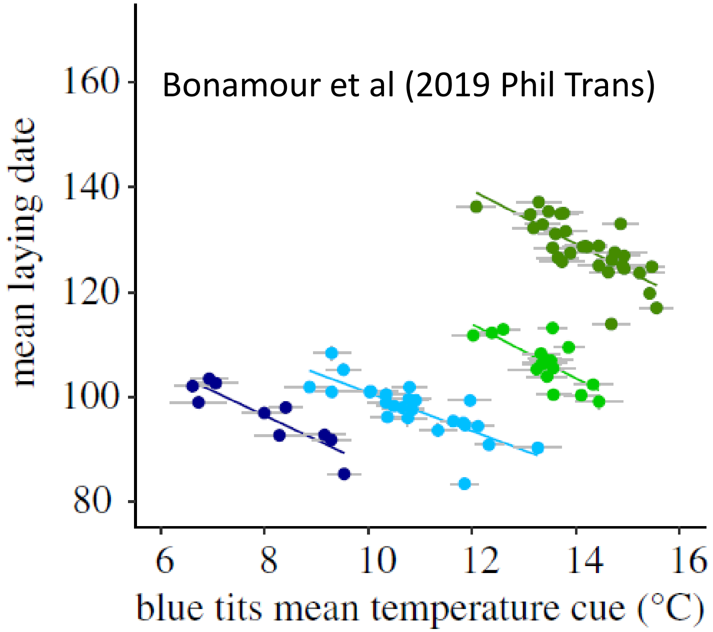
→ Uncertainty needs to be accounted for

Random environments make evolution stochastic

- Source of **fluctuating selection**:
  Different phenotypes/genotypes are favored by natural selection at different times
- Can cause the evolution of specific response mechanisms such as **phenotypic plasticity** = phenotypic change of given genotype in response to environment

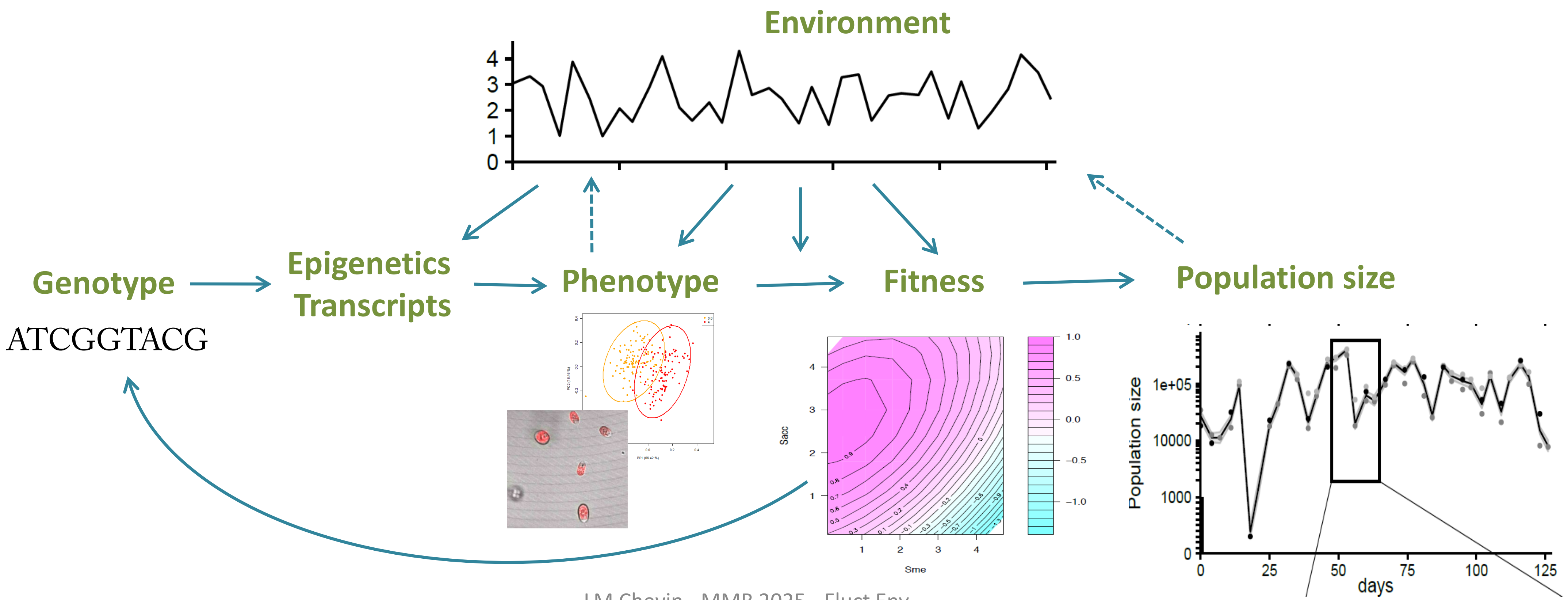
Laying date of blue tits in Mediterranean forests (near Montpellier and Corsica)

Charmantier et al (2015 Evol Appl)



Population responses to stochastic environments

- How do random environmental fluctuations translate into **fluctuations at all levels of population biology**?
- What determines the **predictability of responses** at each level?



2 3

Ecology and evolution in randomly fluctuating environments

- Basics and framework -
- Evolutionary dynamics -
- Phenotypic plasticity -
- Evolutionary demography -
- Experimental results -

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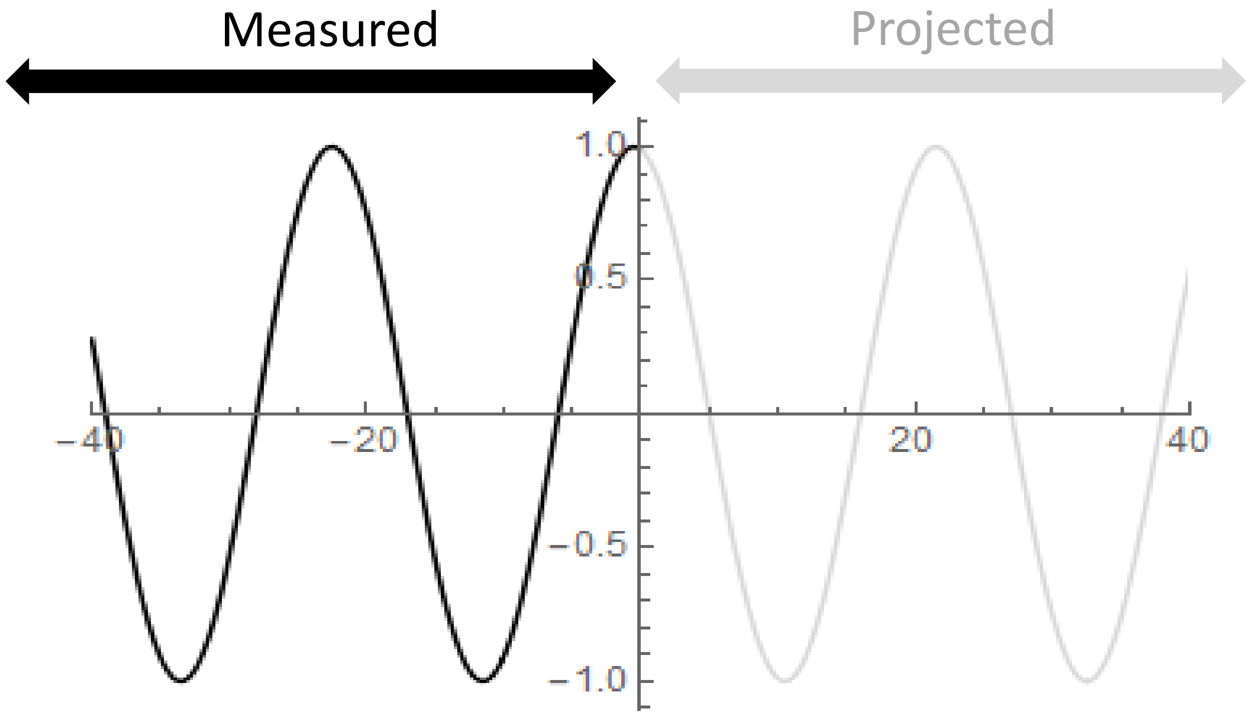
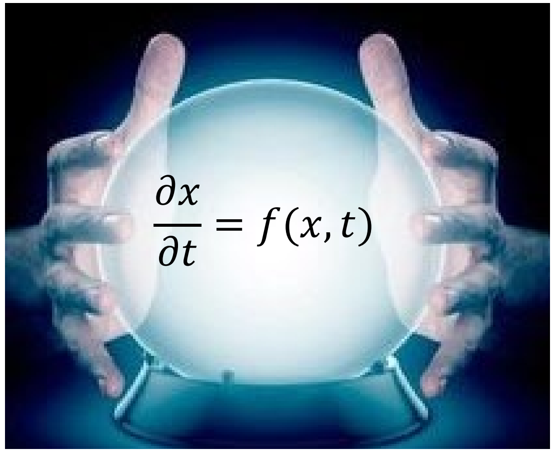
What is a randomness

- Regardless of what randomness means in an absolute sense, treating environments as random accounts for:
  - **Absence of obvious pattern**
  - **Ignorance of underlying causes**,
    some of which may in fact be deterministic, but complex (multifactorial)
  - Imperfect knowledge/measurement

Prediction in stochastic environment

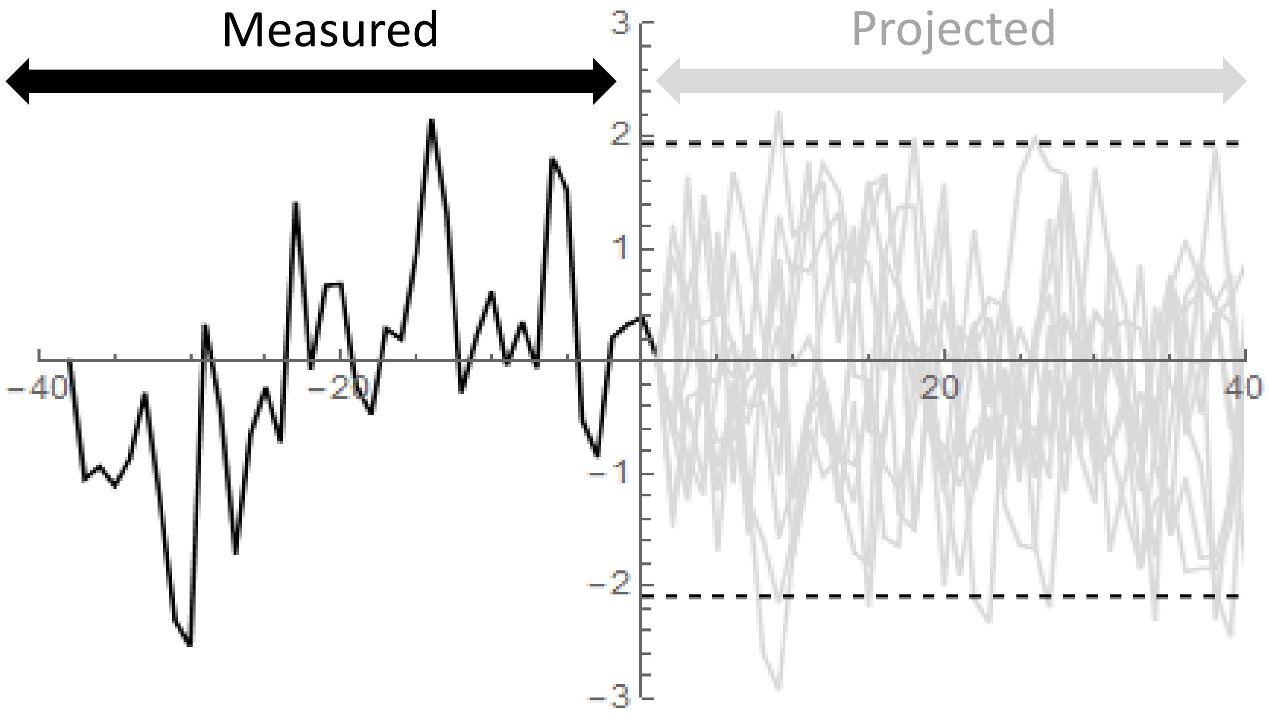
- **Deterministic**: the future is certain provided accurate measurement of the past, and perfect knowledge of causal factors.

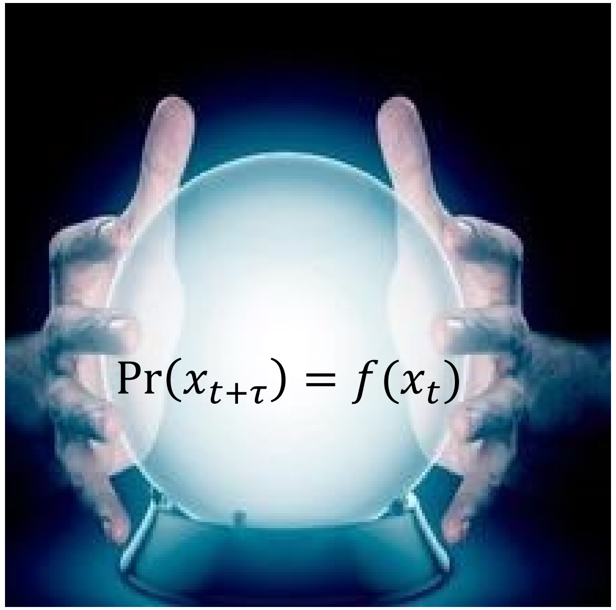




Prediction in stochastic environment

- **Stochastic**: The future is probabilistic even with perfect measurement





Prediction in stochastic environment

- **Temporal** **autocorrelation ρ** determines timescale of predictability
- Related to “colour » of environmental noise[1]

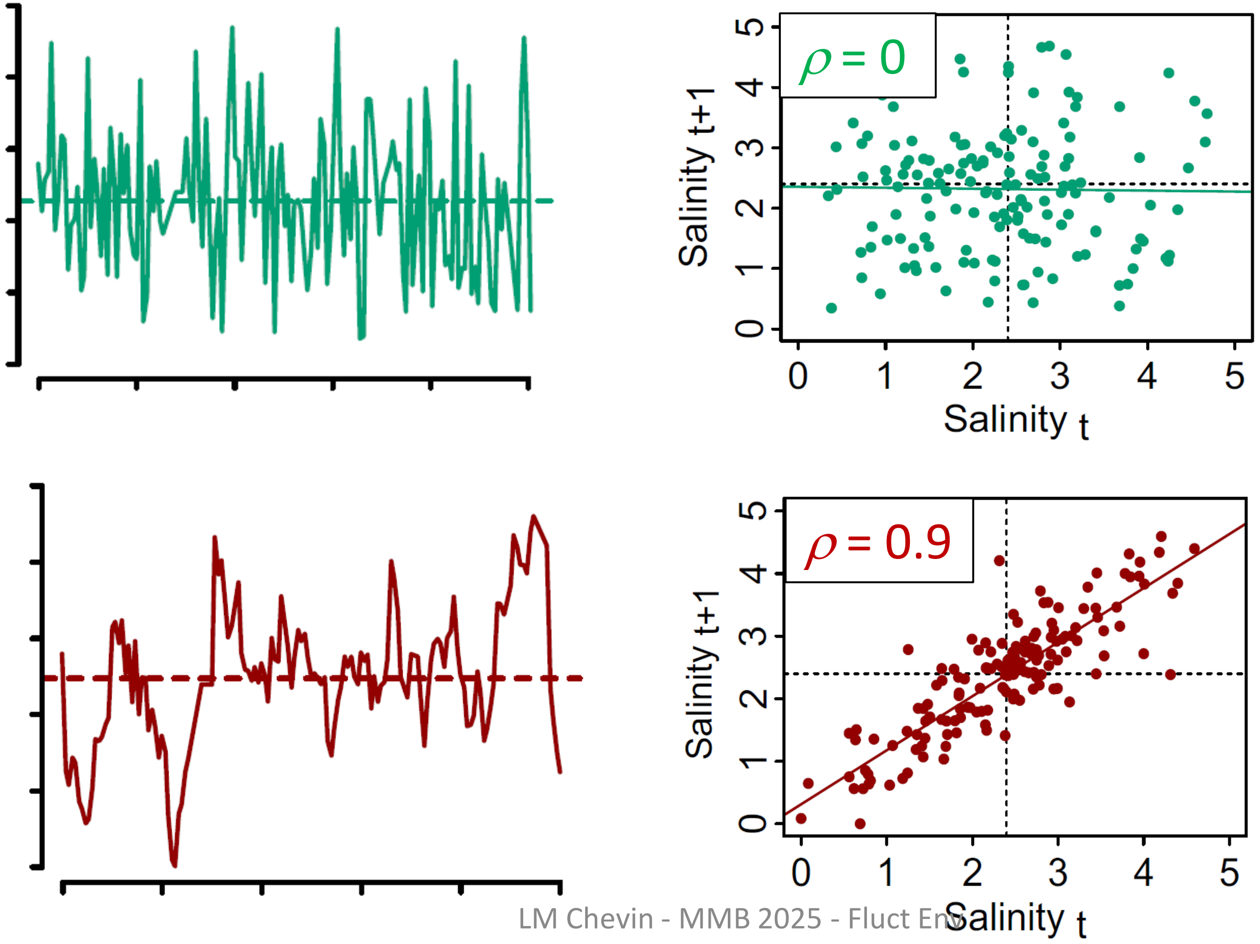


Fig. from Leung et al (2020 Ecol Lett)
1: Vasseur & Yodzis (2004 Ecology)

Evolutionary demography

- Evolution and demography are **connected through the fitness landscape**[1,2]
- In simple discrete-time model where multiplicative fitness (number of offspring per parent) is, with mean $\bar{W}$ in the population:

Demography: $N_{t+1} = \bar{W}_t N_t \rightarrow \ln N_{t+1} = \ln N_t + \ln \bar{W}_t$

Evolution:

- Allelic frequency[1] $\Delta p = pq \frac{\partial ln\bar{W}}{\partial p}$
- Mean of quantitative trait[2] $\Delta \bar{z} = G \frac{\partial ln\bar{W}}{\partial \bar{z}}$ (G: additive genetic variance)

(For frequency-independent selection, i.e. no interaction between genotypes)

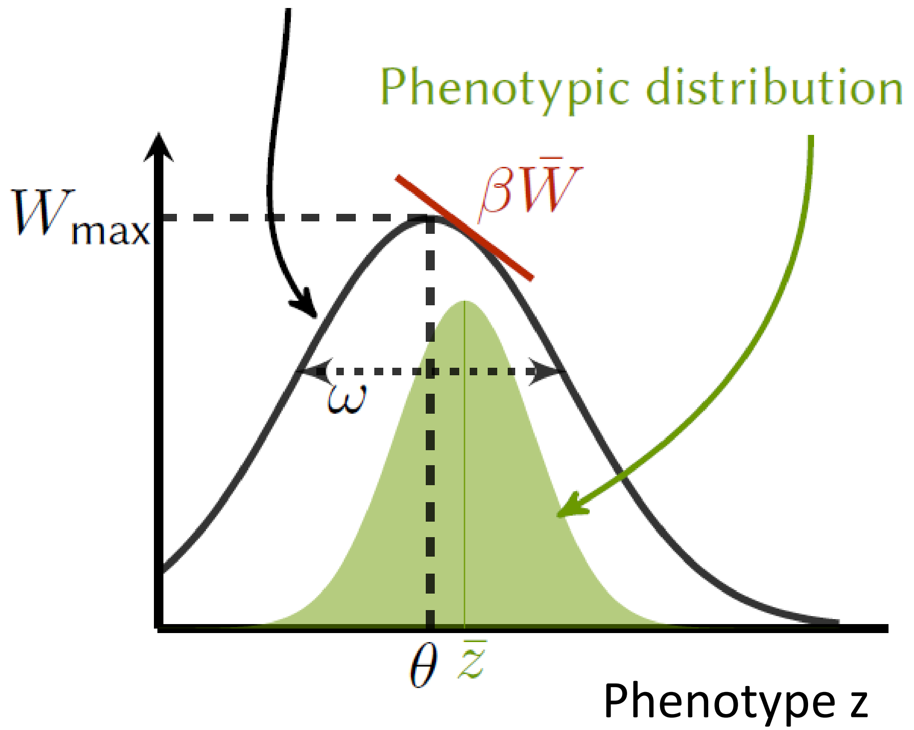
$\partial ln\bar{W}$: selection gradient, local slope of fitness landscape.

1 : Wright (1937 PNAS)
2: Lande (1976 Evolution, 1982 Ecology)
Crow & Kimura (1970)

A conceptual framework: Moving optimum models

- Fitness (reproductive success) depends on phenotypic trait *z*
  Maximized when *z* matches **intermediate phenotypic optimum** θ
- Fitness peak has width ω,
  Strength of stabilizing selection increases with $\frac{1}{\omega^2}$

Fitness $W(z) = \exp\left(-\frac{(z-\theta)^2}{2\,\omega^2}\right)$



1: Lande (1976, 1979 Evolution)
reviewed by Kopp & Matuszewski (2014 Evol Appl)
Figure from de Villemereuil et al (2020 PNAS)

A conceptual framework: Moving optimum models

- The optimum phenotype θ is assumed to **move with the environment**
- Gaussian process:
  Random environmental fluctuations lead to normal distribution of θ with
  $\left\{ \begin{array}{l} \text{variance } \sigma_\theta^2 \\ \text{autocorrelation } \rho \text{ per generation} \end{array} \right.$

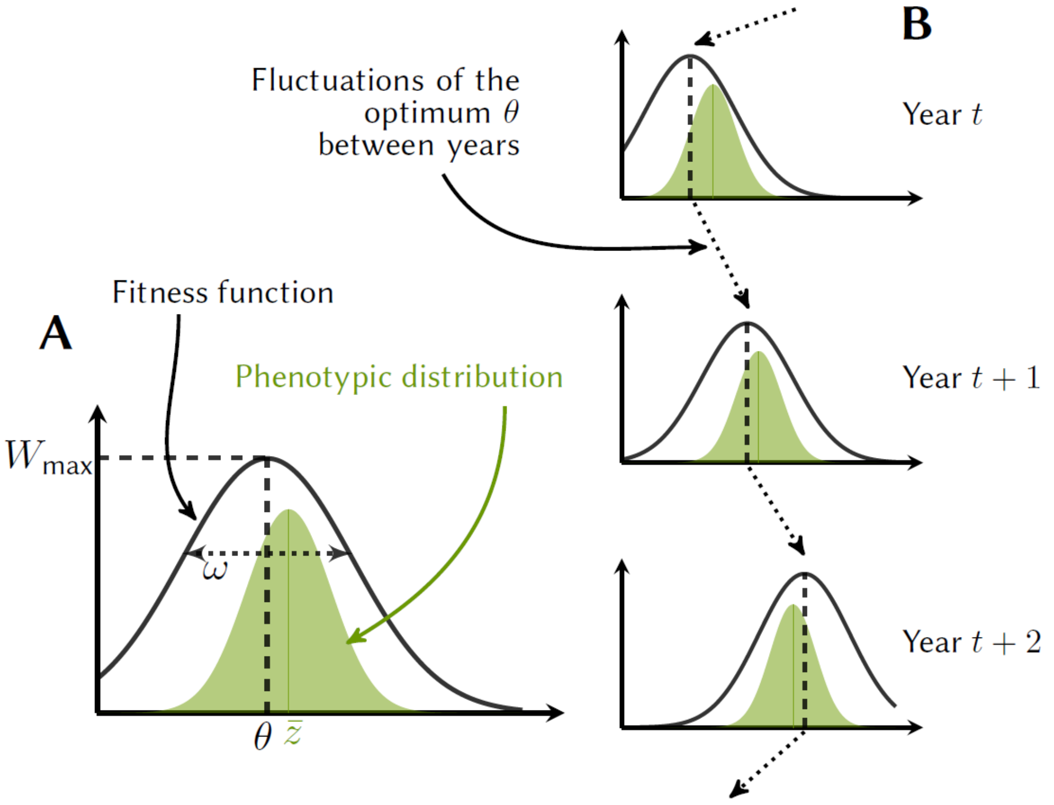


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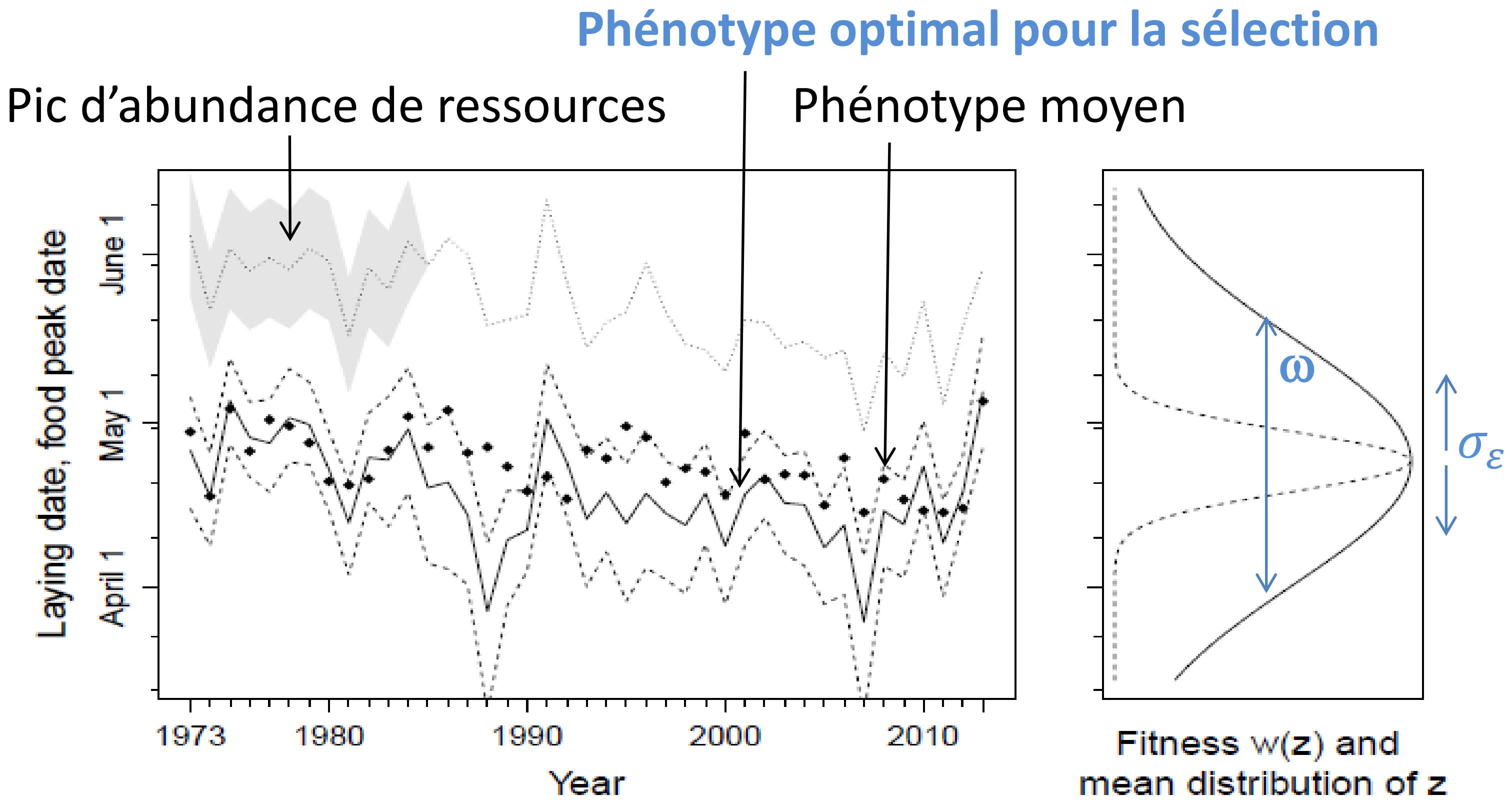
Figure from de Villemereuil et al (2020 PNAS)

A conceptual framework: Moving optimum models

- Empirical evidence from wild populations: great tits in Netherland (40 years)[1]



Parameter	Posterior mean ± S.E.
ω (days)	20.55 ± 1.7
σ_ϵ (days)	6.75 ± 1.66
Autocorrelation α	0.3029 ± 0.2419
Intercept *A* (April day)	19.43 ± 1.95
Slope *B* (days/°C)	−5.01 ± 1.09

1: Chevin, Visser & Tufto (2015 Evolution)

Evidence for moving optimum

Pierre de Villemereuil

- Fluctuating selection estimated as movements of Gaussian fitness peak, for breeding time across birds and mammals in the wild[1] :
  39 populations, 21 species, average 33.2 yrs [9-63]

Sheep
(*Ovis aries*)

Eurasian oystercatcher
(*Haematopus ostralegus*)

Superb fairywren
(*Malurus cyaneus*)

Hi hi
(*Notiomystis cincta*)

Eastern grey kangaroo
(*Macropus giganteus*)

Savannah sparrow
(*Passerculus sandwichensis*)

Red squirrel
(*Tamiasciurus hudsonicus*)

Mountain goats
(*Oreamnos americanus*)

Northern wheatear
(*Oenanthe oenanthe*)

Great tits
(*Parus major*)

Collared flycatcher
(*Ficedula albicollis*)

Dipper
(*Cinclus cinclus*)

Alpine swift
(*Tachymarptis melba*)

Red-winged Fairy-wren
(*Malurus elegans*)

Blue tits
(*Cyanistes caeruleus*)

House sparrow
(*Passer domesticus*)

Pied flycatcher
(*Ficedula hypoleuca*)

Red deer
(*Cervus elaphus*)

Columbian ground squirrel
(*Urocitellus columbianus*)

1: de Villemereuil et al (2020 PNAS)

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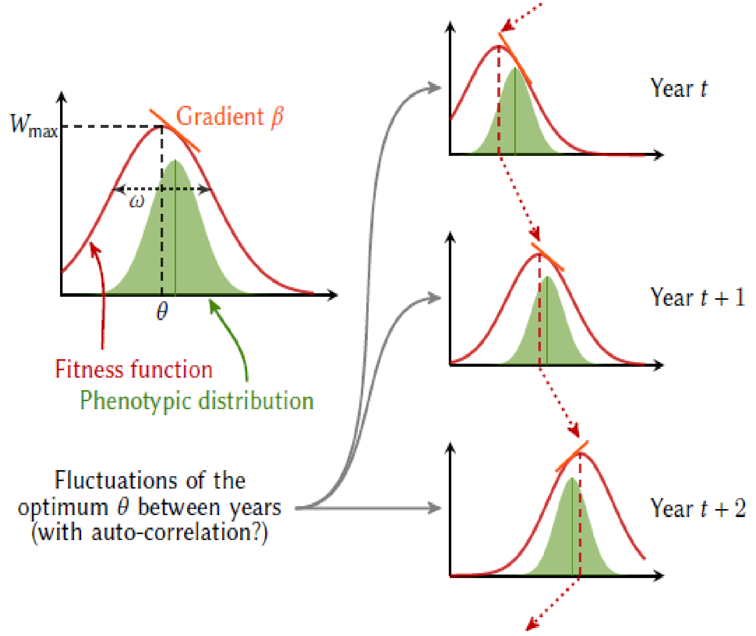
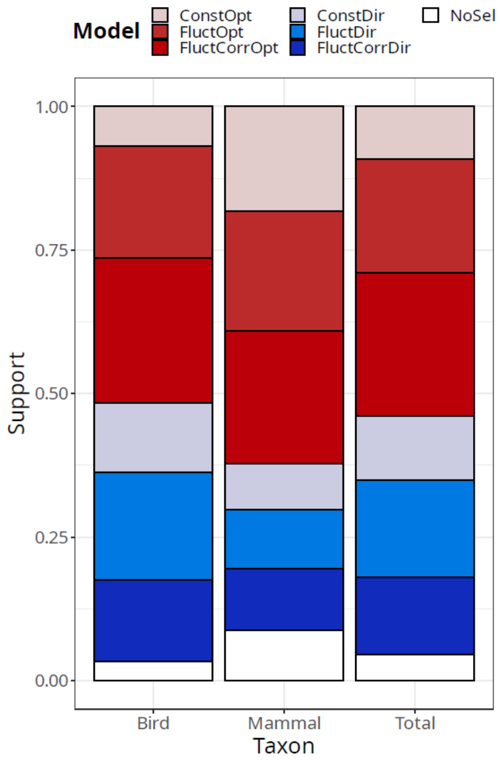
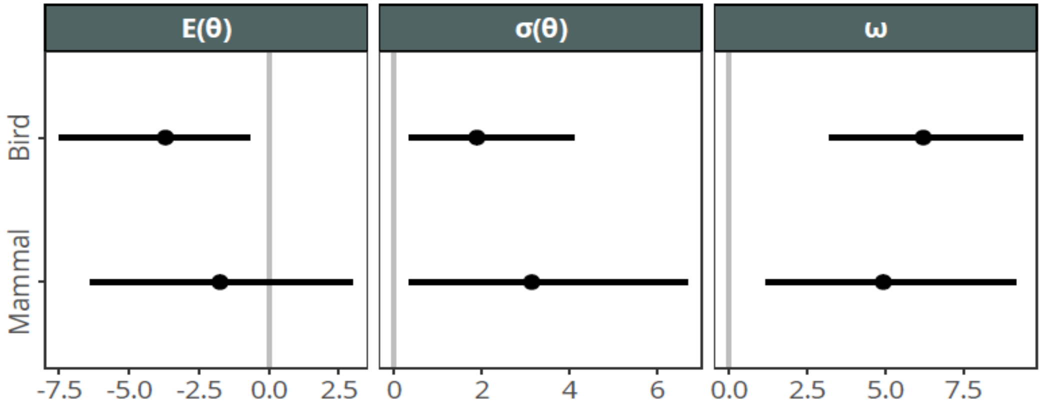




Majority of support across datasets for models with optimum

Also evidence for substantial optimum fluctuations

Mean optimum | SD of optimum | Peak width



1: de Villemereuil et al (2020 PNAS)

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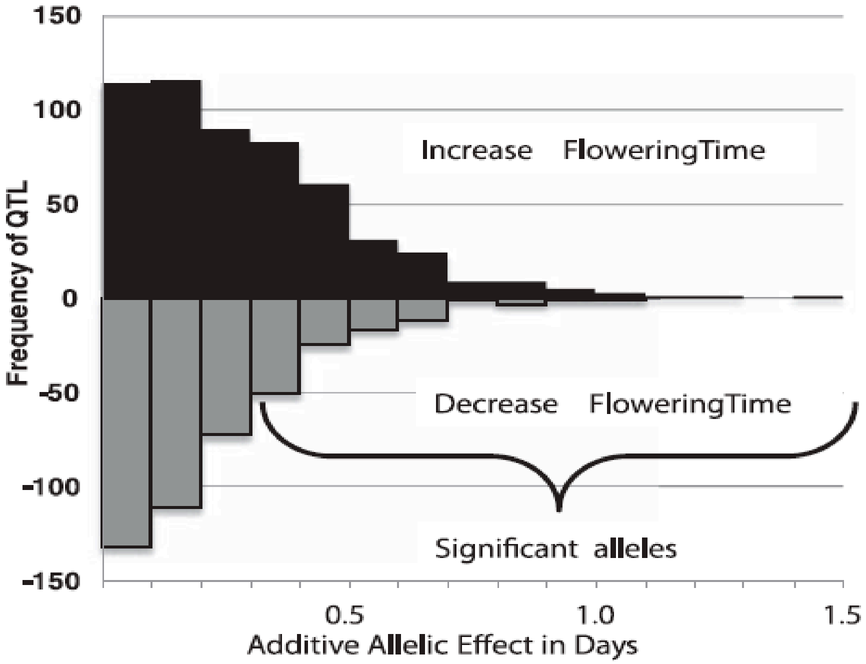
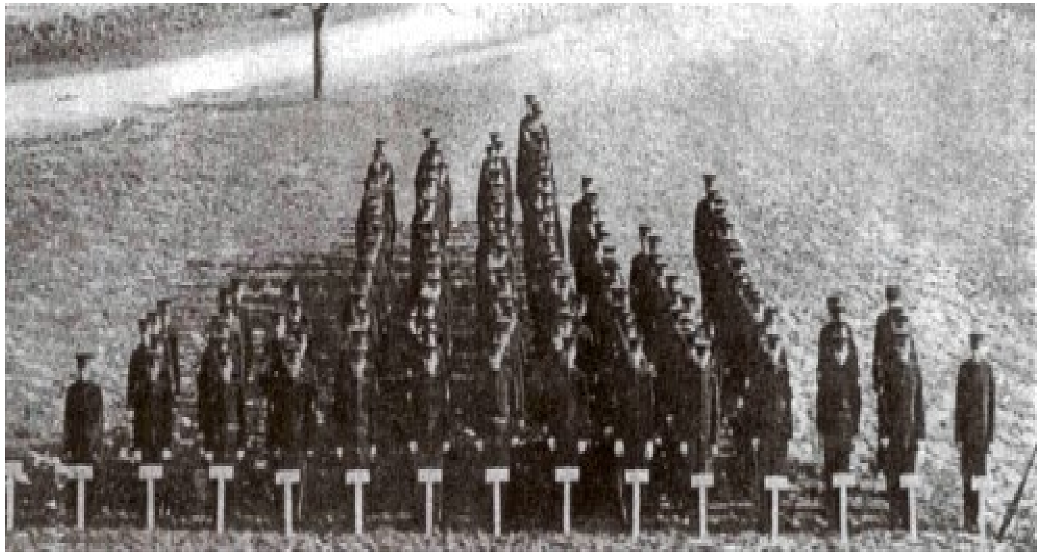
Quantitative traits and adaptation

- Many ecologically important phenotypic traits are determined by many genes of weak effects → Polygenic inheritance

Maize flowering time (Buckler al 2009, Science)



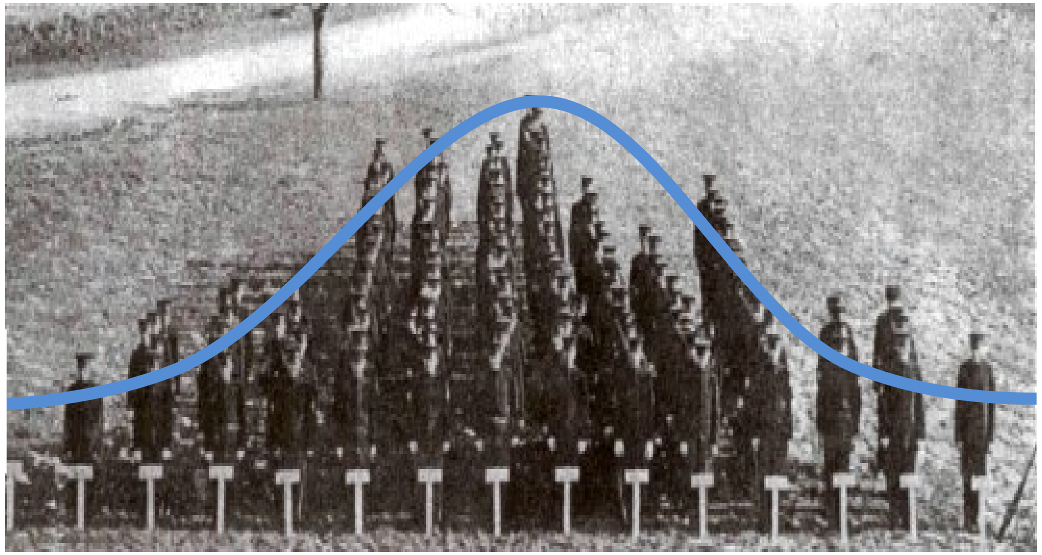
Human height



"*We show that 12111 independent SNPs that are significantly associated with height account for nearly all of the common SNP-based heritability [that is,] for 40% (45%) of phenotypic variance in populations of European ancestry*" (Yengo et al 2022 Nature)

Quantitative traits and adaptation

- Many ecologically important phenotypic traits are determined by many genes of weak effects → Polygenic inheritance
- These traits tend to continuous, normal distributions (infinitesimal model[1])



1: Fisher (1918), Barton et al (2017)

Quantitative traits and adaptation

- Many ecologically important phenotypic traits are determined by many genes of weak effects → Polygenic inheritance
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→ Can be studied using quantitative genetics, robust to departures from normality[2]

- Response to selection by mean phenotype[3]: $\Delta\bar{z} = G\,\frac{\partial ln\bar{W}}{\partial\bar{z}}$

$\beta = \frac{\partial ln\bar{W}}{\partial\bar{z}}$ is the directional selection gradient

G is the additive genetic variance of the trait

1: Fisher (1918), Barton et al (2017)
2: Turelli & Barton (1994 Genetics)
3: Lande (1976)

Quantitative traits and adaptation

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- Response to selection by mean phenotype[3]: $\Delta\bar{z} = G\,\frac{\partial ln\bar{W}}{\partial\bar{z}}$
- Genetic variance G is maintained trough segregation and recombination among loci[1], as well as polygenic mutation[4].
- With stationary fluctuations of an optimum, G will reach an expected equilibrium. To first order G can be approximated as constant to study changes in the mean phenotype across generations

1: Fisher (1918), Barton et al (2017)
2: Turelli & Barton (1994 Genetics)
3: Lande (1976)
4: Kimura (1965); Turelli (1984)

Quantitative trait tracking a fluctuating optimum

- A **Gaussian fitness peak** approximates well any phenotype-fitness map with an optimum for multiplicative fitness:

$$W(z) = W_{\max} \exp\left(-\frac{(z-\theta)^2}{2\,\omega^2}\right)$$

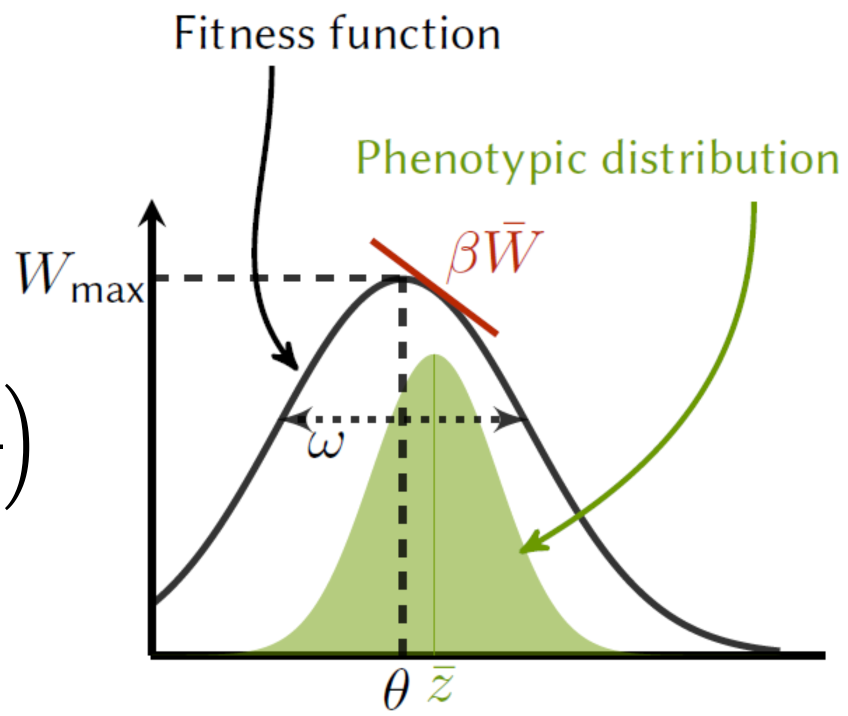
- When the trait z is has normal distribution $p(z)$, then mean fitness is also Gaussian (convolution):

$$\bar{W} = \int_{-\infty}^{\infty} p(z)W(z)dz = W_{\max}\sqrt{\frac{\omega^2}{\omega^2+\sigma_z^2}}\exp\left(-\frac{(\bar{z}-\theta)^2}{2(\omega^2+\sigma_z^2)}\right)$$

- Response to selection becomes[1]:

$$\Delta\bar{z} = G\frac{\partial ln\bar{W}}{\partial\bar{z}} = -GS(\bar{z}-\theta) \quad \text{with} \quad S = \frac{1}{(\omega^2+\sigma_z^2)}$$

Linear restoring force on mean phenotype towards optimum



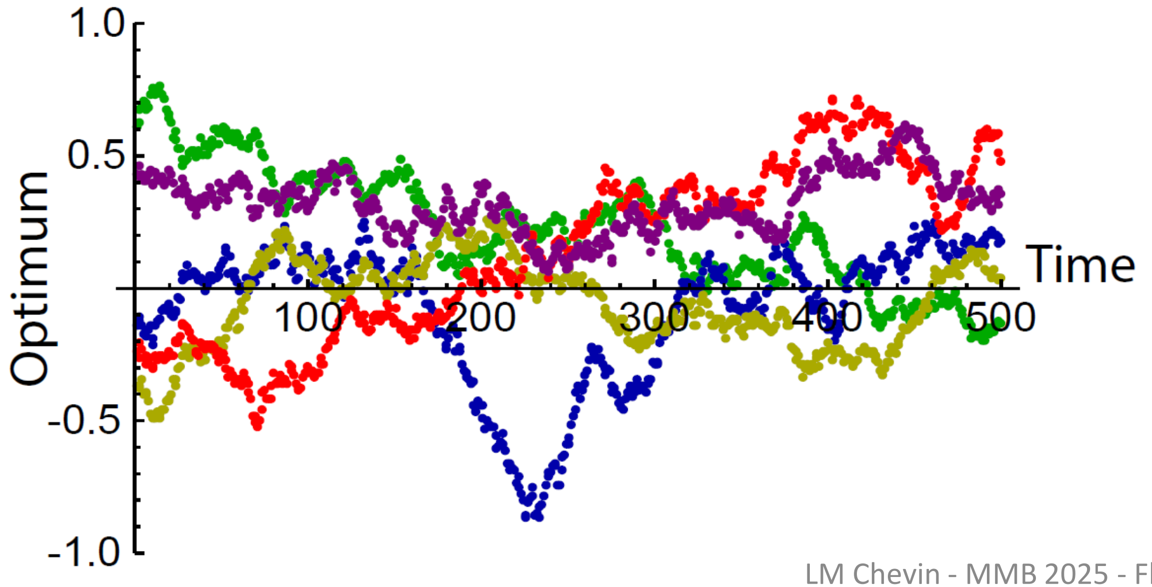
Lande (1976 Evolution)

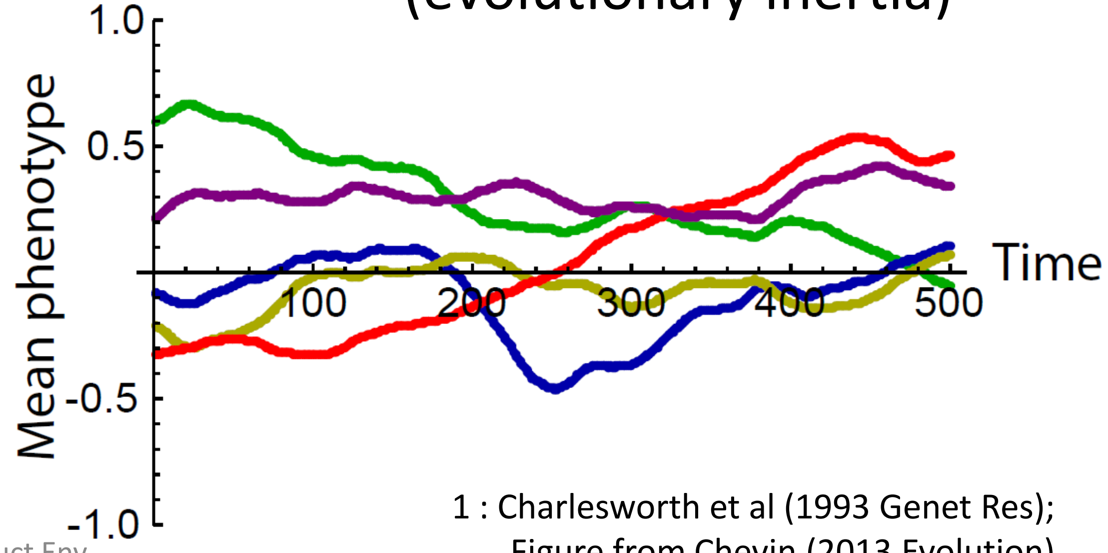
Quantitative trait tracking a fluctuating optimum

- Iterating over generations assuming constant genetic variance, we have[1]

$$\bar{z}_t = \bar{z}_0(1-GS)^t + GS\sum_{j=1}^{t}(1-GS)^{j-1}\theta_{t-j} \underset{t\to\infty}{\rightarrow} GS\sum_{j=1}^{\infty}(1-GS)^{j-1}\theta_{t-j}$$

→ Mean phenotype is weighted average of past optima, with more weight on more recent. Smoothes environmental "signal", all the more as adaptive potential SG is small (evolutionary inertia)





1 : Charlesworth et al (1993 Genet Res); Figure from Chevin (2013 Evolution)

Quantitative trait tracking a fluctuating optimum

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- If optimum undergoes Gaussian process, so do:
  - the mean phenotype $\bar{z}$ (linear combination of Gaussians)
  - the mismatch with optimum $x = \bar{z} - \theta$

→The distribution of maladaptation can be summarized by its mean and variance.

- At stationarity:

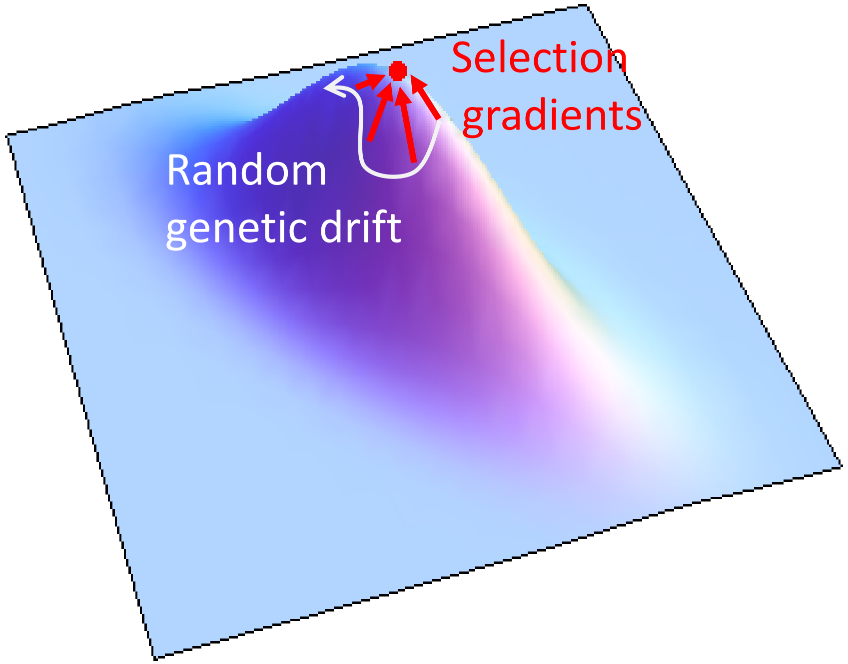
➢The expected mean phenotype matches the expected optimum

➢But the **variance and autocorrelation of mismatch** play important roles.

1 : Charlesworth et al (1993 Genet Res);
Figure from Chevin (2013 Evolution)

Fluctuations of mismatch & selection gradient

- Directional selection gradient is proportional to phenotypic mismatch, $\beta = -S(\bar{z} - \theta)$
- Even with a constant optimum, **drift causes temporal variation in mismatch** $(\bar{z} - \theta)$



- The variance of directional selection caused by drift around the constant optimum is $V(\beta) = \frac{S}{(2-SG)N_e}$

→ **Lower bound for fluctuations** in directional selection, larger for lower N_e and larger S.

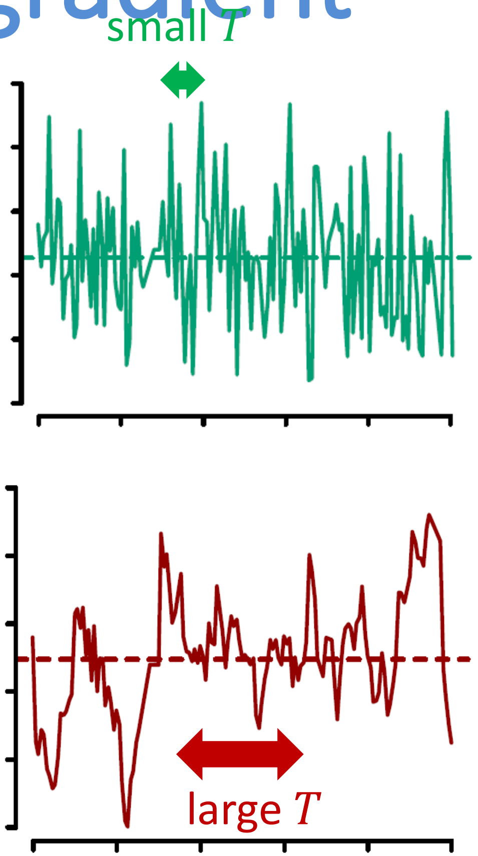
- The autocorrelation function of selection gradients is $$\mathrm{ACF}(\beta, \tau) = (1 - SG)^{\tau}$$

→ **Evolutionary inertia** over timescale $1/(SG)$ longer with lower evolutionary potential

Chevin & Haller (2014 Evolution)

Fluctuations of mismatch & selection gradient

- Autocorrelated fluctuating optimum (AR1),
  with T the characteristic time over which optimum is autocorrelated



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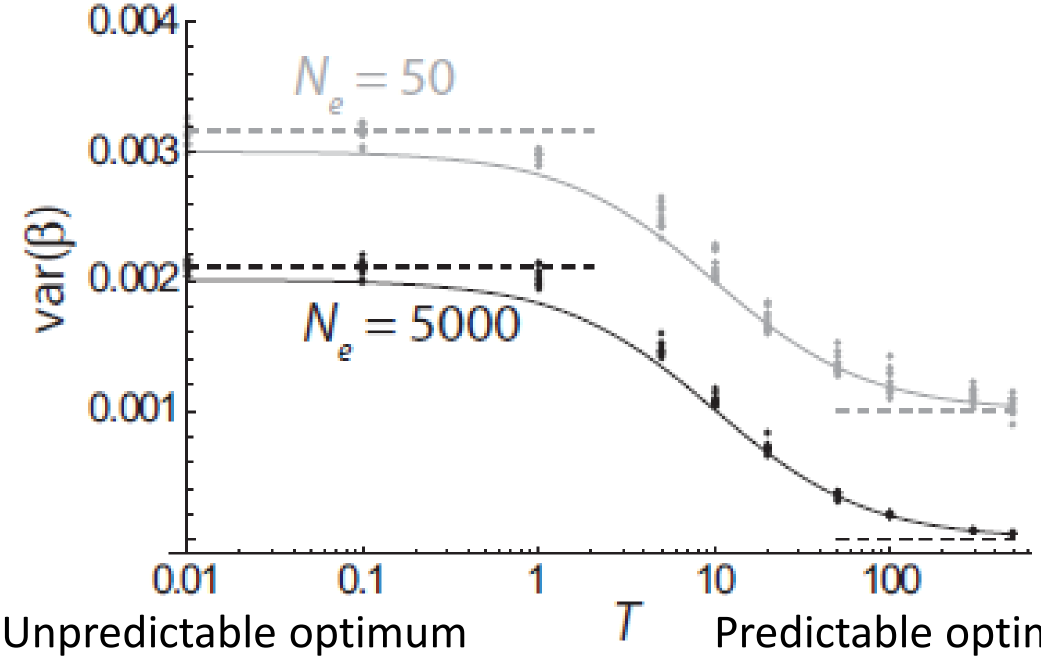
Fluctuations of mismatch & selection gradient

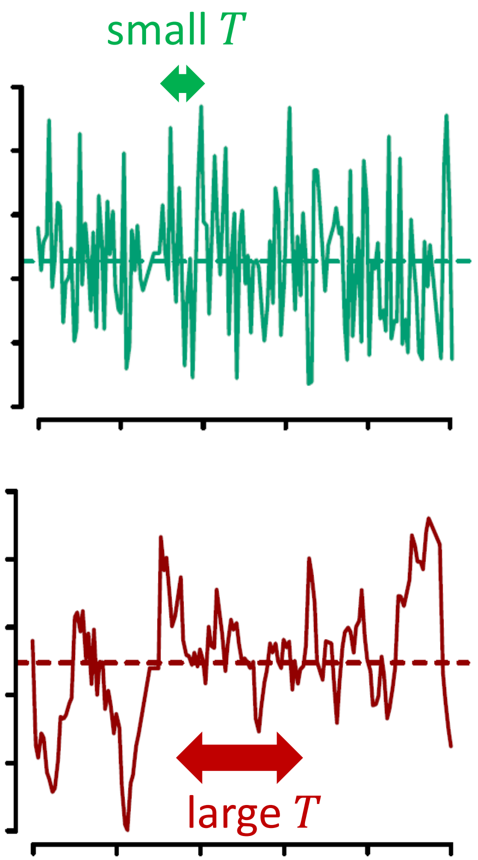
- Autocorrelated fluctuating optimum (AR1), with T the characteristic time over which optimum is autocorrelated
- Without drift: $\mathrm{V}(\beta) \approx \frac{S^2\sigma_\theta^2}{1+SGT}$



Unpredictable optimum

Predictable optimum

- ➢ Higher autocorrelation leads to **better adaptive tracking**, thus smaller fluctuations in β
- ➢ The variance due to drift around optimum adds up to that of optimum fluctuations



Chevin & Haller (2014 Evolution)

Fluctuations of mismatch & selection gradient

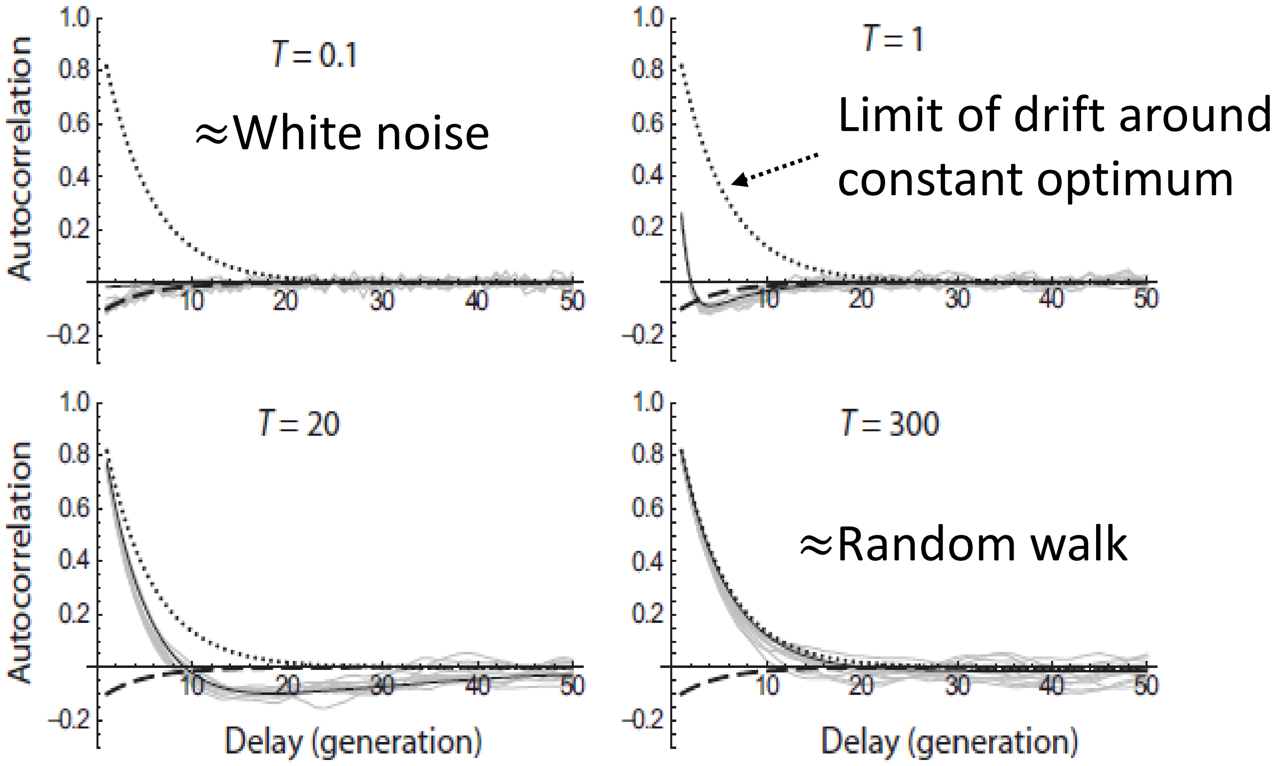
- Autocorrelated fluctuating optimum (AR1),
  with T the characteristic time over which optimum is autocorrelated

- Without drift: $\mathrm{V}(\beta) \approx \frac{S^2\sigma_\theta^2}{1+SGT}$

$$\mathrm{ACF}(\beta,\tau) = \frac{e^{-\frac{\tau}{T}} - SGTe^{-SG\tau}}{1-SGT}$$

(Weighted) difference between autocorrelation of optimum and evolutionary inertia

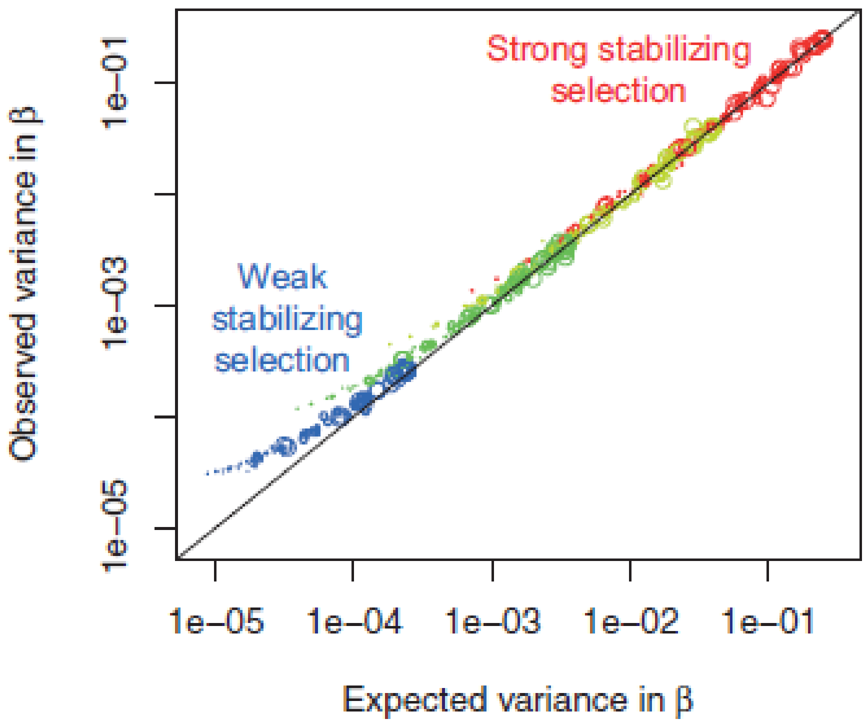
→ Fluctuations in β do not tell the whole story about fluctuating selection!

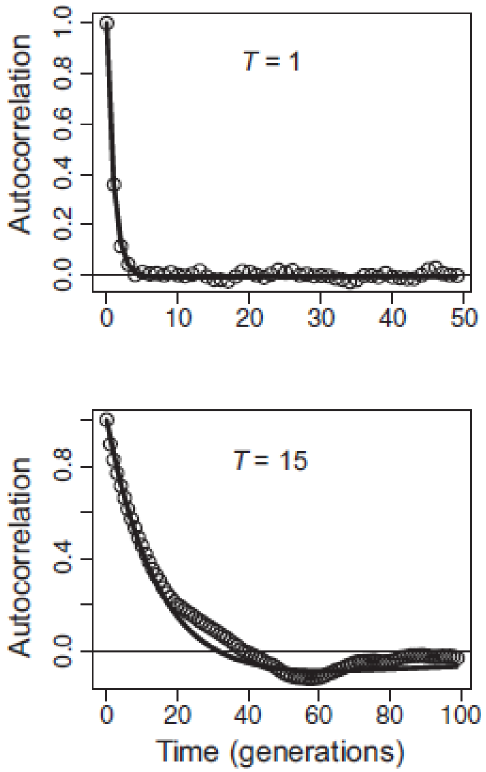


Chevin & Haller (2014 Evolution)

Fluctuations of mismatch & selection gradient

- Analytical predictions assuming constant genetic variance work well on individual-based simulations with explicit loci and high mutation rates

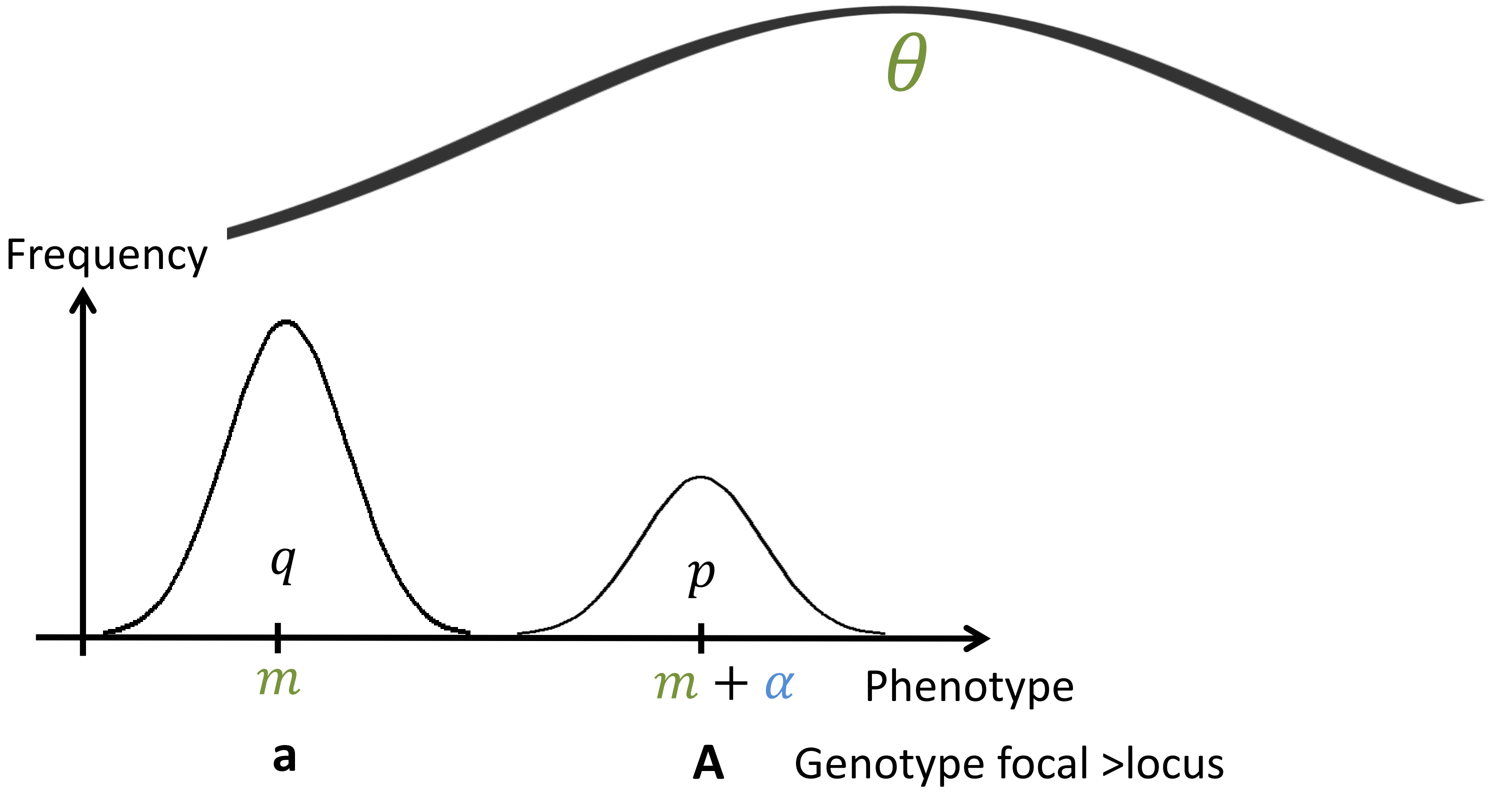




Chevin & Haller (2014 Evolution)

Selection on large-effect mutation

- Haploid model: mutation in frequency p (with $q = 1 - p$), with phenotypic effect α, arising in background genotype with mean phenotype m, selected towards optimum θ



Selection on large-effect mutation

- Haploid model: mutation in frequency p (with $q = 1 - p$), with phenotypic effect α, arising in background genotype with mean phenotype m, selected towards optimum θ
- Effect of selection on frequency change:

$$p' = \frac{pW_{m+\alpha}}{pW_{m+\alpha}+qW_m} \text{ and } q' = \frac{qW_m}{pW_{m+\alpha}+qW_m}\text{, so } \frac{p'}{q'} = \frac{W_{m+\alpha}}{W_m}\frac{p}{q}$$

- On logit scale $\psi = \ln\left(\frac{p}{q}\right)$: $\Delta\psi = \ln W_{m+\alpha} - \ln W_m = -\frac{S\alpha}{2}[\alpha + 2(m-\theta)]$

→Mutations compensating for mean mismatch $m - \theta$ are favored

- After t generation of selection: $\psi_t = \psi_0 - \frac{S\alpha}{2}\left[\alpha\, t + 2\sum_{i=0}^{t-1}(m_i - \theta_i)\right]$

Linear in mismatch $m - \theta$ → **If the optimum $\boldsymbol{\theta}$ follows a Gaussian process, so does $\boldsymbol{\psi}$.**

ψ simply **integrates all past mismatches, with equal weight on all times**

1: Kimura (1954 Genetics), Gillespie (1991), Chevin (2019 Genetics)

Selection on large-effect mutation

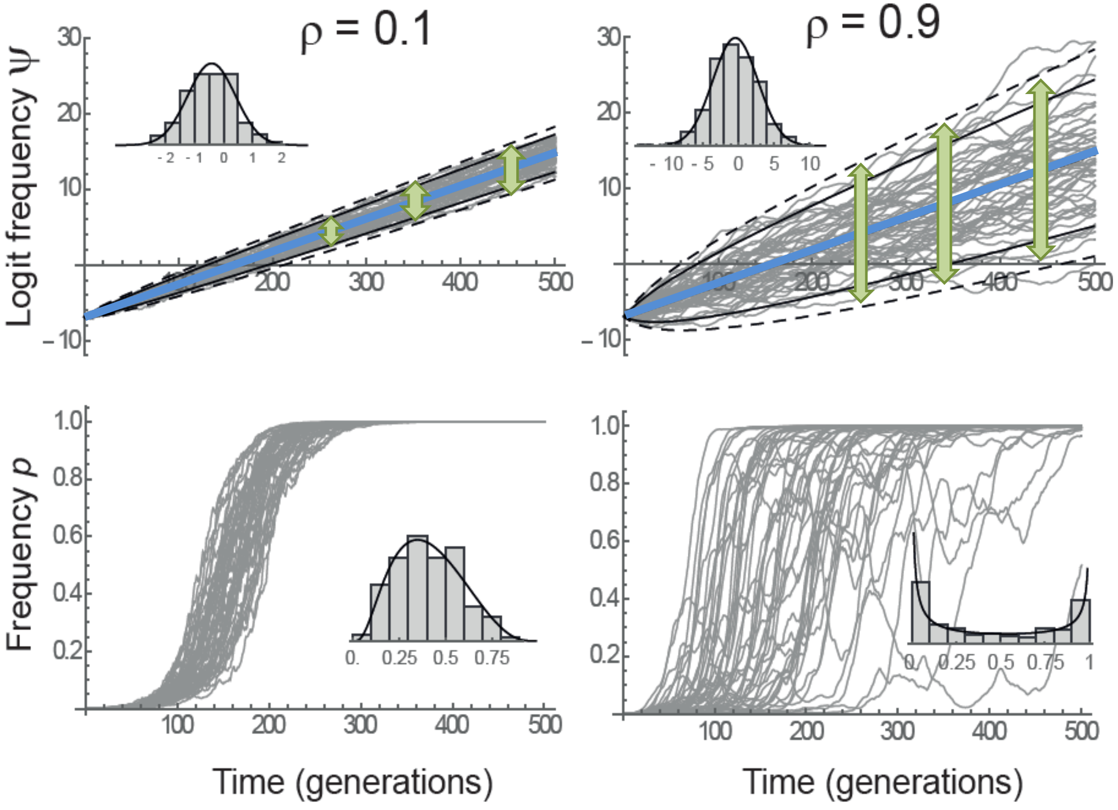
- Assume the optimum follows a stationary autocorrelated Gaussian process (AR1), and background mean phenotype m is constant.

- Fluctuation pattern has **no influence on expected change** in (logit) frequency

- Stochastic **variance of ψ** is
  $\sigma^2_{\psi,t} \approx \sigma^2_s \frac{1+\rho}{1-\rho} t$, with $\sigma^2_s = (S\alpha\sigma_\theta)^2$

→ Increases linearly, faster under higher autocorrelation

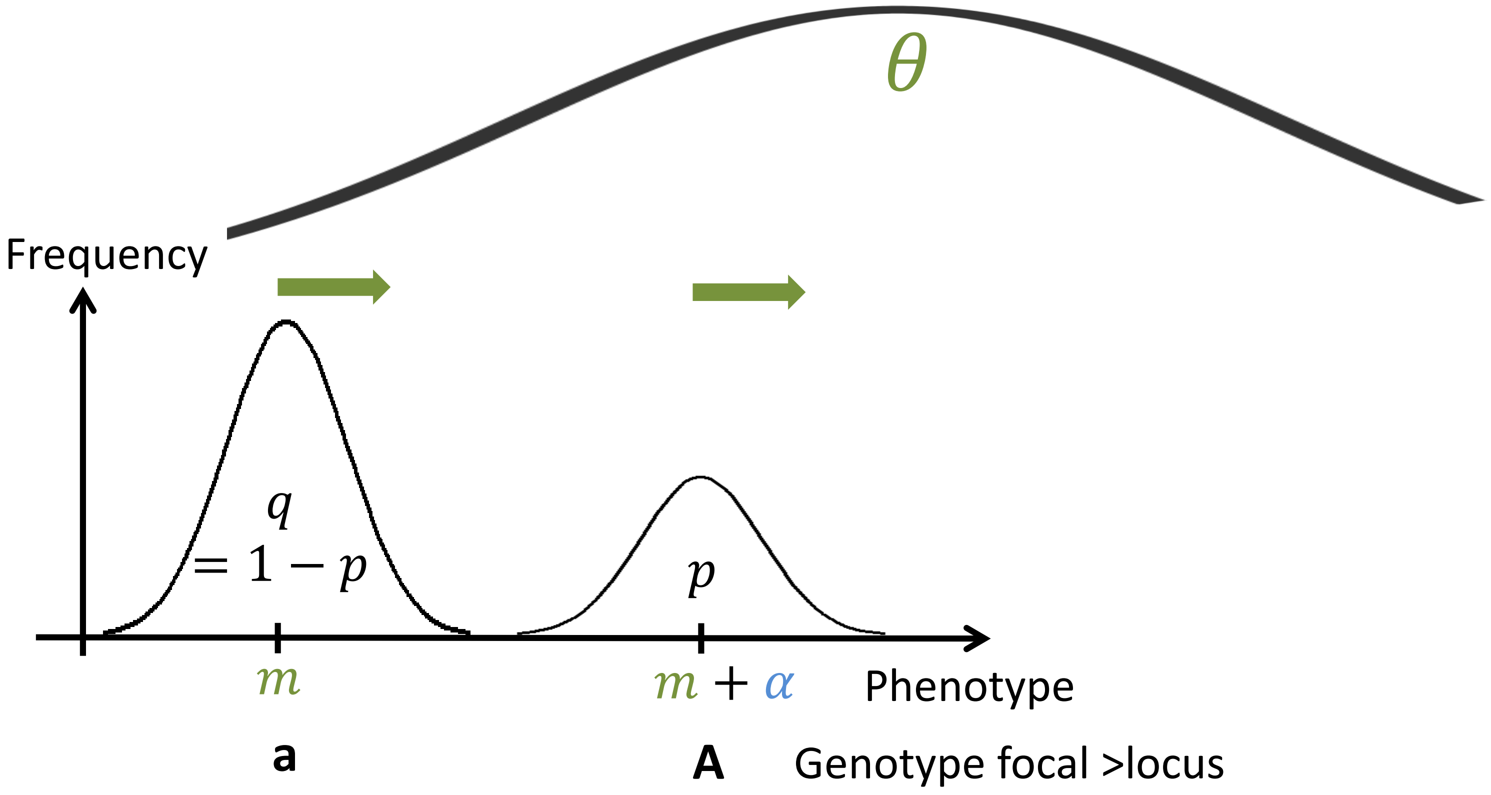
- On p scale, variance of ψ translates into variance in the timing of selective sweeps



Chevin (2019 Genetics)

Influence of background genetic variation

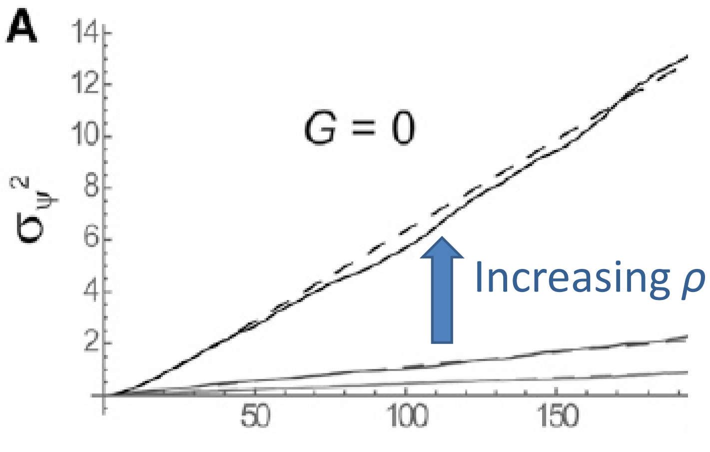
- If other small effect loci cause normally distributed background genetic variance, then **mean background m also evolves in response to fluctuating optimum**.



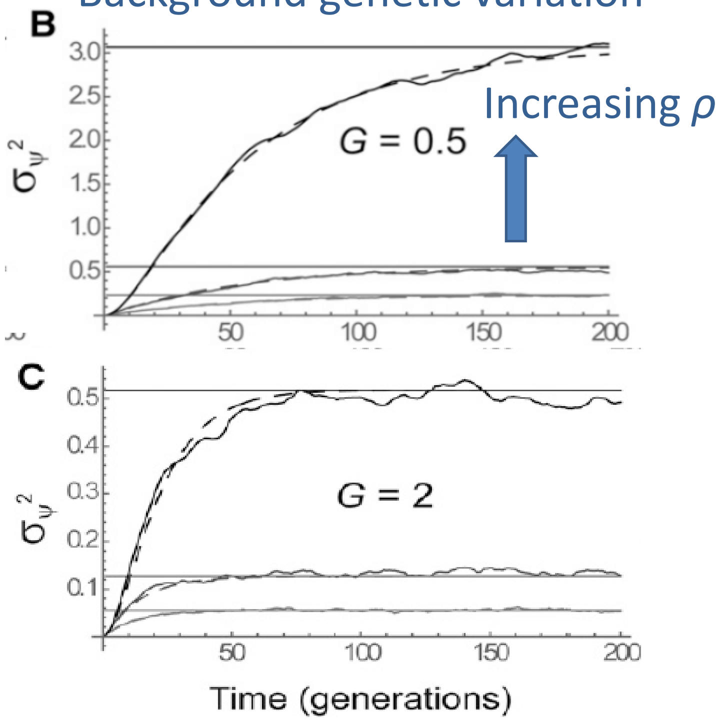
Influence of background genetic variation

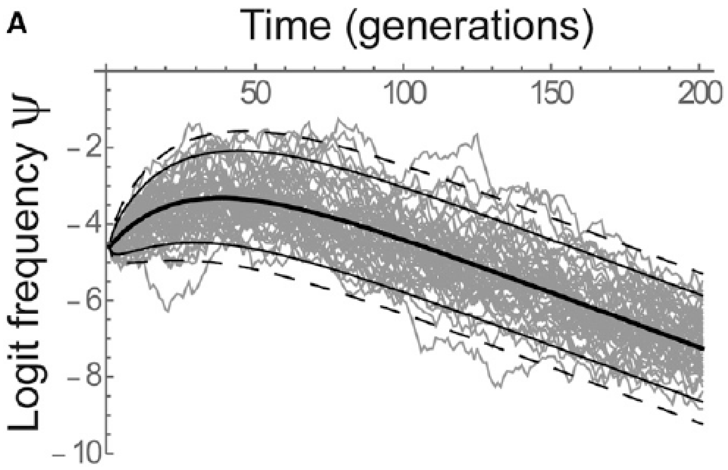
- If other small effect loci cause normally distributed background genetic variance, then **mean background m also evolves in response to fluctuating optimum**.
- The process for $\psi = \mathrm{logit}(p)$ then becomes **stationary: variance plateaus**
  → Polygenic background variation buffers the stochasticity perceived by major gene

No background genetic variation



Background genetic variation



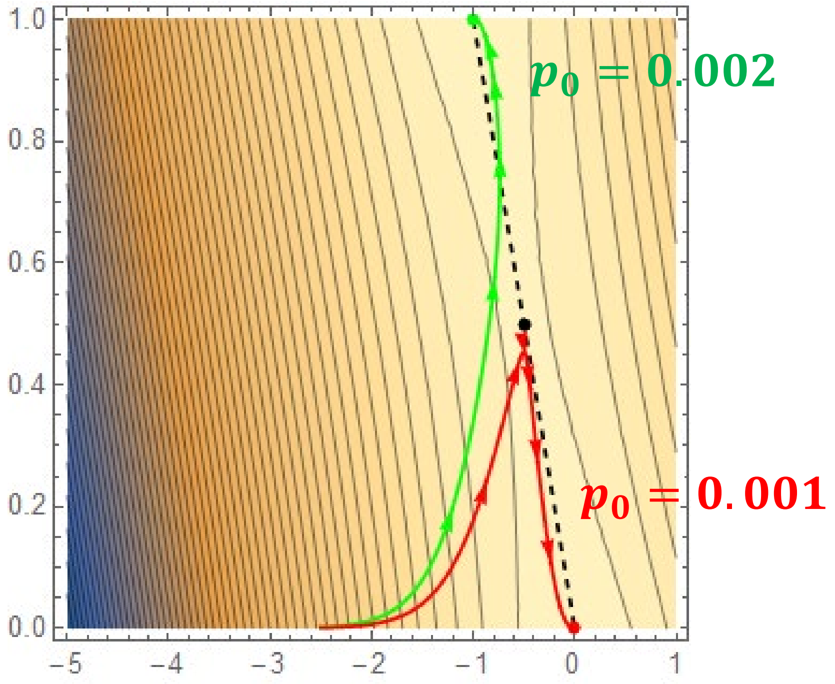


Chevin (2019 Genetics)

Influence of background genetic variation

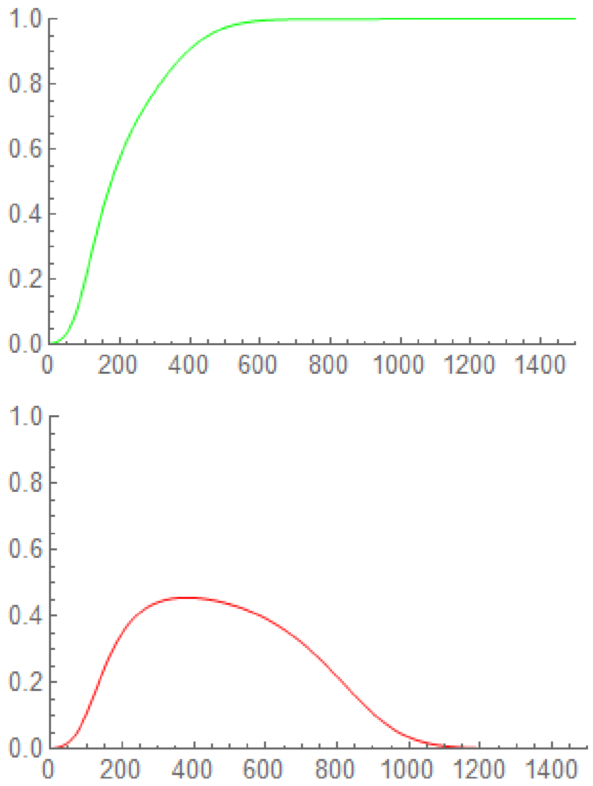
- Bistability: Evolution of mean background phenotype towards optimum via polygenic background variation may interrupt sweep at QTL[1]

Frequency p at QTL



Background mismatch $m - \theta$

Frequency p

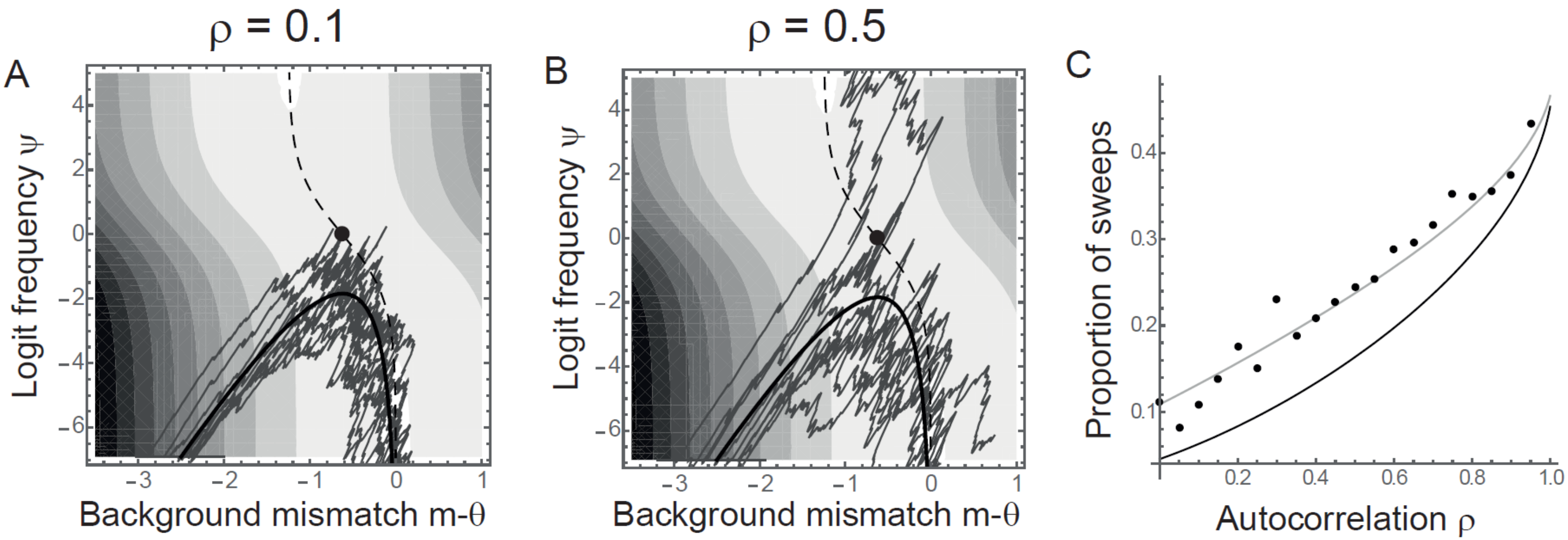


Time

1: Adapted from Lande (1983 Heredity), Chevin & Hospital (2008 Genetics)

Influence of background genetic variation

- Bistability: Evolution of mean background phenotype towards optimum via polygenic background variation may interrupt sweep at QTL[1]
- In stochastic environment: autocorrelation ρ changes probability of complete sweep, by increasing the stochastic variance of this process.



Chevin (2019 Genetics)

Ecology and evolution in randomly fluctuating environments

- Basics and framework -

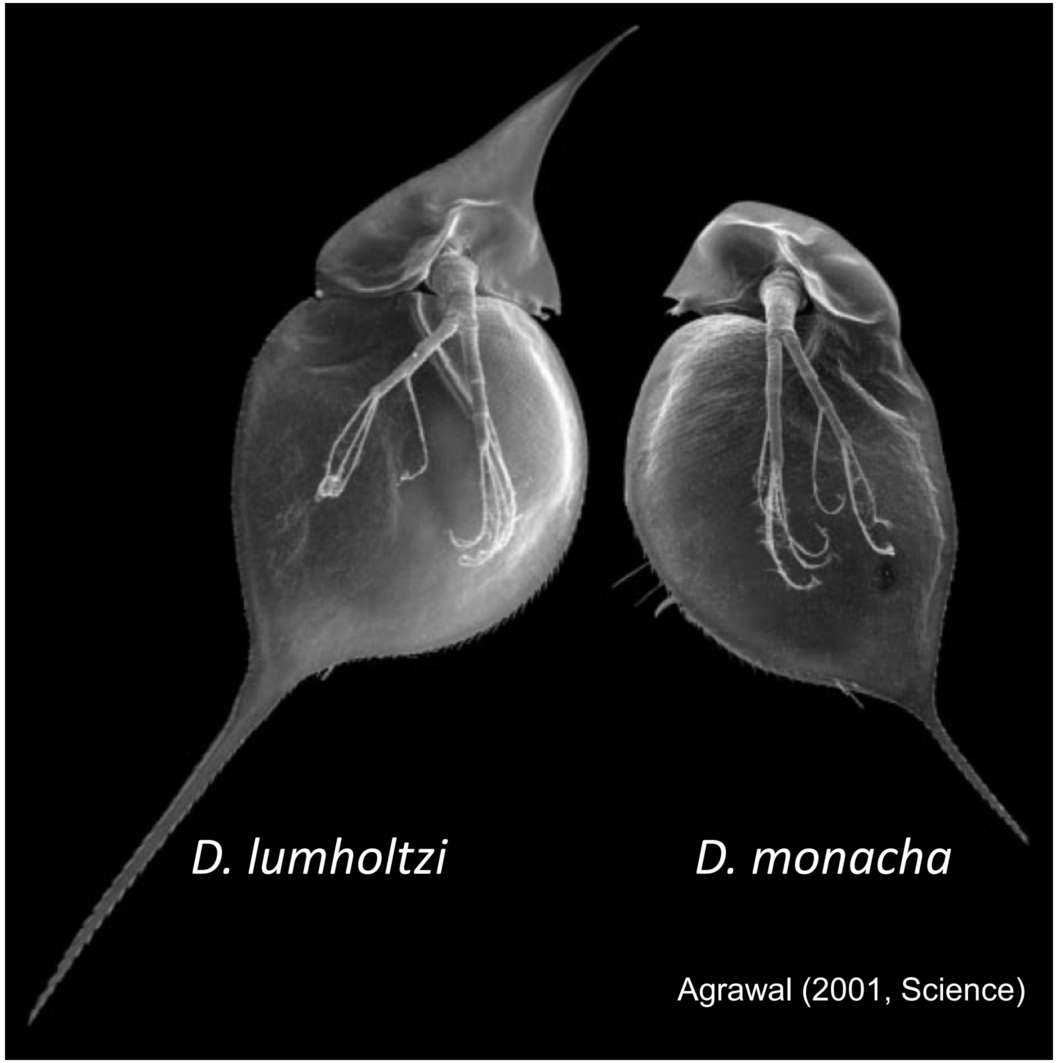
- Evolutionary dynamics -

- Phenotypic plasticity -

- Evolutionary demography -

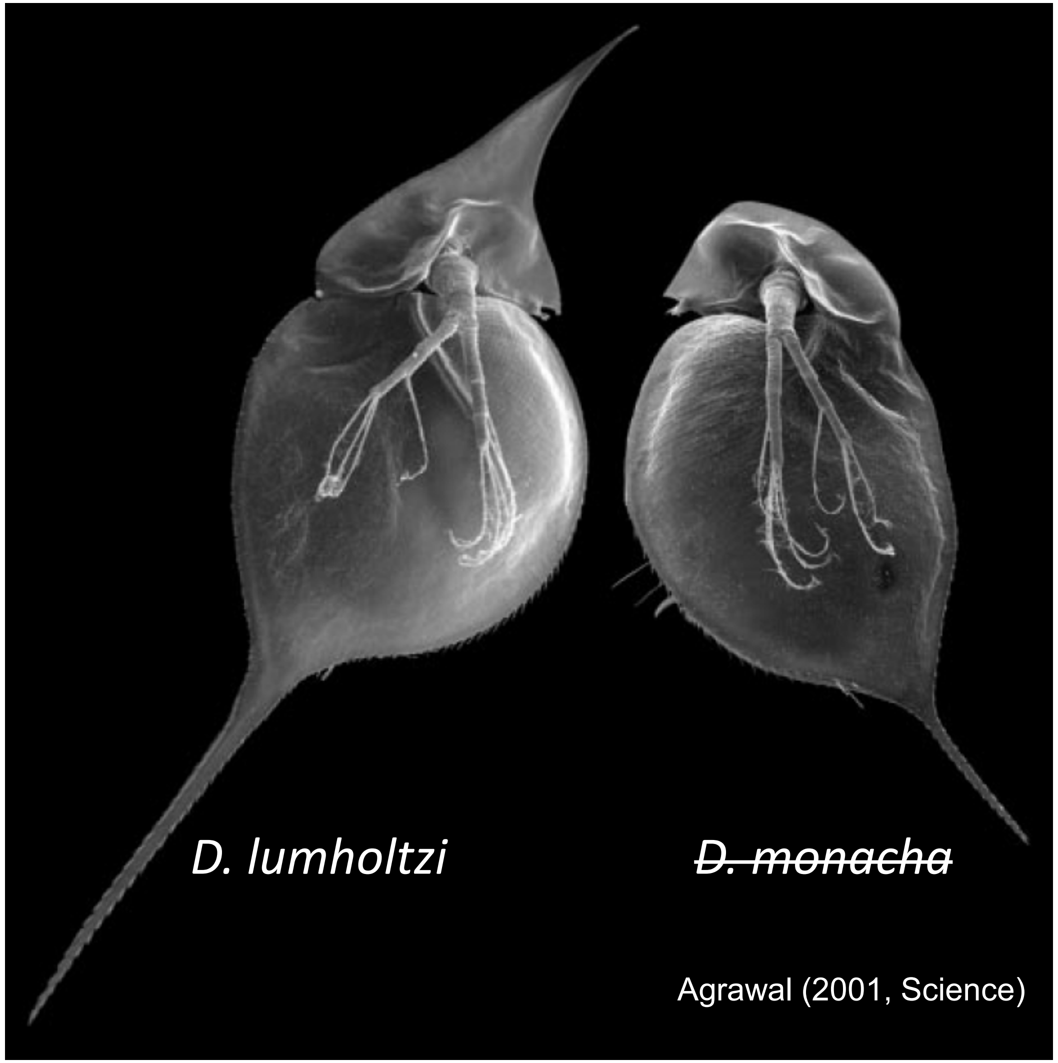
- Experimental results -

2 daphnia species



~~2 daphnia species~~

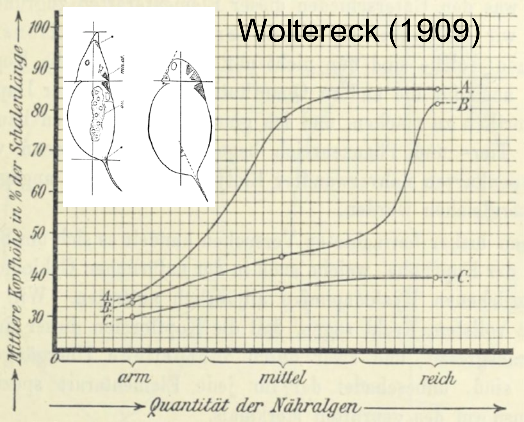
The **same clone**, with and without **predator cues**



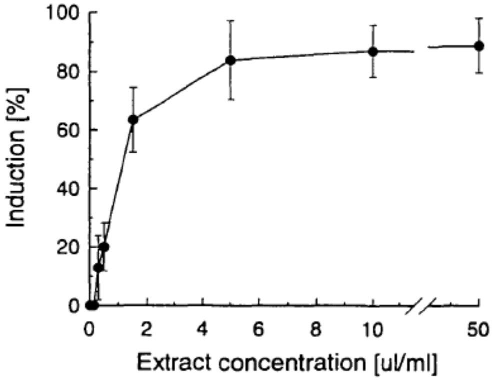
Phenotypic plasticity

- Ability of a given genotype to produce different phenotypes in different environments
- Captured by the **reaction norm** relating trait to environment

Body shape vs resources … or predator cues

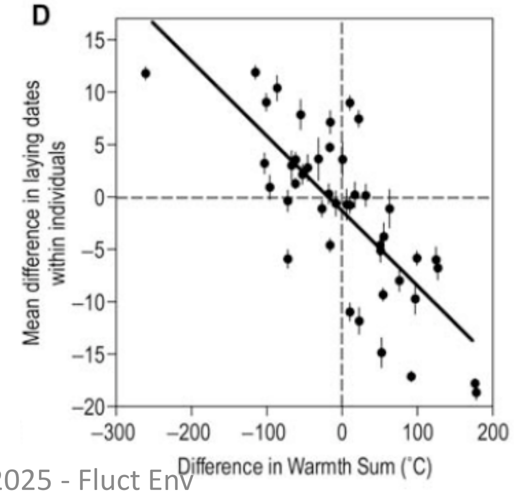


Tollrian (1993 J Plankt Res)



Breeding time vs temperature

Charmantier et al (2008 Science)

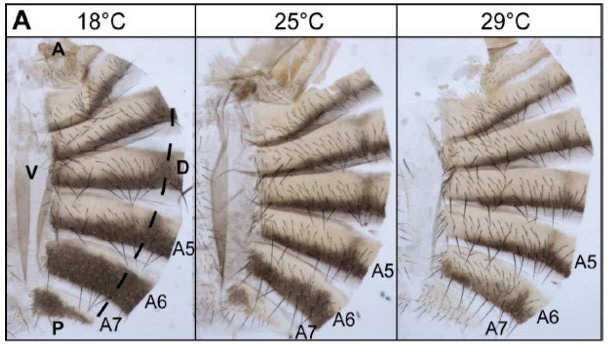


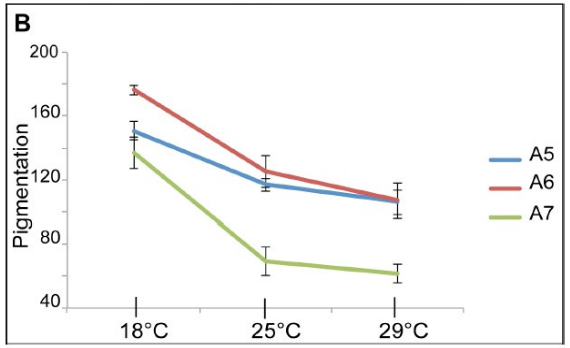
Wet-season
vs dry-season forms

(F. Nijhout, in Pfennig et al 2010 TREE)

Darkness vs temperature

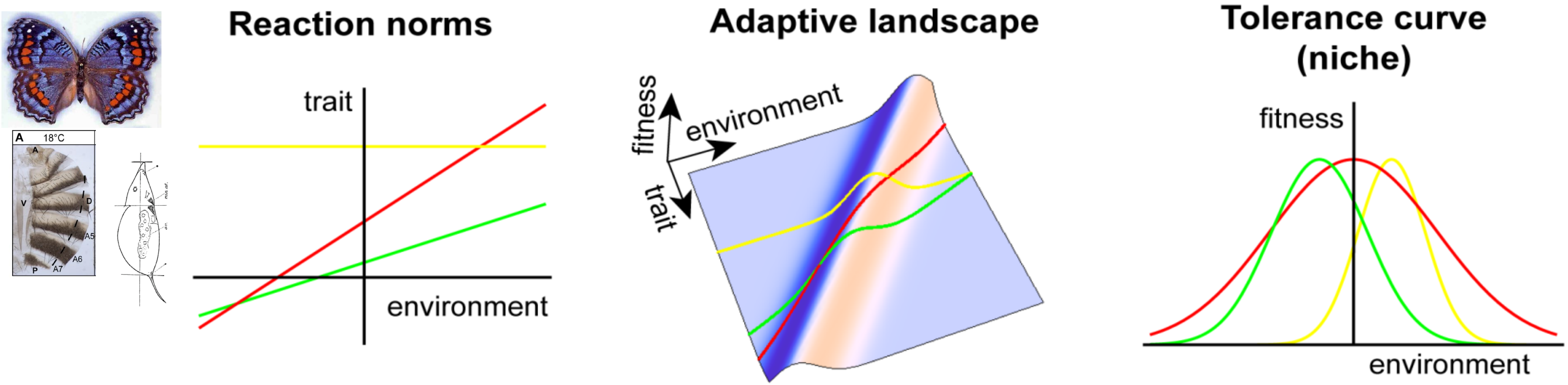
Gibert et al (2016, PLoS Genetics)





Environmental tolerance curves

- Fitness (or survival, performance, etc) against environment: **Environmental tolerance curve**[1] = one axis of fundamental niche.
- Emerges from phenotypic plasticity & selection of underlying traits.



→ Predictions about **plastic tracking of a moving optimum phenotype** can be translated into predictions about **environmental tolerance curves**[2].

1: Lynch & Gabriel (1987 Am Nat); Buckley & Kingsolver (2021 ARESE)
2: Chevin, Lande & Mace (2010 PLoS Biol); Lande (2014 JEB)

Plastic tracking of moving optimum in the wild

- Moving optimum for breeding time estimated across birds and mammals in the wild

Eurasian oystercatcher (*Haematopus ostralegus*)

Superb fairywren (*Malurus cyaneus*)

Hi hi (*Notiomystis cincta*)

Sheep (*Ovis aries*)

Eastern grey kangaroo (*Macropus giganteus*)

Savannah sparrow (*Passerculus sandwichensis*)

Red squirrel (*Tamiasciurus hudsonicus*)

Mountain goats (*Oreamnos americanus*)

Northern wheatear (*Oenanthe oenanthe*)

Great tits (*Parus major*)

Collared flycatcher (*Ficedula albicollis*)

Dipper (*Cinclus cinclus*)

Alpine swift (*Tachymarptis melba*)

Red-winged Fairy-wren (*Malurus elegans*)

Blue tits (*Cyanistes caeruleus*)

House sparrow (*Passer domesticus*)

Pied flycatcher (*Ficedula hypoleuca*)

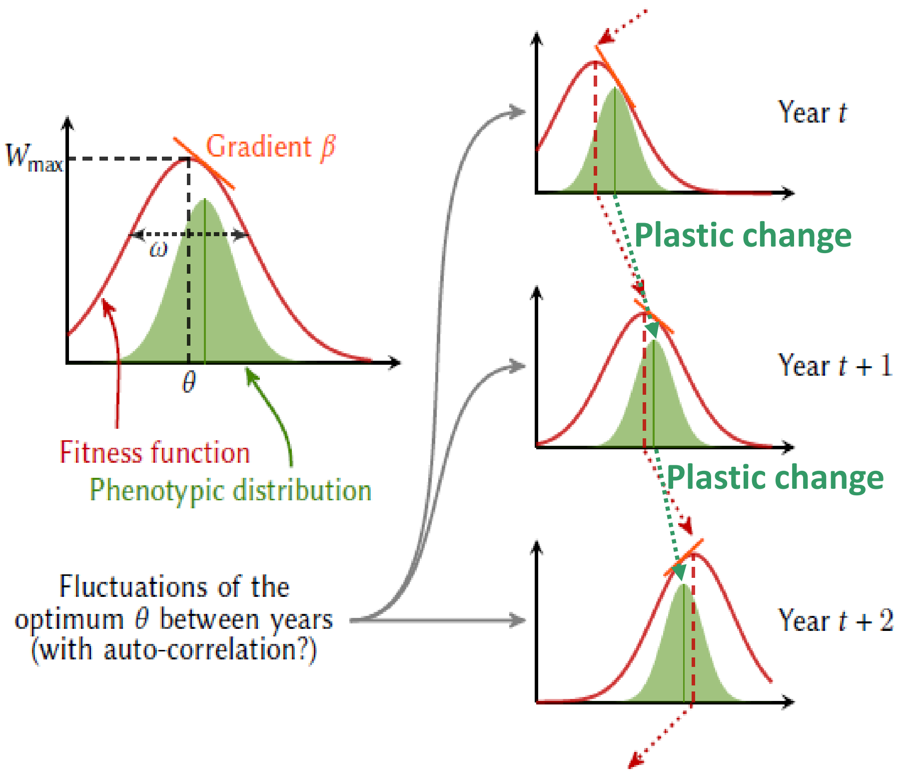
Red deer (*Cervus elaphus*)

Columbian ground squirrel (*Urocitellus columbianus*)

De Villemereuil et al (2020 PNAS)

Plastic tracking of moving optimum in the wild

- Moving optimum for breeding time estimated across birds and mammals in the wild
- **Plastic phenological changes** across years can be estimated from **individuals that breed repeatedly**



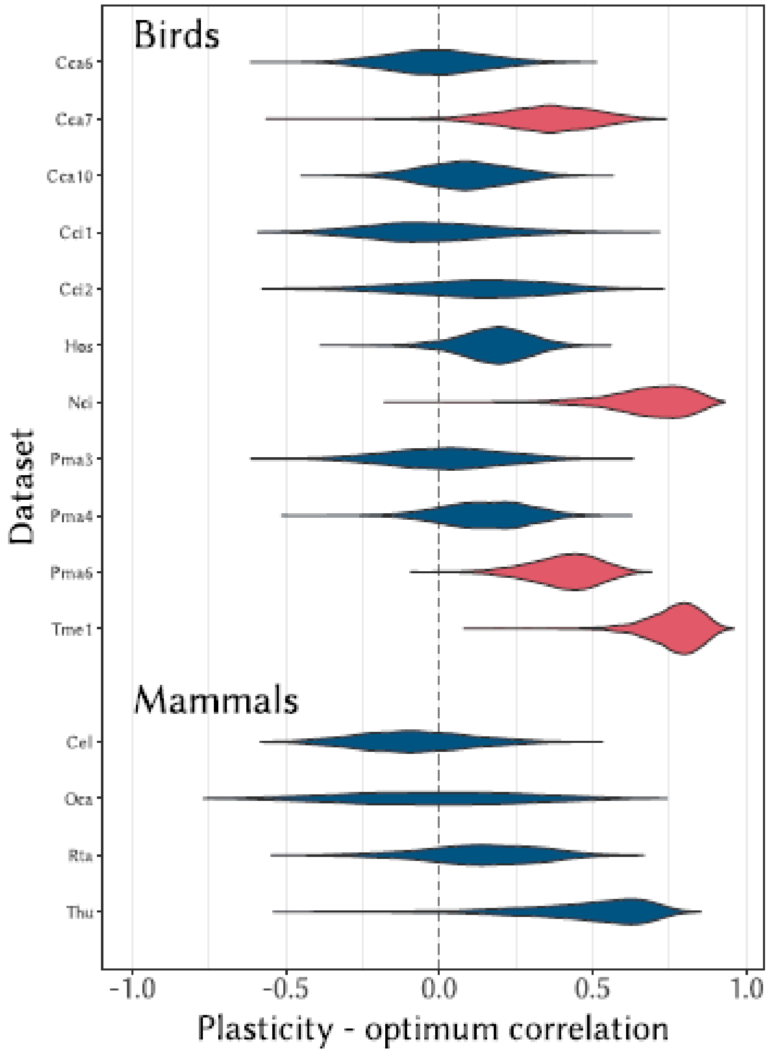
De Villemereuil et al (2020 PNAS)

Plastic tracking of moving optimum in the wild

- Moving optimum for breeding time estimated across birds and mammals in the wild
- **Plastic phenological changes** across years can be estimated from **individuals that breed repeatedly**
- Significantly correlated to movements of optimum across birds.

→ **Plastic tracking of optimum** reduces magnitude of phenotypic mismatch:

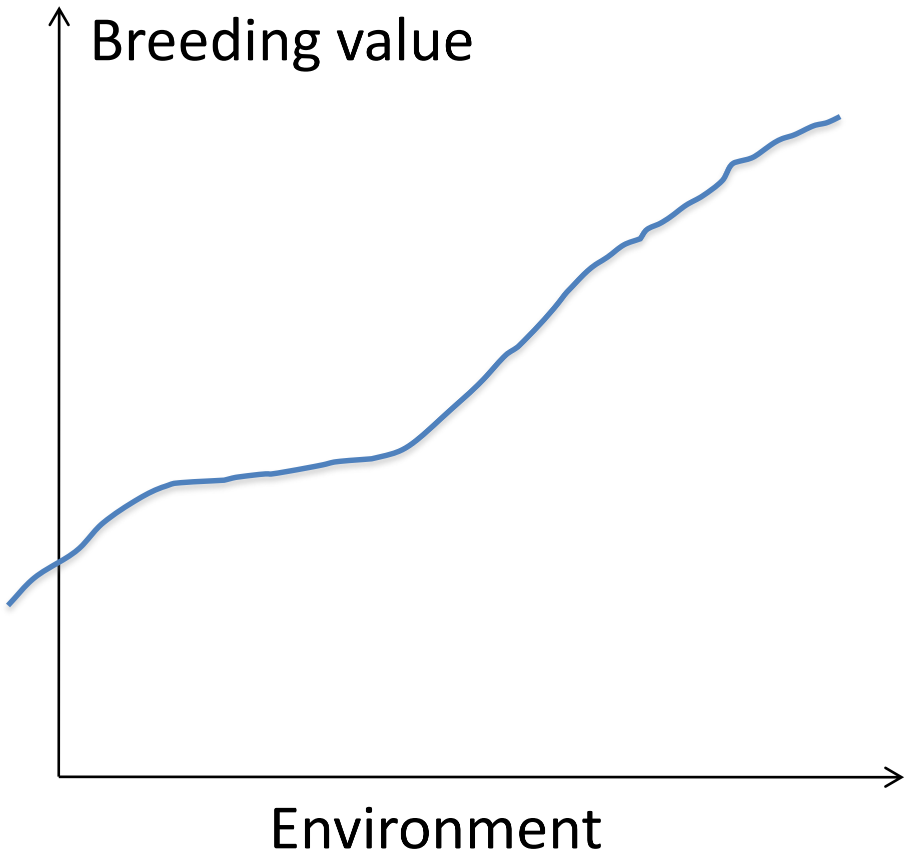
$$V(\bar{z}-\theta) = V(\theta) + V(\bar{z}) - 2\mathrm{Cov}(\bar{z},\theta)$$



De Villemereuil et al (2020 PNAS)

Inheritance of plasticity

- For continuous, polygenic traits:
  plasticity investigated by **applying quantitative genetics to reaction norms**.



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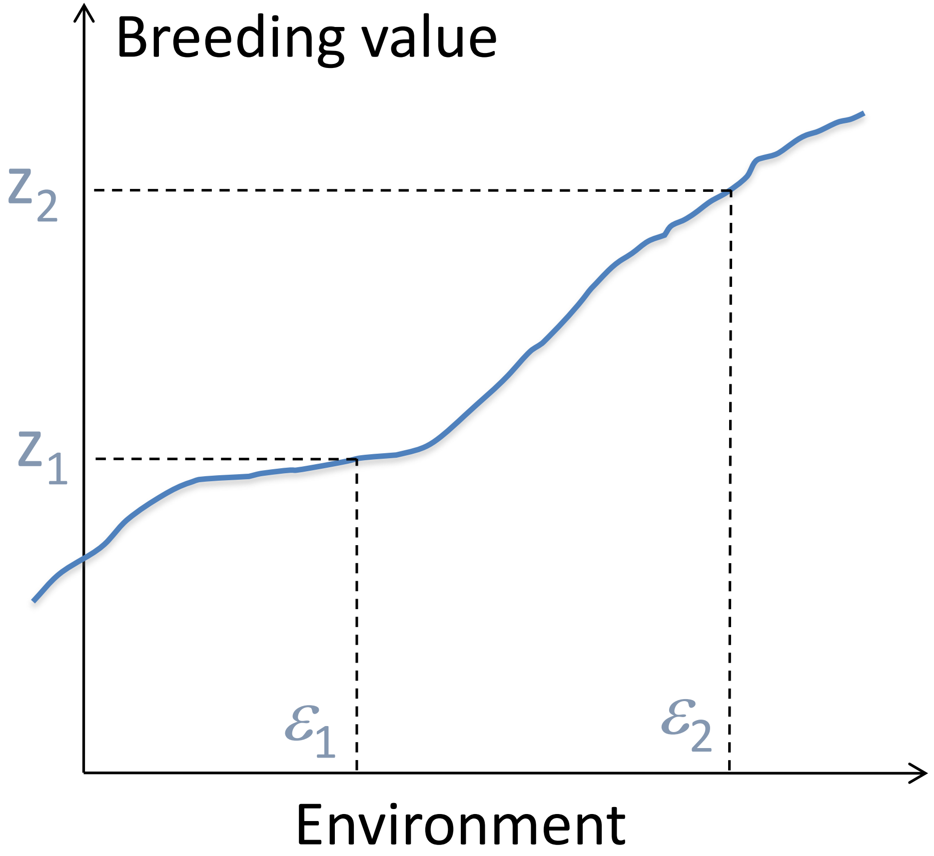

- **Character state approach**[1]
  z_1 and z_2 = 2 traits,
  possibly genetically correlated.

1: Falconer 1952 Am Nat; Via & Lande 1985 Evolution

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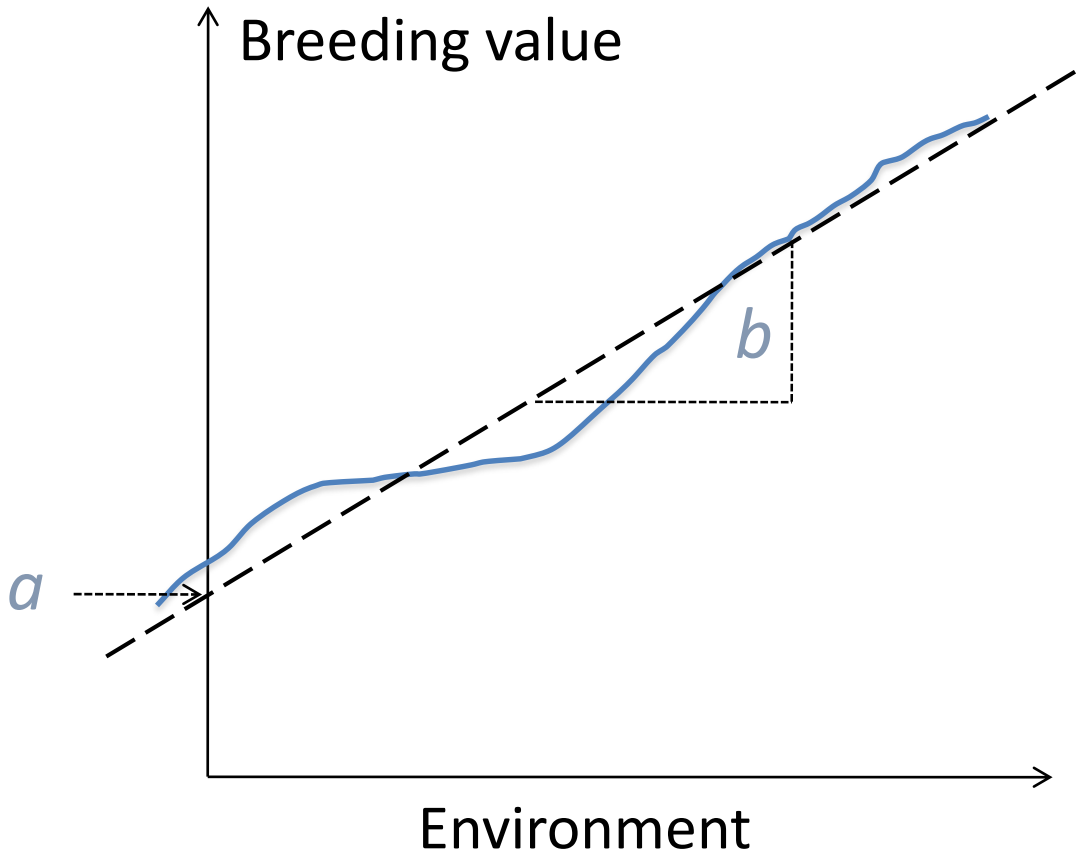


- **Character state approach**[1]
  z_1 and z_2 = 2 traits,
  possibly genetically correlated.
- **Reaction norm approach**[2]
  Reaction norm shape parameters
  (intercept *a*, slope *b*, …)
  are quantitative traits.
  If linear, slope *b* quantifies plasticity

1: Falconer 1952 Am Nat; Via & Lande 1985 Evolution
2: de Jong 1990; Gavrilets & Scheiner 1993 JEB

Selection on plasticity

- Parameters of reaction shape are **selected indirectly via their effects on the expressed trait** across environments.
- Directional selection on any normally distributed polygenic reaction norm parameter ϑ is

$$\beta_\vartheta = \frac{\partial ln\bar{W}}{\partial\vartheta} = \underbrace{\frac{\partial ln\bar{W}}{\partial\bar{z}}}_{\text{Selection gradient on expressed trait}} \underbrace{\frac{\partial\bar{z}}{\partial\vartheta}}_{\text{Reaction norm gradient, depends on environment}}$$

- With linear reaction norms $z = a + b\varepsilon_D + e$ (with ε_D the env of development) , the vector of selection gradients on reaction norm parameters is

$$\begin{pmatrix}\beta_a\\ \beta_b\end{pmatrix} = -S(\bar{z}-\theta)\begin{pmatrix}\frac{\partial\bar{z}}{\partial\bar{a}}\\ \frac{\partial\bar{z}}{\partial\bar{b}}\end{pmatrix} = -S(\bar{z}-\theta)\begin{pmatrix}1\\ \varepsilon_D\end{pmatrix}$$

Gavrilets & Scheiner 1993 JEB, de Jong 1999 JEB

Evolution in fluctuating environment

- Assuming the optimum also changes linearly with environment of selection, $\theta = A + B\varepsilon_S$, the expected selection gradient in a stationary fluctuating environment (with $\bar{\varepsilon} = 0$) is

$$\mathrm{E}\begin{pmatrix}\beta_a \\ \beta_b\end{pmatrix} = -S\,\mathrm{E}\begin{pmatrix}\bar{a} - A + (\bar{b}\varepsilon_D - B\varepsilon_S) \\ (\bar{a} - A)\varepsilon_D + (\bar{b}\varepsilon_D - B\varepsilon_S)\varepsilon_D\end{pmatrix} = -S\begin{pmatrix}\bar{a} - A \\ (\bar{b} - B\rho_{DS})\sigma_\varepsilon^2\end{pmatrix}$$

→ Plasticity evolves towards slope of optimum B **discounted by correlation ρ_{DS} between environment of development of selection** (predictability of selection)

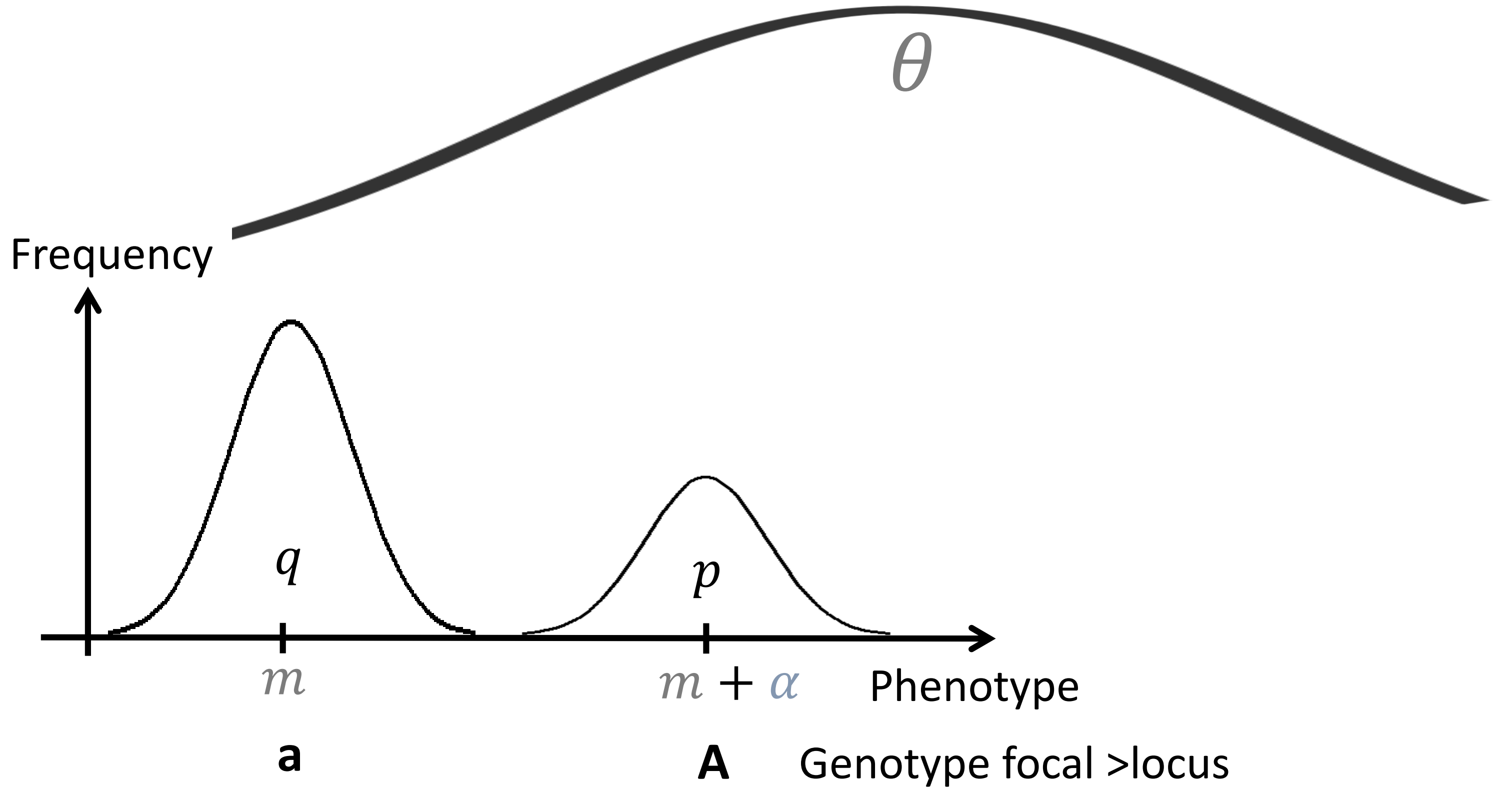
→ Faster evolution under larger magnitude σ_ε^2 of environmental fluctuations

- In general $\rho_{DS} < 1$ because of **developmental delay (and possibly dispersal) between development and selection**, and imperfect cue reliability
  → Reaction norm shallower than changes in optimum.

1: Gavrilets & Scheiner 1993 JEB, de Jong 1999 JEB
2: Lande 2009 JEB

Selection at QTL for plasticity

- Mutation at locus with environment-dependent effect on trait: $\alpha = a_\alpha + b_\alpha \varepsilon$



Chevin (2019 Genetics)

Selection at QTL for plasticity

- Mutation at locus with environment-dependent effect on trait: $\alpha = a_\alpha + b_\alpha \varepsilon$
- Expected selection coefficient in fluctuating environment ε:

$$\mathrm{E}(\Delta\psi) = -\frac{S}{2}\{a_\alpha^2 + b_\alpha[(b_\alpha - 2(b_\theta - b_m)]\sigma_\varepsilon^2\}$$

Chevin (2019 Genetics)

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→Environmental **fluctuations influence <u>expected</u> frequency change**, <u>unlike</u> for non-plastic QTL

→Selection strength also scales with **background mismatch with optimal plasticity,** which depends on predictability of selection

Chevin (2019 Genetics)

Selection at QTL for plasticity

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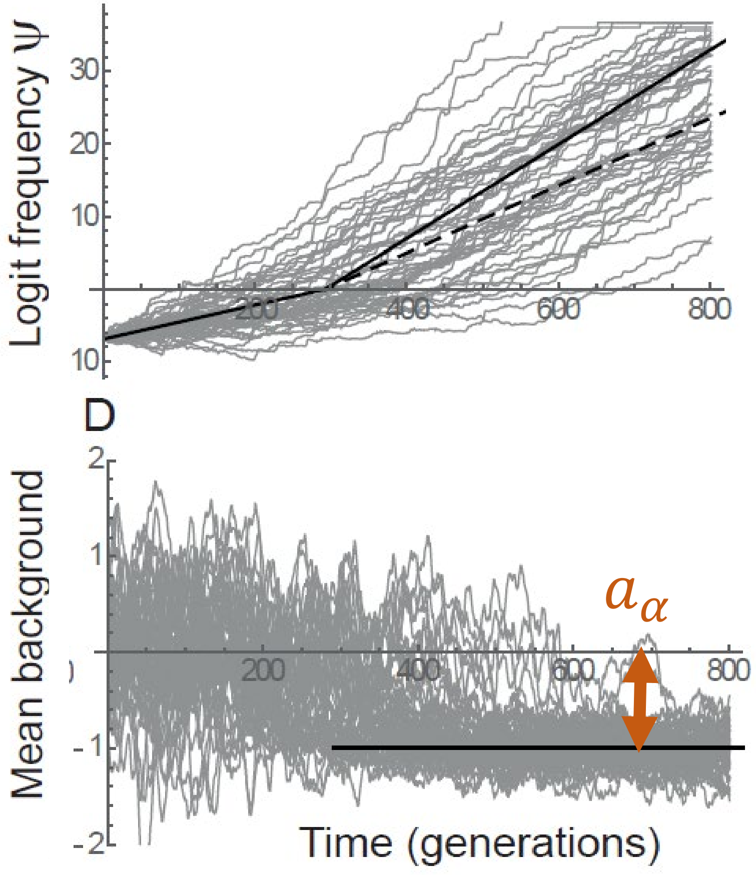

- An allele **favored through its effect on plasticity** (buffering environmental fluctuations) can spread despite a **deleterious side effect on the mean trait** (optimum displacement in average environment)
- The mean background trait *m* can then evolve to **compensate for the pleiotropic effect**

Chevin (2019 Genetics)

Ecology and evolution in randomly fluctuating environments

- Basics and framework -

- Evolutionary dynamics -

- Phenotypic plasticity -

- Evolutionary demography -

- Experimental results -

Population dynamics under moving optimum

- **Evolution and demography are connected through the fitness landscape**[1] relating population mean fitness $\bar{W}$ to the mean phenotype $\bar{z}$
- Simple discrete-time model:

Demography: $\ln N_{t+1} - \ln N_t = \ln \bar{W}_t$

Evolution: $\bar{z}_{t+1} - \bar{z}_t = G \frac{\partial ln\bar{W}}{\partial \bar{z}}$ (G : additive genetic variance of z)

1 : Wright (1937 PNAS)
Crow & Kimura (1970)
Lande (1976 Evolution, 1982 Ecology)

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- With Gaussian fitness peak, mean mismatch with optimum drives eco-evo dynamics

Demography: $\ln N_{t+1} - \ln N_t = r_{\max} - \dfrac{S}{2}(\bar{z}_{\mathrm{t}} - \theta_{\mathrm{t}})^2 - g(N_t)$

Evolution: $\bar{z}_{t+1} - \bar{z}_t = -GS(\bar{z}_{\mathrm{t}} - \theta_{\mathrm{t}})$

$g(N_t)$ accounts for density-dependent regulation (increasing function).

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Crow & Kimura (1970)
Lande (1976 Evolution, 1982 Ecology)

Population dynamics under moving optimum

- **Neglecting density dependence** (eg under severe stress):
  $$\ln N_t = n_t = n_0 + r_{\max} t - \frac{S}{2}\sum_{k=0}^{t-1}(\bar{z}_k - \theta_k)^2$$
  Unweighted sum of all **past maladaptations**
  → Extreme events in the past may have long-lasting consequences

Chevin et al 2017 (Am Nat)

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- **With density regulation** of Gompertz form, $g(N) = \gamma \ln N = \gamma n$, asymptotically:
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  → More sensitive to recent events, especially if density dependence is strong

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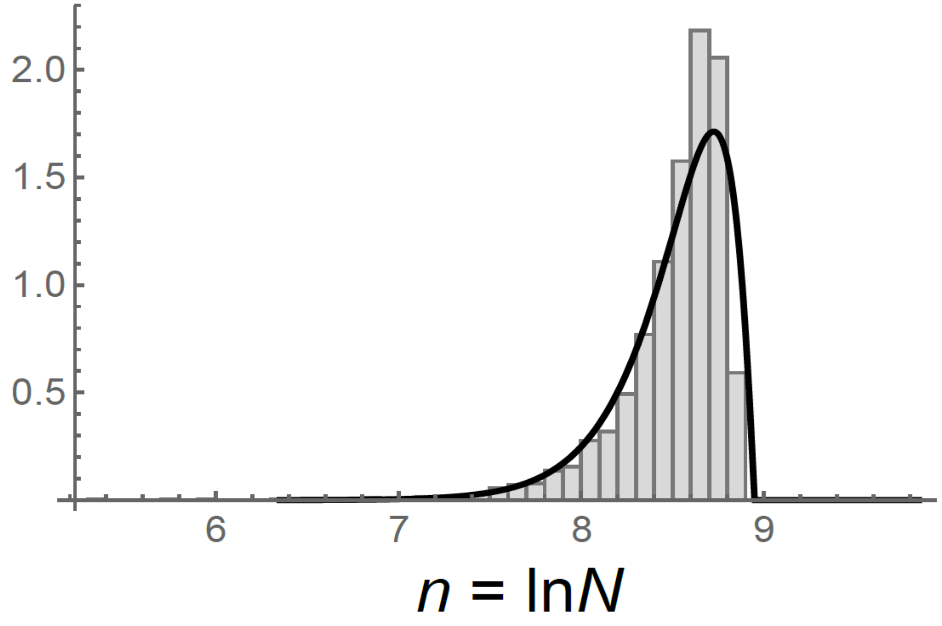
- Stationary distribution of mismatch $(\bar{z} - \theta)$ is shaped by **plasticity and evolution**
  If θ is a Gaussian process, so are $\bar{z}$ and $(\bar{z} - \theta)$
  Then $n = \ln N$ is ~ (reverse non-central) chi-square/gamma

Chevin et al 2017 (Am Nat)

Distribution of population size

- The reverse gamma distribution is:
  - **Bounded above** by growth of optimum phenotype
  - **Skewed downward** (towards small *N*)



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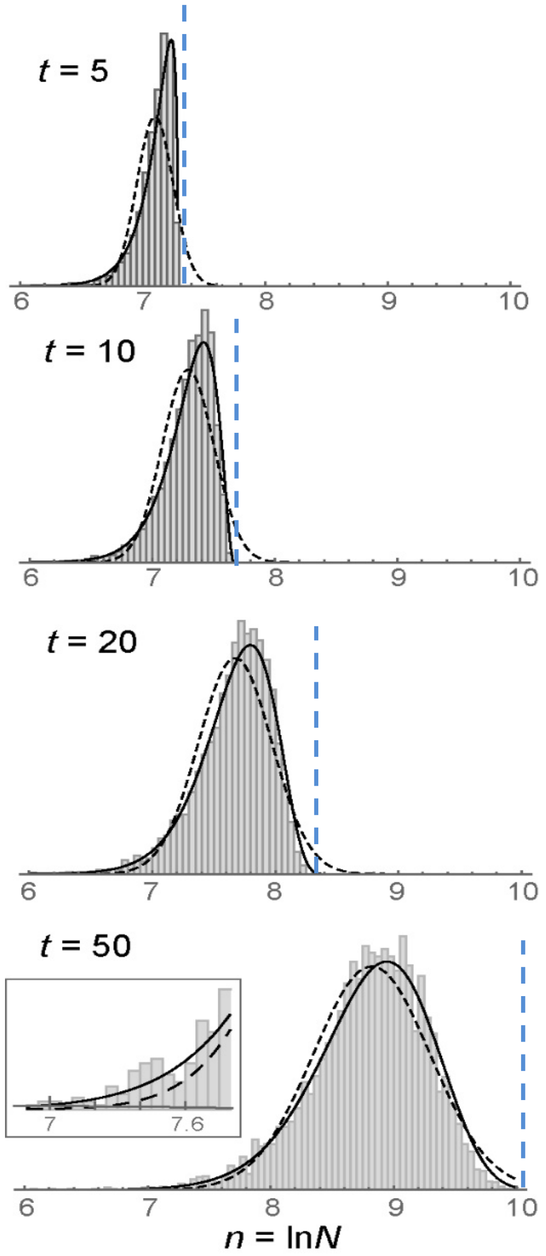

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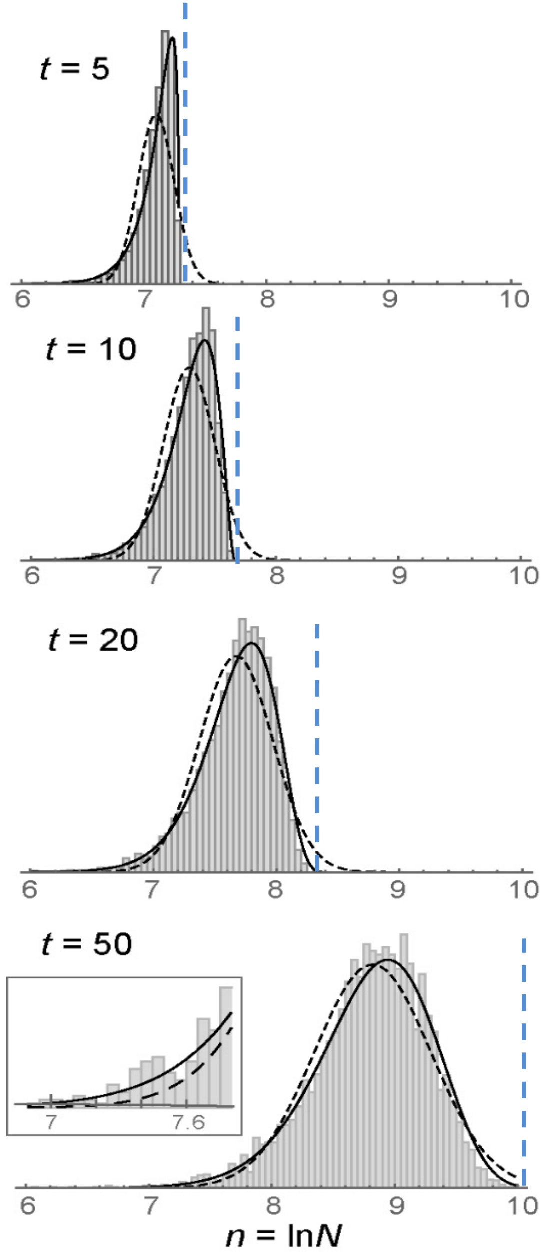
    → **Residual excess of small population sizes** with high extinction risk
  - **Autocorrelation** of optimum :
    - **increases** the **expected growth rate and pop size** (facilitates adaptive tracking of optimum)
    - increases **variance** of population size (among independent lineages)[1].
    → possibly antagonistic for persistence



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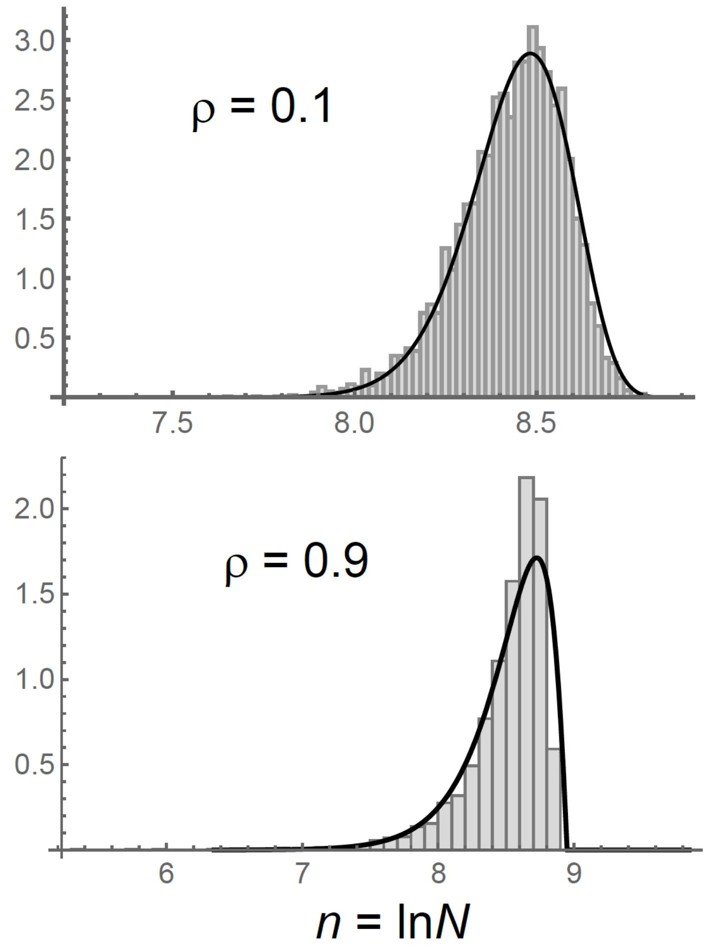
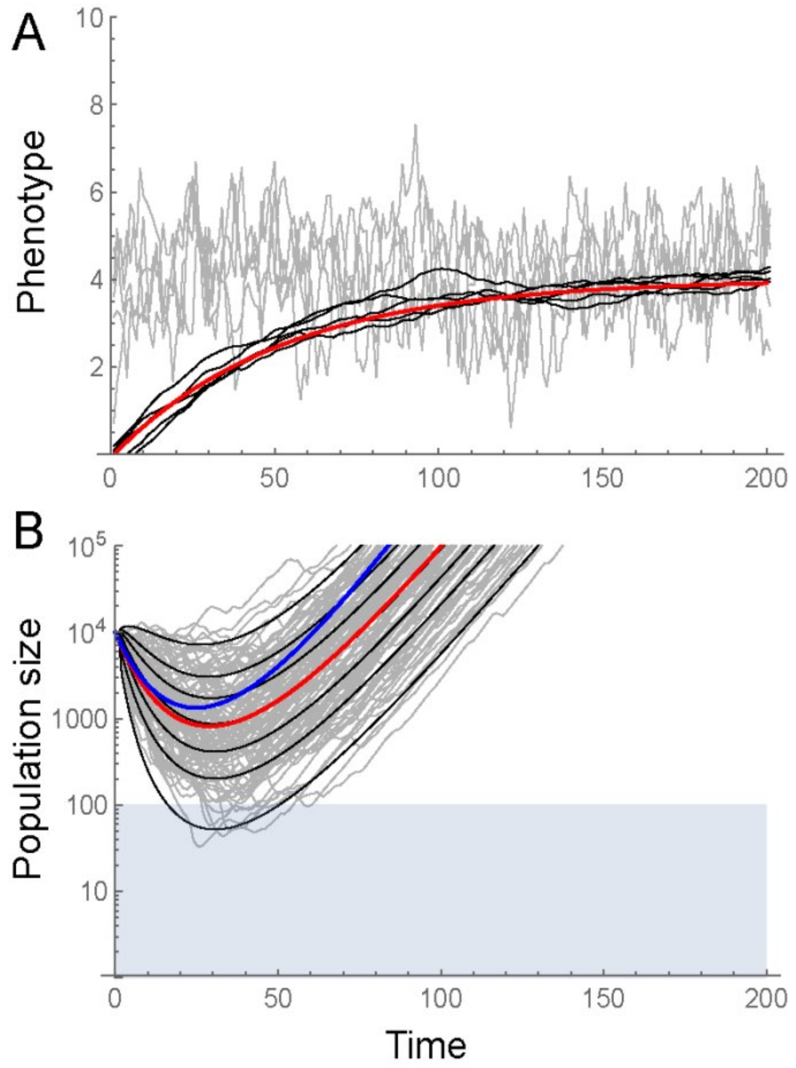
  - **With Gompertz density regulation**, distribution becomes **stationary**. **More skewed under more autocorrelated mismatch.** Why? Fewer effective generations of maladaptation are summed → χ^2 with lower DOF



Chevin et al 2017 (Am Nat)

Evolutionary rescue in stochastic environment

- Abrupt shift + random fluctuations in environment
- Population starts declining because of maladaptation, risking extinction unless it evolves fast enough
  = **Evolutionary rescue**
- Mean phenotype evolves towards new mean optimum, and also tracks stochastic fluctuations
- Stochasticity causes pop size to **span several orders of magnitude, increasing extinction risk when rescue would occur deterministically**[1]



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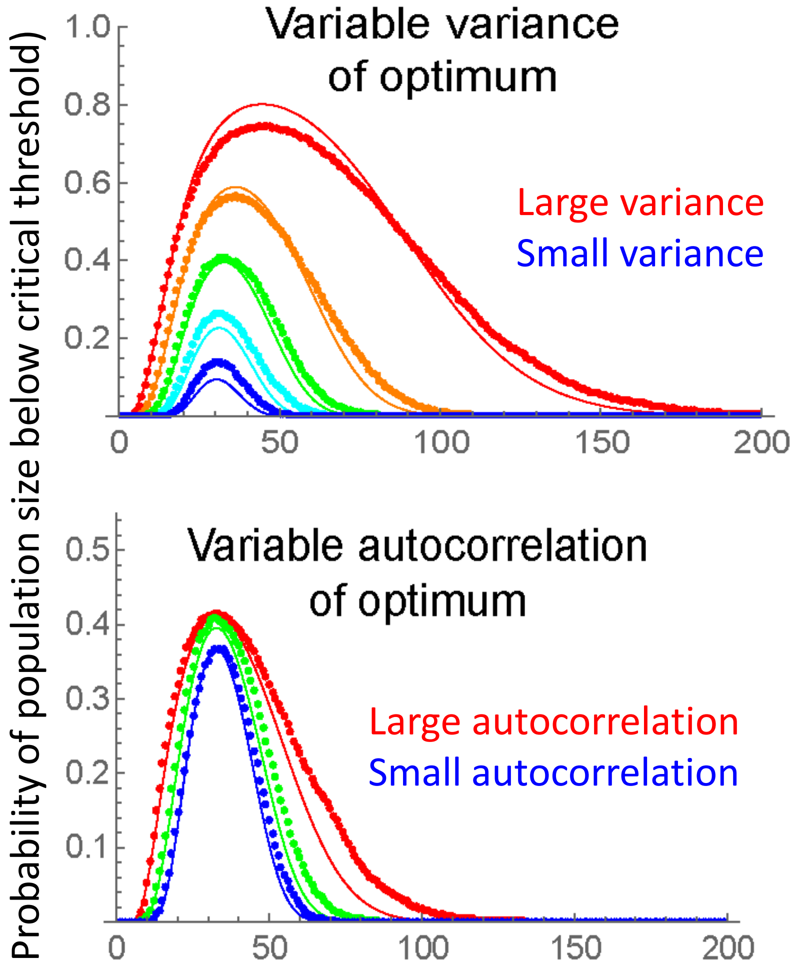

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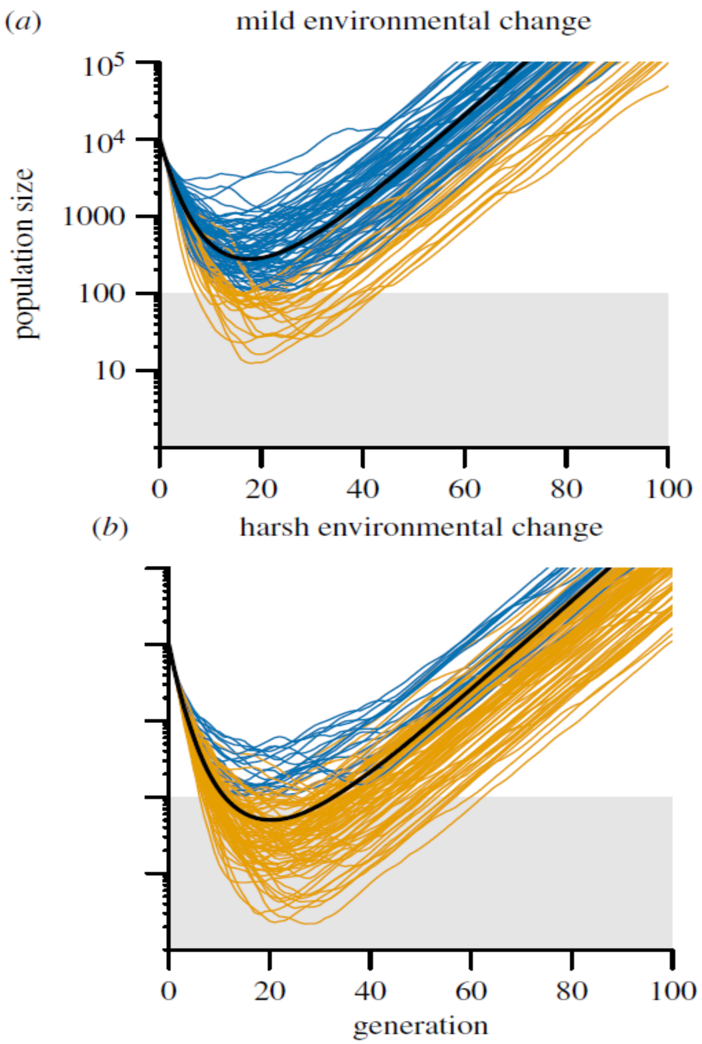
- Stochasticity causes pop size to **span several orders of magnitude, increasing extinction risk when rescue would occur deterministically**[1]
- Conversely, environmental stochasticity can facilitate ER in population that would be doomed in constant environment[2]



1: Chevin et al (2017 Am Nat)
2: Peniston et al (2020 Proc B)

Plasticity and stochastic demography

- Under stationary fluctuations, reaction norm slope (plasticity) affects the **variance of phenotypic mismatch with optimum**.
- Effective variance of fluctuating optimum as "perceived " by reaction norm elevation (« non-plastic » phenotypic component) is[1]

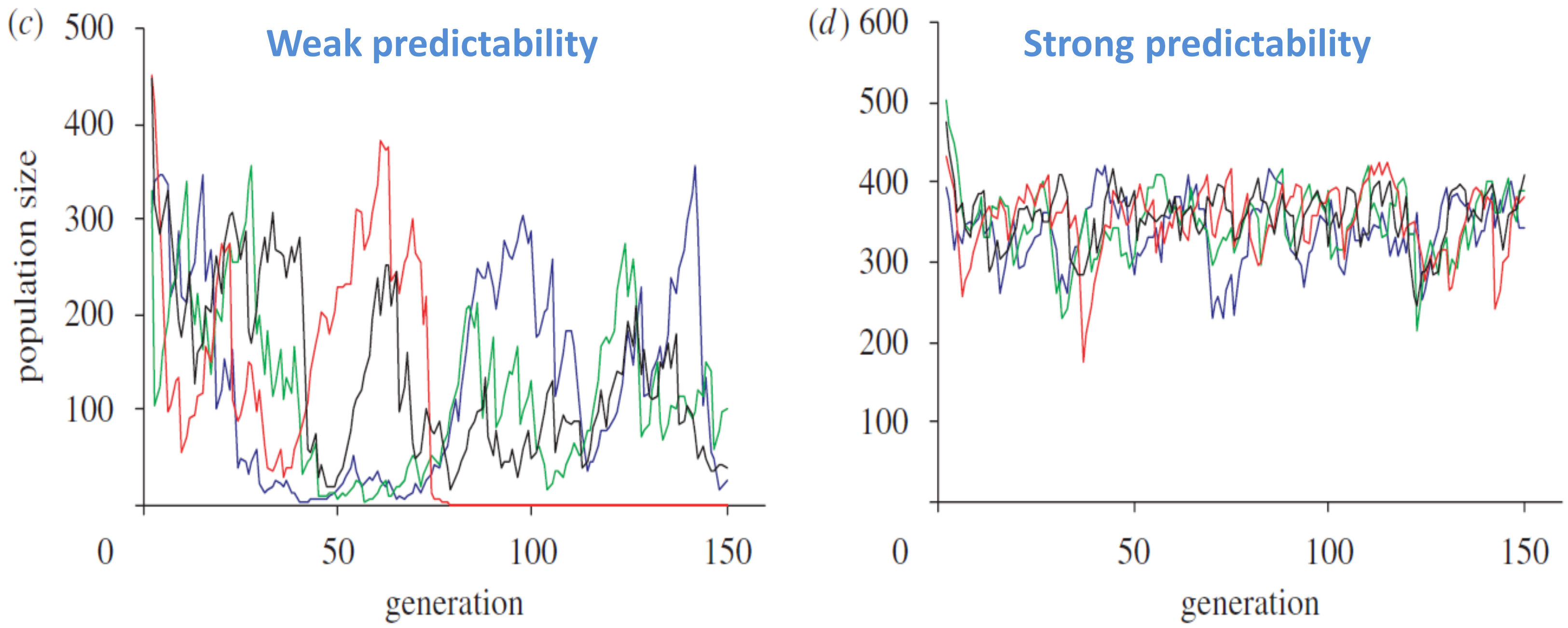
$$\sigma_\psi^2 = \sigma_\theta^2\left[1 + \alpha(\alpha - 2\rho_{DS})\right]$$

  $\alpha = b/B$: slope of reaction norm scaled to slope of optimum vs environment
  $\boldsymbol{\rho_{DS}}$: environmental correlation between development and selection

- Plasticity close to environmental predictability ρ_{DS} **buffers fluctuations**
  BUT: Plasticity larger than $2\rho_{DS}$ **amplifies fluctuations**
- Variance of deviations from optimum decreases expected population size

Plasticity and stochastic demography

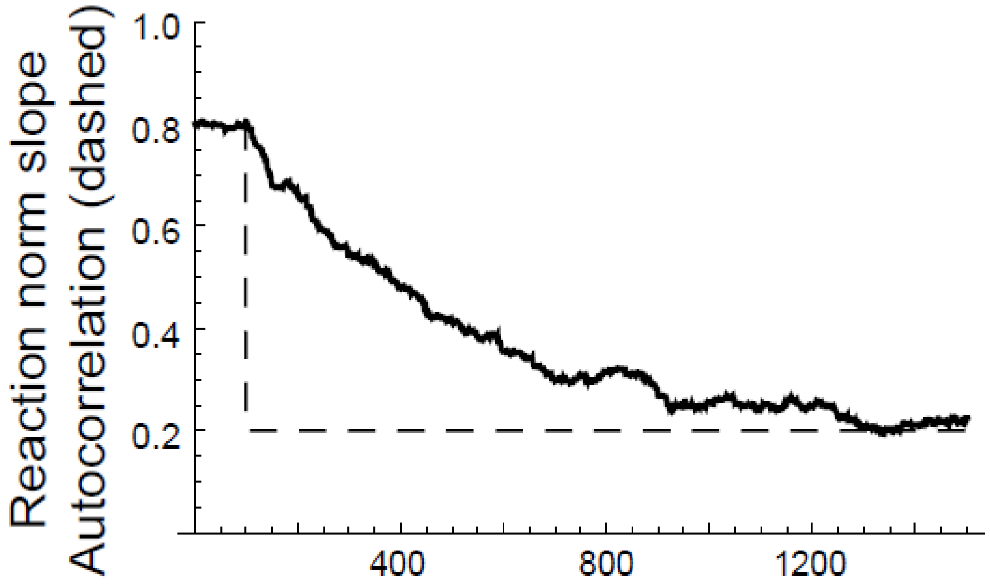
- Plasticity buffers demographic impacts of fluctuating environment **only if the inducing environment accurately predicts future selective pressure**
- Otherwise plasticity increases phenotypic mismatches (eg overshoots optimum), amplifies population fluctuations, and may cause extinction[1]

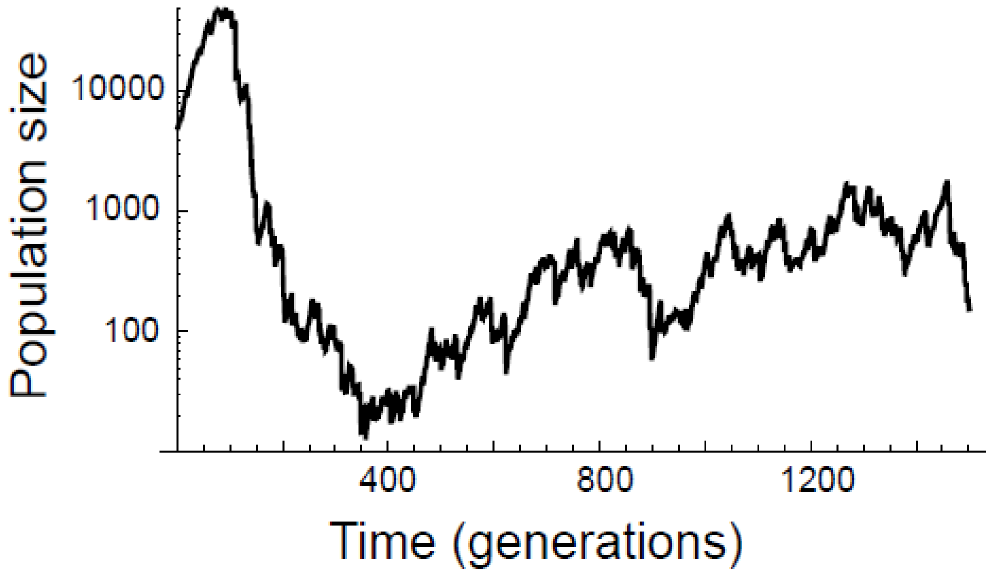


1: Reed et al (2010 Proc B)

Plasticity and stochastic demography

- Climate change alters environmental (auto)correlations and predictability
- A change in cue nature / reliability can **increase variance of mismatch with optimum**, reducing expected population growth rate.
- Evolution of plasticity may then be required for evolutionary rescue

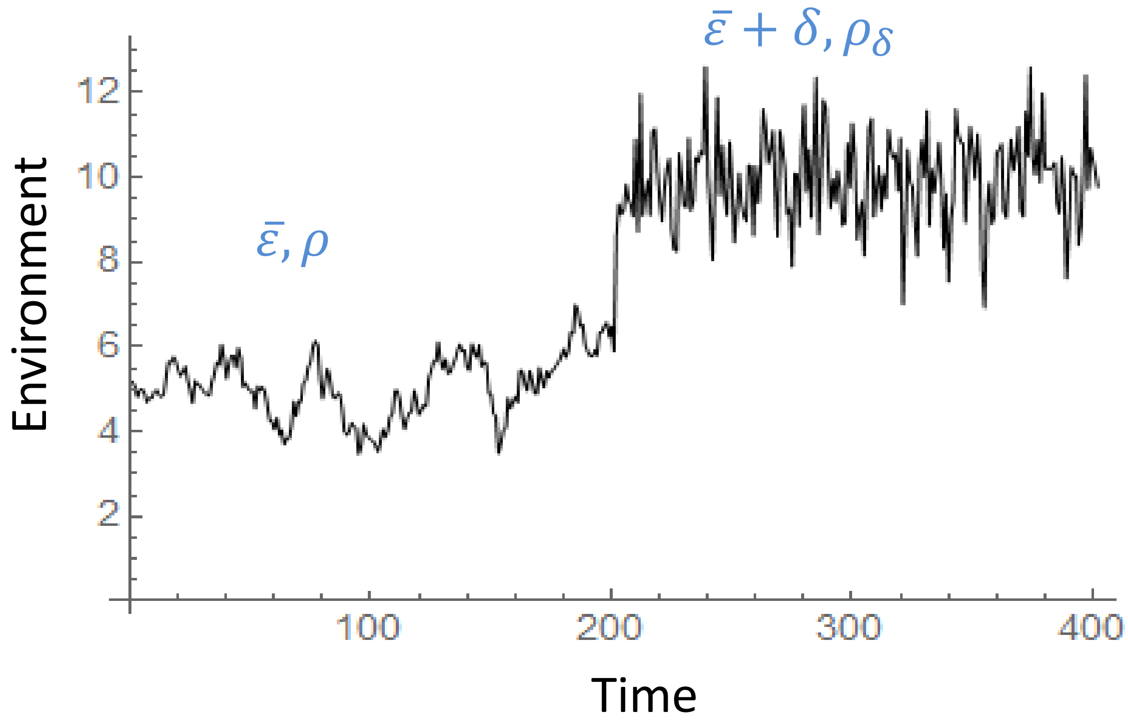




Chevin et al (2013 Phil Trans B)
Ashander, Chevin & Baskett (2016 Proc B)

ER by evolving plasticity in stochastic environment

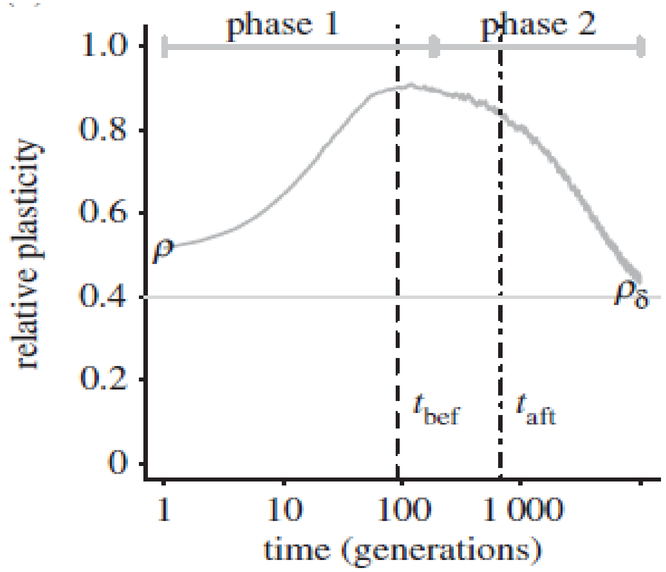
- Model where environmental shift modifies the **mean** (δ) and **autocorrelation** (ρ_δ) **of random fluctuations** in environment



1: Ashander, Chevin & Baskett (2016 Proc B)

ER by evolving plasticity in stochastic environment

- Evolutionary dynamics in two phases[1]:
  1 - Adaptation to the new mean environment by transient increase in plasticity.
  2 - Evolution of plasticity to match new level of environmental predictability



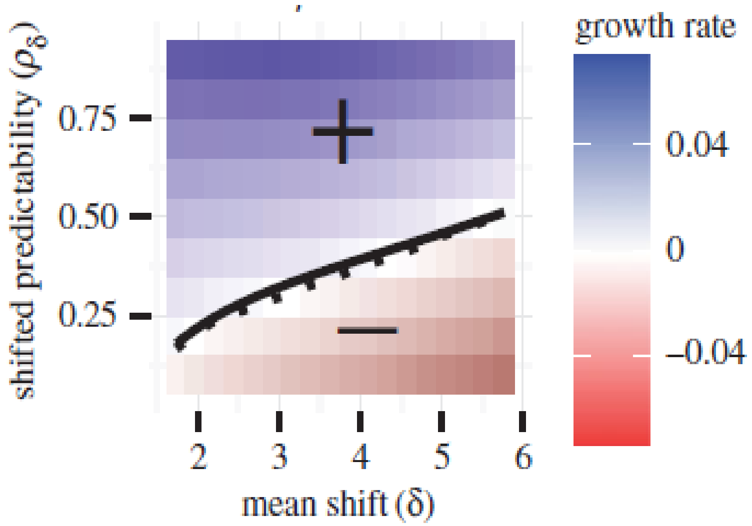
- **Transient increase in plasticity in phase I causes increased stochastic lag load[2]**
  (caused by variance of mismatch with optimum)

1: Lande (2009 JEB)
2: Ashander, Chevin & Baskett (2016 Proc B)

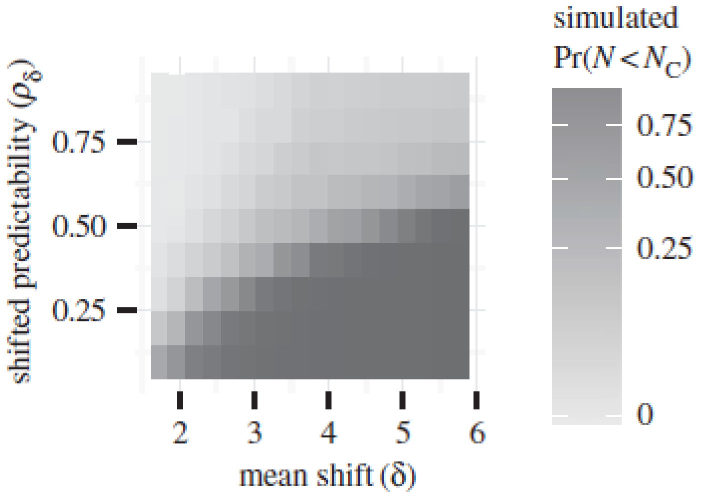
ER by evolving plasticity in stochastic environment

- **Potential for ER** at end of phase 1, when mean phenotype largely matches mean optimum:

Time-averaged growth rate



Probability of population below critical size



- **ER more likely under high predictability after the shift**
  With low predictability, the high plasticity that evolves transiently in phase 1 amplifies the negative demographic impact of environmental stochasticity

1: Ashander, Chevin & Baskett (2016 Proc B)

Ecology and evolution in randomly fluctuating environments

- Basics and framework -

- Evolutionary dynamics -

- Phenotypic plasticity -

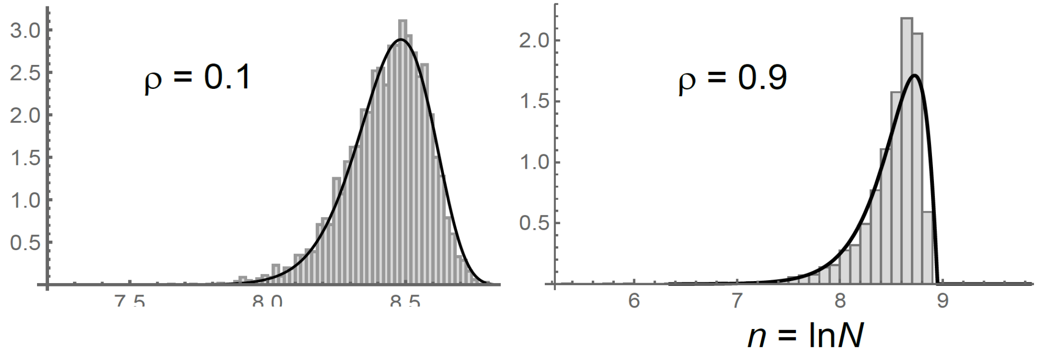
- Evolutionary demography -

- Experimental results -

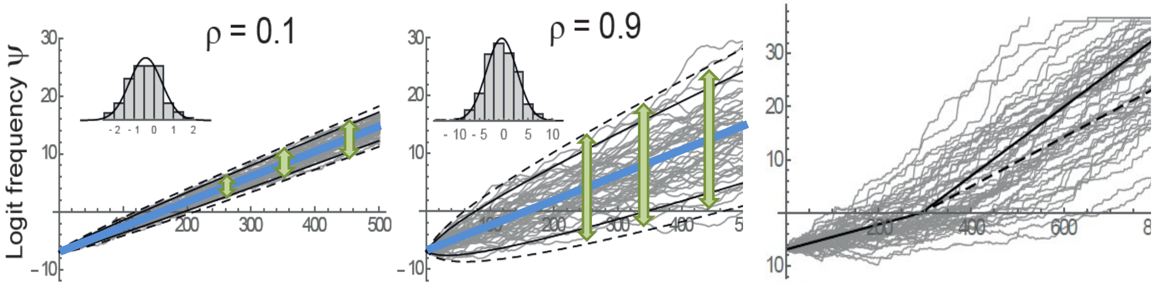
Population responses to stochastic environments

Reminder of predictions from moving optimum theory:

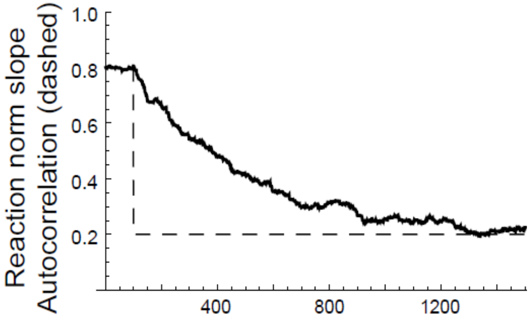
- **Population dynamics**: $\ln(N)$
  - ➢ Reverse gamma distributed
  - ➢ Mean and variance influenced by autocorrelation, through adaptive tracking by plasticity and/or evolution

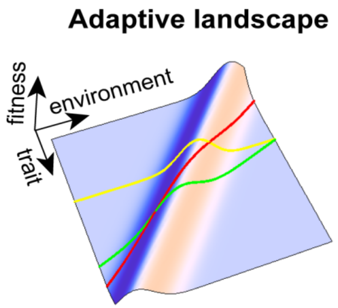


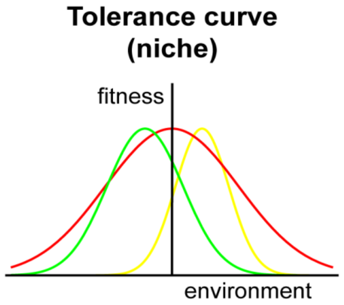
- **Selection at single locus**: $\mathrm{logit}(p)$
  - ➢ Expected change not affected by fluctuations, unless allele influences plasticity/tolerance breath
  - ➢ Change in variance depends on env autocorrelation



- **Evolution of plasticity: reaction norm slope**
  - ➢ Higher plasticity evolves in more predictable environments (and reciprocally)

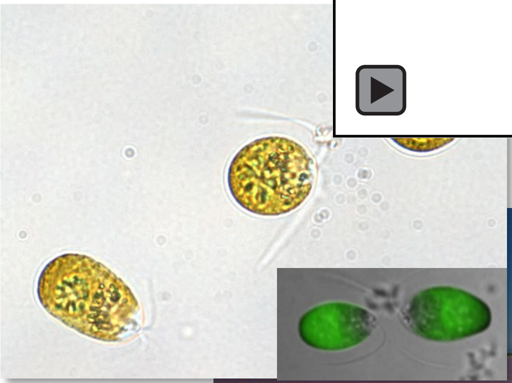






Dunaliella salina:
A model organism for salinity tolerance

- Micro-algae, **most halotolerant eucaryote** (freshwater to NaCl saturation).
- Common in coastal lagoons & salterns. Shallow → **salinity fluctuates** with precipitation, wind, sunlight…
- **Extremophile**: few ecological interactions → Niche easily mimicked in the lab
- **Short generation time** ~ 1 day → multigenerational experiments



Long-term experiment under fluctuating salinity

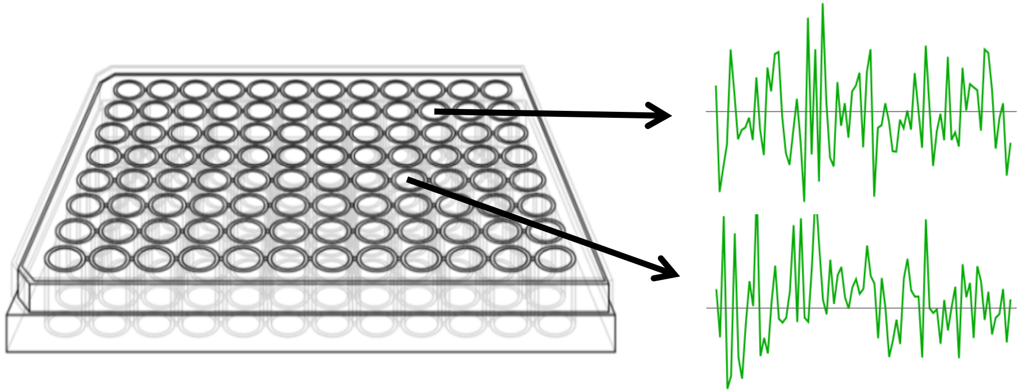
- Salinity changed twice a week using a pipetting robot
  - ➢ High replication
  - ➢ Complex fluctuation pattern

- Exposed during several months → hundreds of generations.

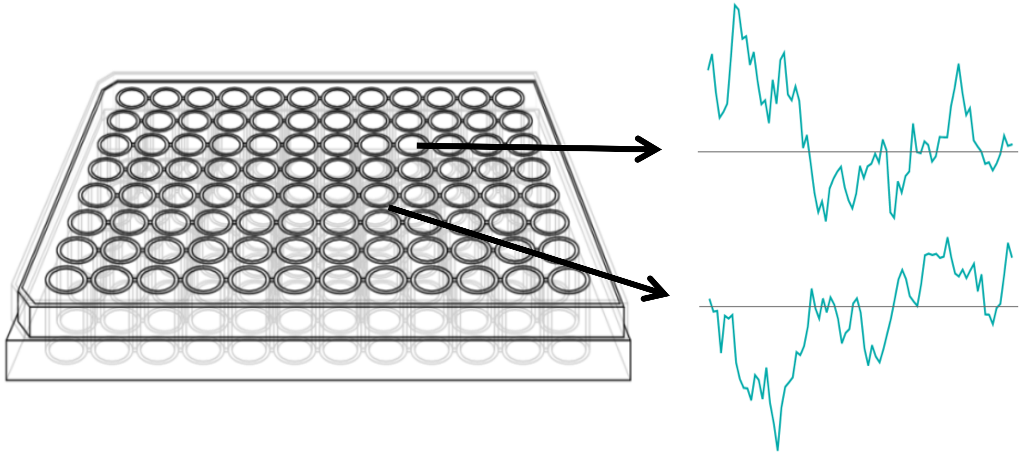
Predictability treatment

- Random change, with environmental autocorrelation as the treatment

Low predictability



High predictability

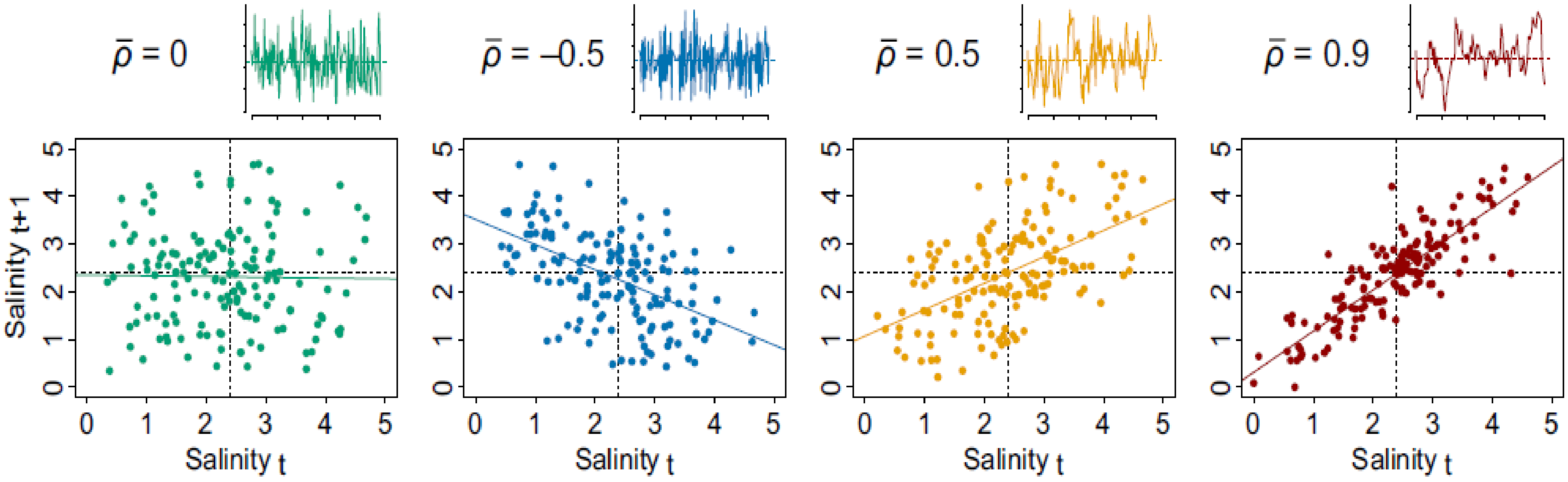


Predictability treatment

- Random change, with environmental autocorrelation as the treatment

Time series

Subsequent time points

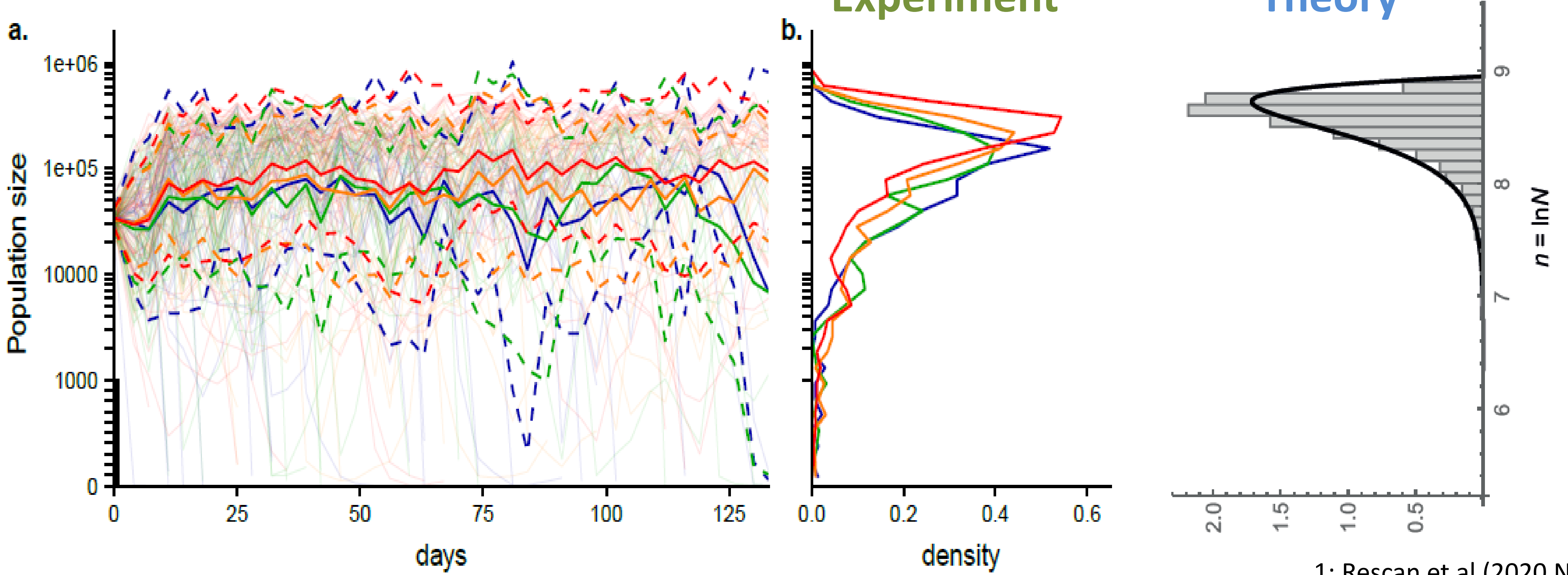


Predictability

Population fluctuations

- Tracking population size through time
- Populations reach stationary distribution **similar to moving optimum theory**[1]
- Is it for the same reason?

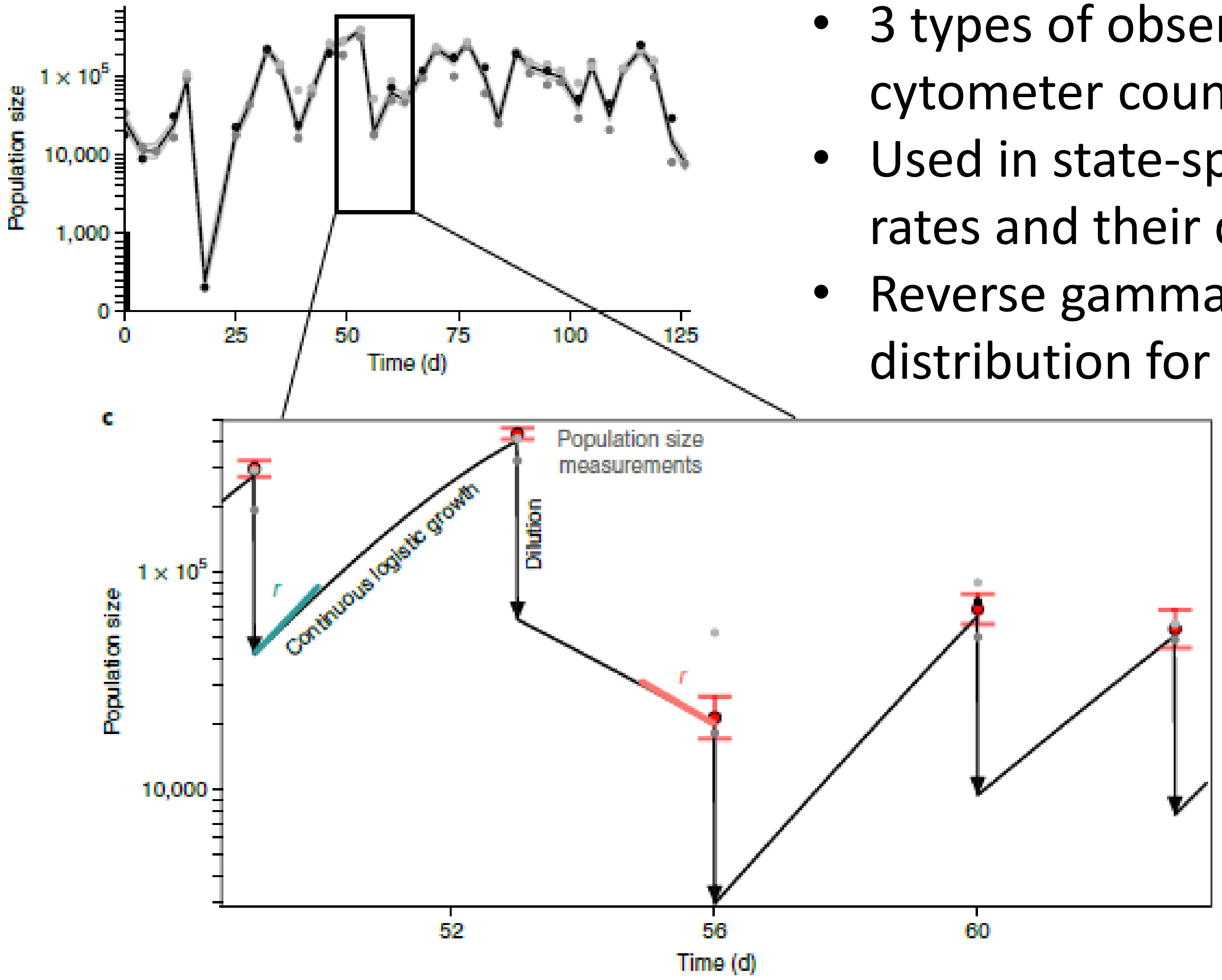
Experiment[1] **Theory**[2]



1: Rescan et al (2020 Nat Ecol Evol)
2: Chevin et al (2017 Am Nat)

Salinity tolerance curve

- **Analysis of population growth rates from times series of *N***



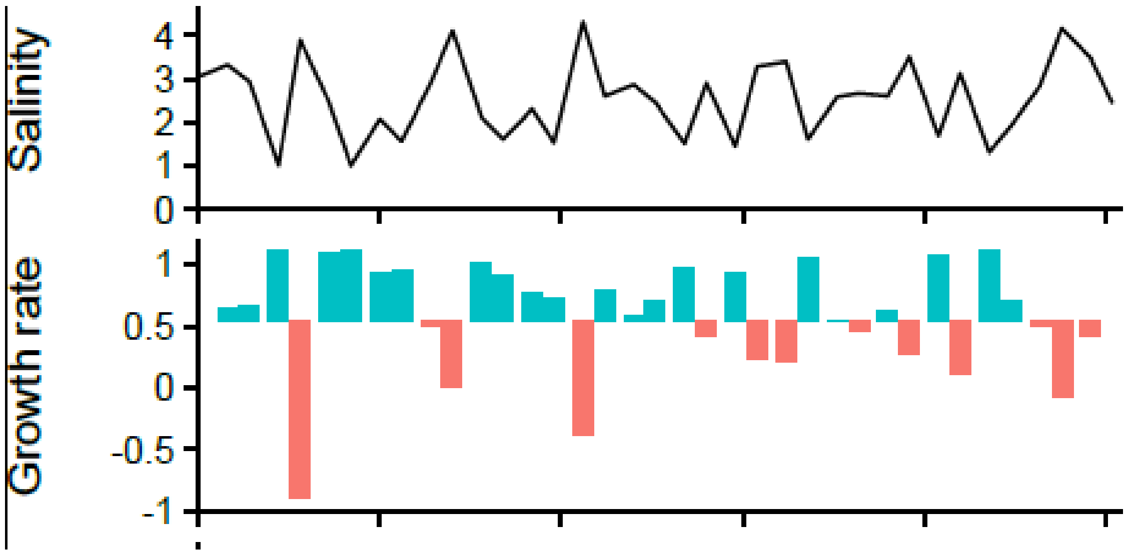
- 3 types of observations (colored dots): cytometer counts, fluorescence, and absorbance
- Used in state-space model to extract intrinsic growth rates and their distributions
- Reverse gamma distribution favored over normal distribution for *r*

Rescan et al (2020 Nat Ecol Evol)

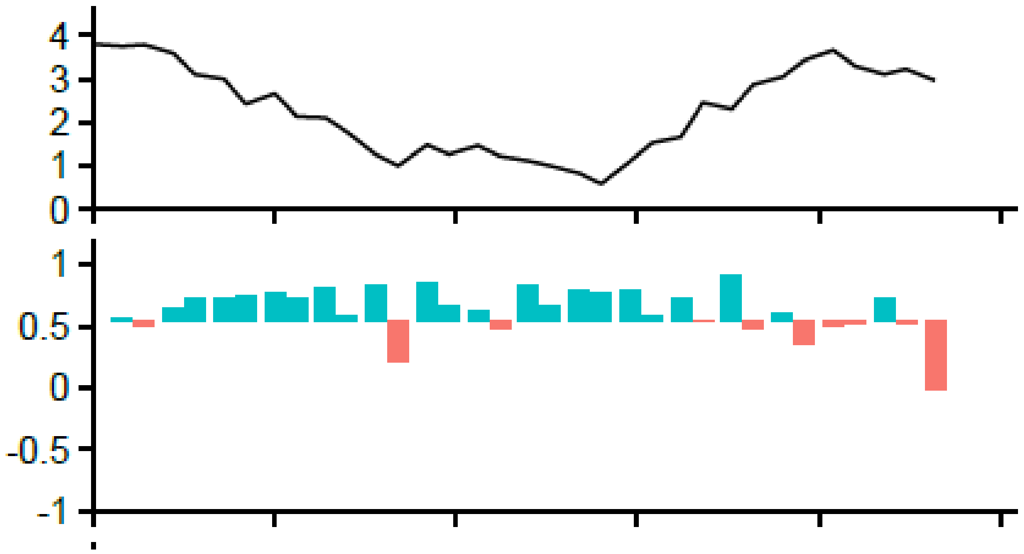
Salinity tolerance curve

- **Informed model: salinity included as covariate for *r***

Small autocorrelation



Large autocorrelation



Rescan et al (2020 Nat Ecol Evol)

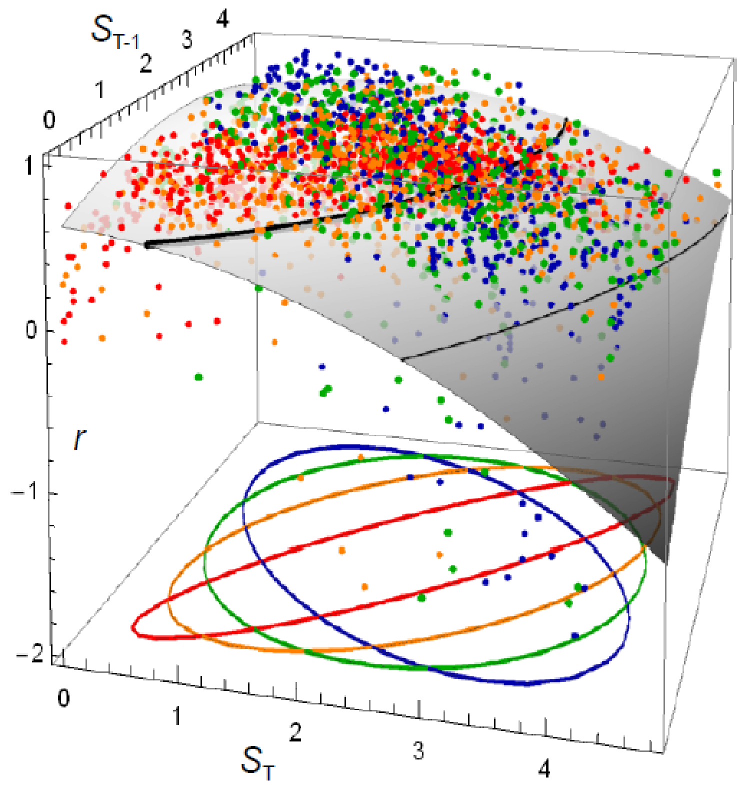
Salinity tolerance curve

- Population growth rate well predicted by **[tolerance curve with optimum environment]()**,

Rescan et al (2020 Nat Ecol Evol)

Salinity tolerance curve

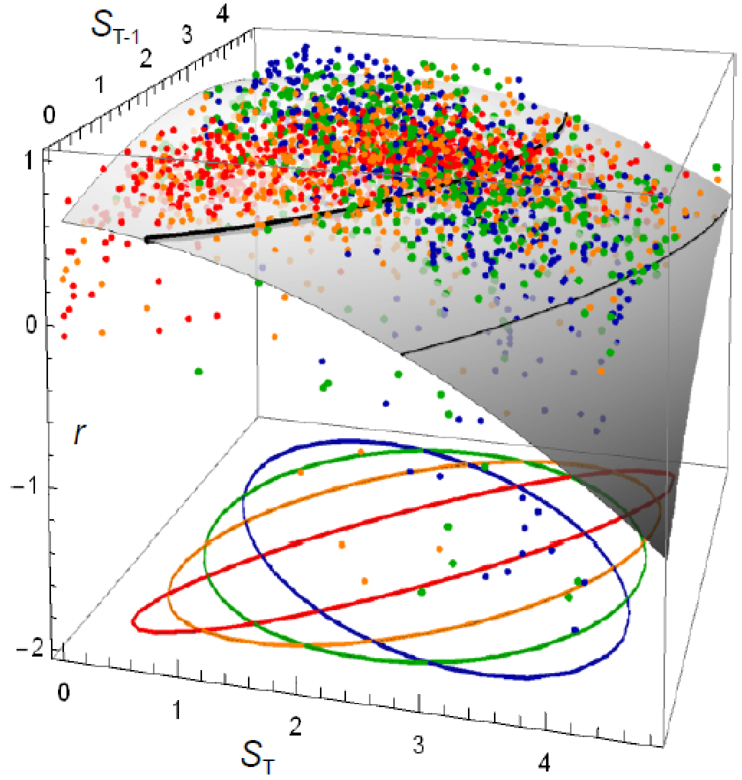
- Population growth rate well predicted by **tolerance curve with optimum environment**, BUT with respect to both **current and previous salinity**
  → **Phenotypic memory, lagged plasticity**



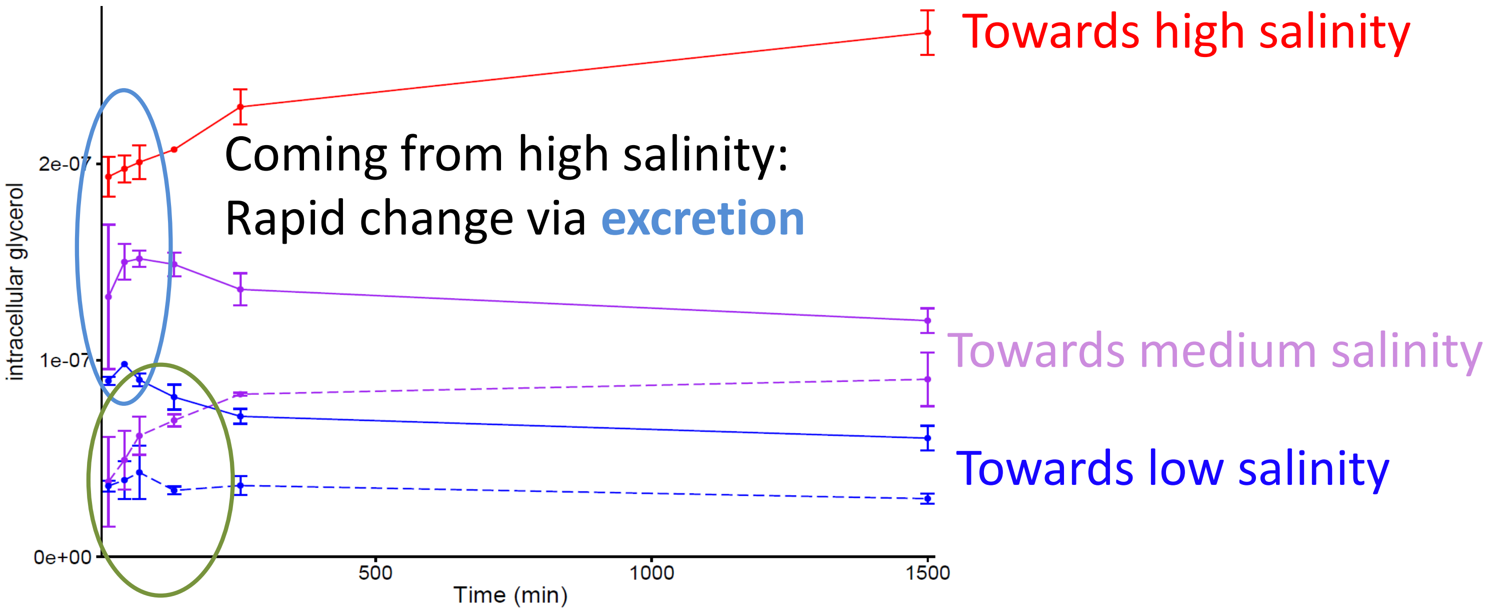
Rescan et al (2020 Nat Ecol Evol)

Salinity tolerance curve

- Population growth rate well predicted by **tolerance curve with optimum environment**, BUT with respect to both **current and previous salinity**
  → **Phenotypic memory, lagged plasticity**



- Likely **contribution from glycerol**, main osmoprotectant

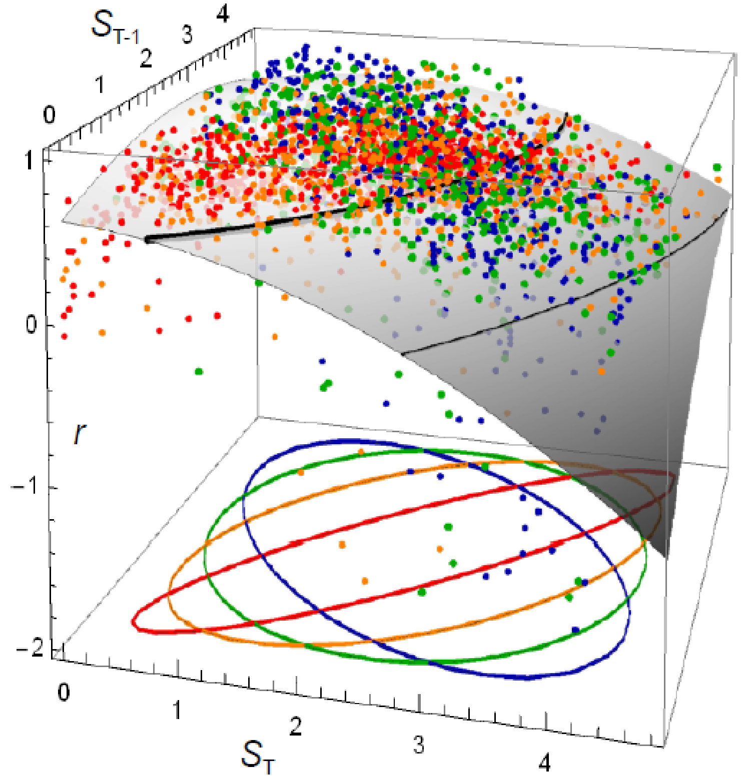


Coming from low salinity:
Slower change requiring **production**

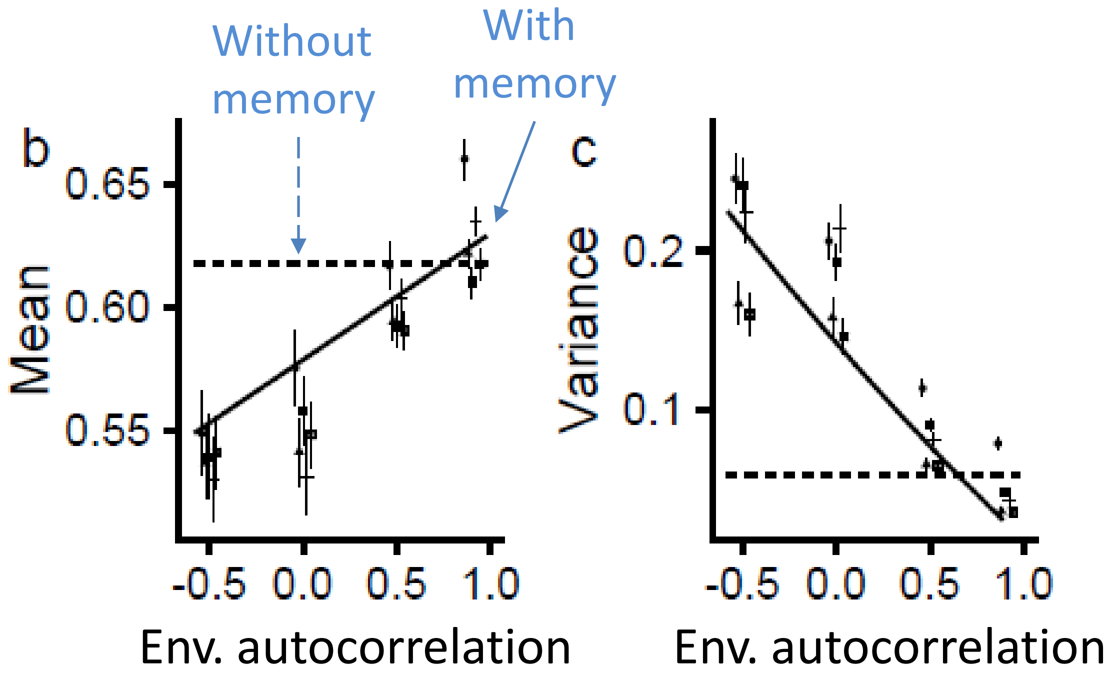
Rescan et al (2020 Nat Ecol Evol)

Salinity tolerance curve

- Population growth rate well predicted by **tolerance curve with optimum environment**, BUT with respect to both **current and previous salinity**
  → **Phenotypic memory, lagged plasticity**



- Explains effect of env autocorrelation on *r* distribution

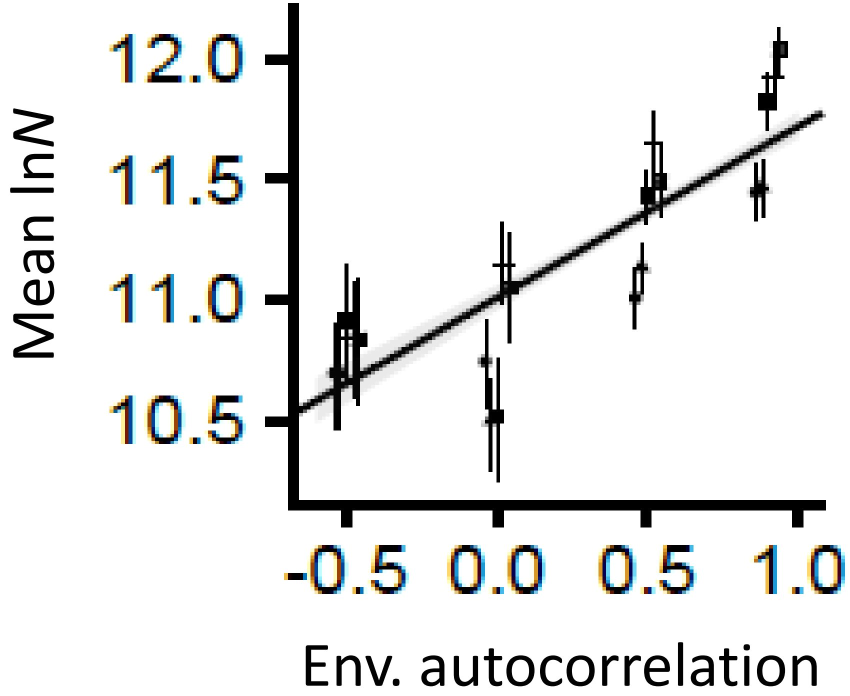


Rescan et al (2020 Nat Ecol Evol)

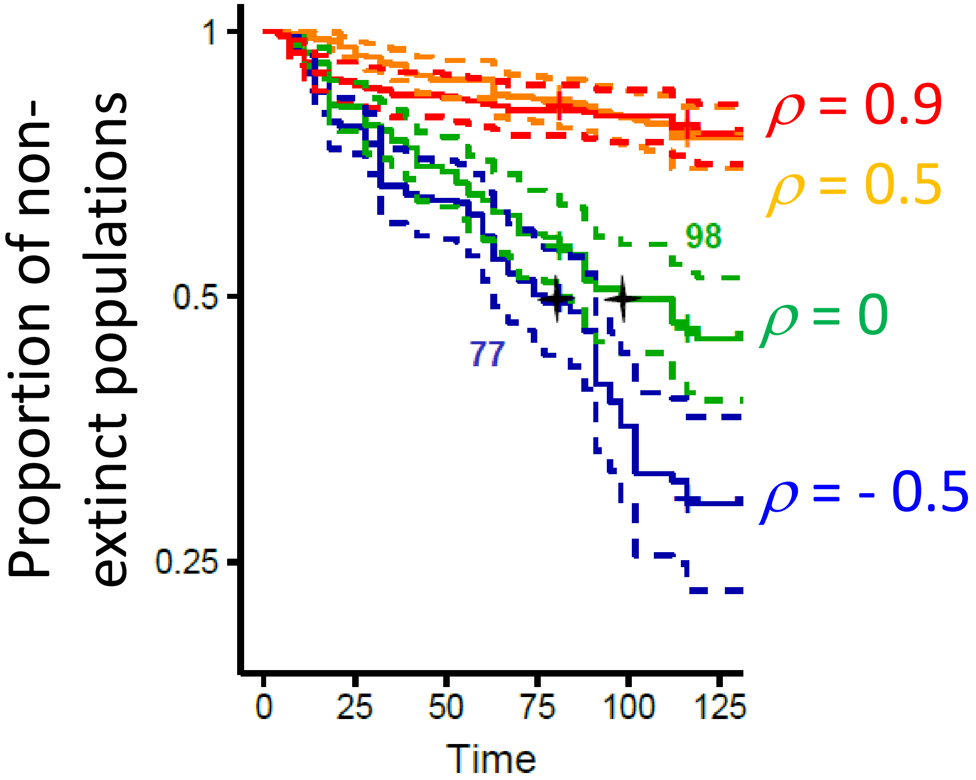
Environmental predictability & population dynamics

- **Large effect of environmental autocorrelation** on pop size and extinction risk

- Mean population size



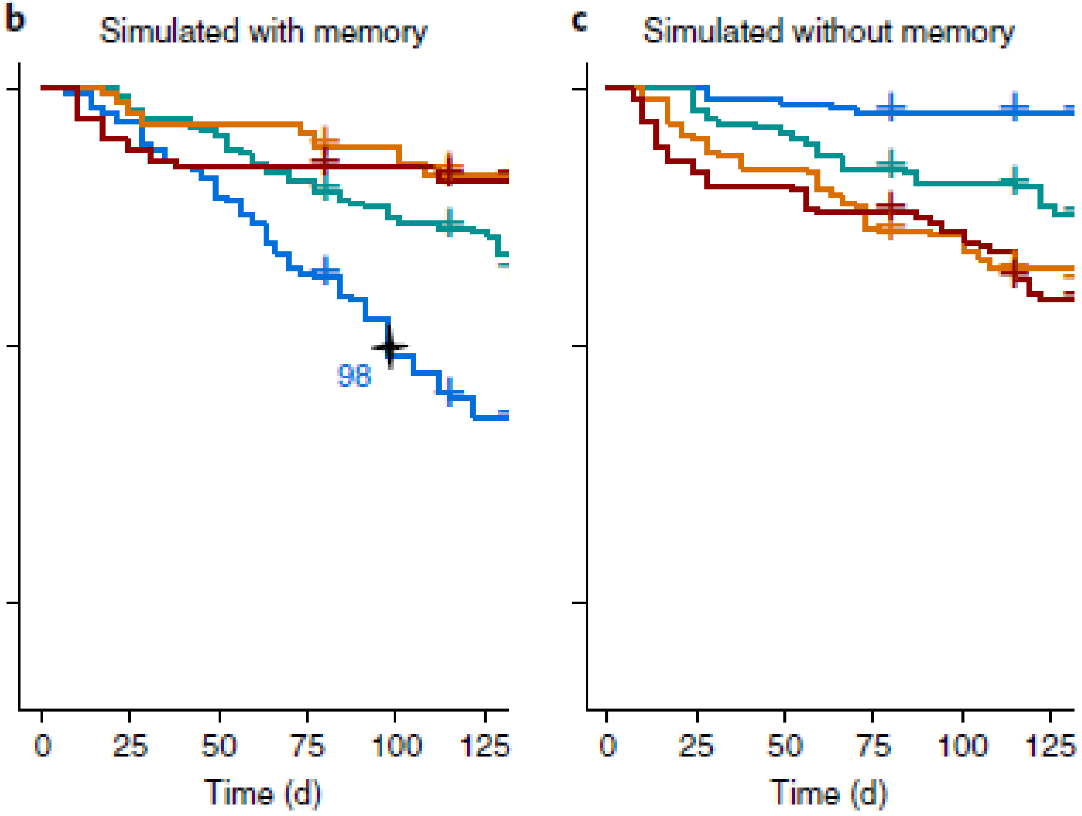
- Extinction risk



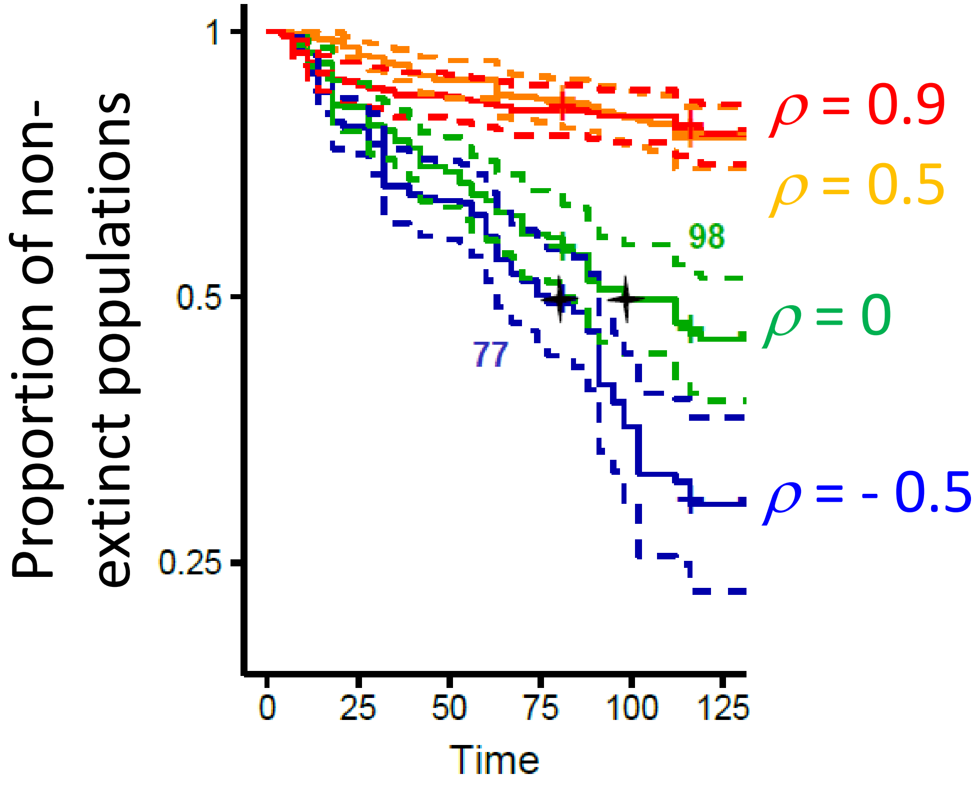
Rescan et al (2020 Nat Ecol Evol)

Environmental predictability & population dynamics

- **Large effect of environmental autocorrelation** on pop size and extinction risk
- Consistent with predicted salinity responses with memory, otherwise reversed



- Extinction risk

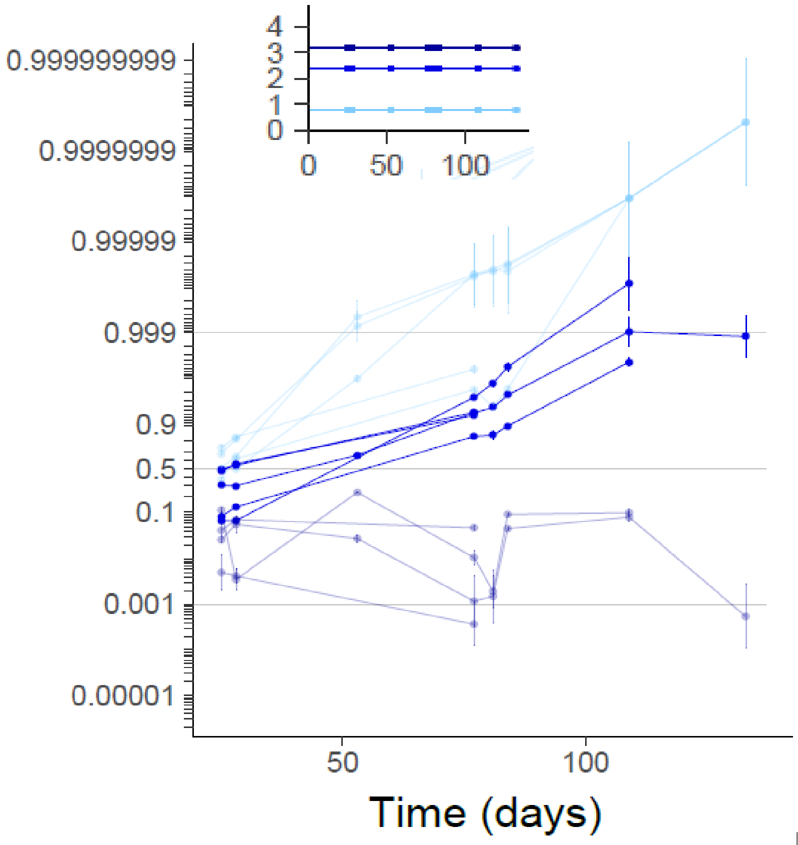


Rescan et al (2020 Nat Ecol Evol)

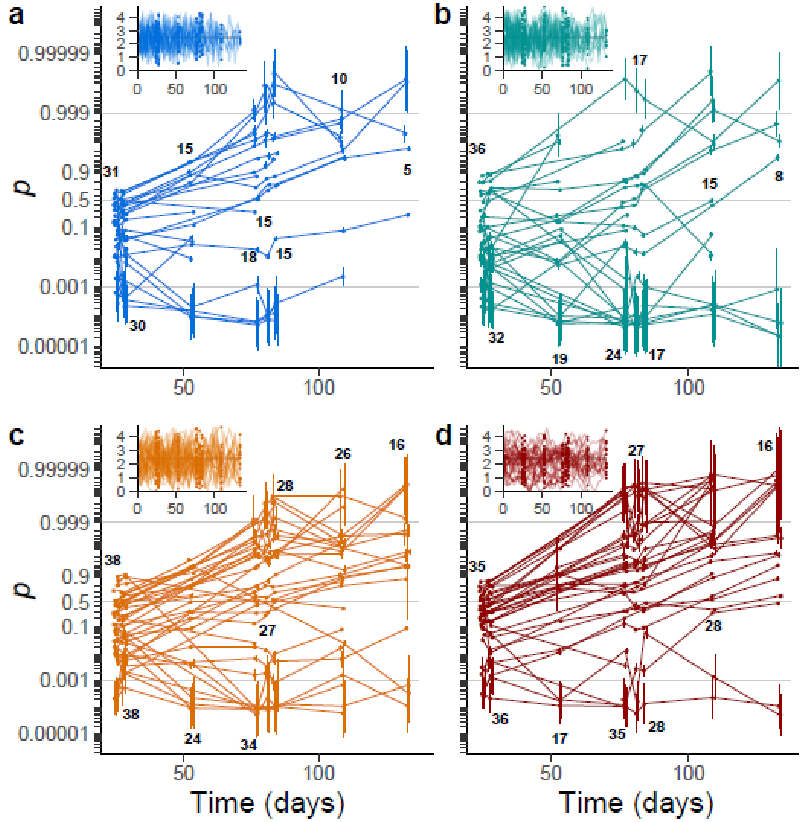
Population genetics in stochastic environment

- Tracking frequency of one strain among two in a mixture, by amplicon sequencing of two loci at regular time points

Constant salinity



Fluctuating salinity



Rescan et al (2021 Plos Gen)

Population genetics in stochastic environment

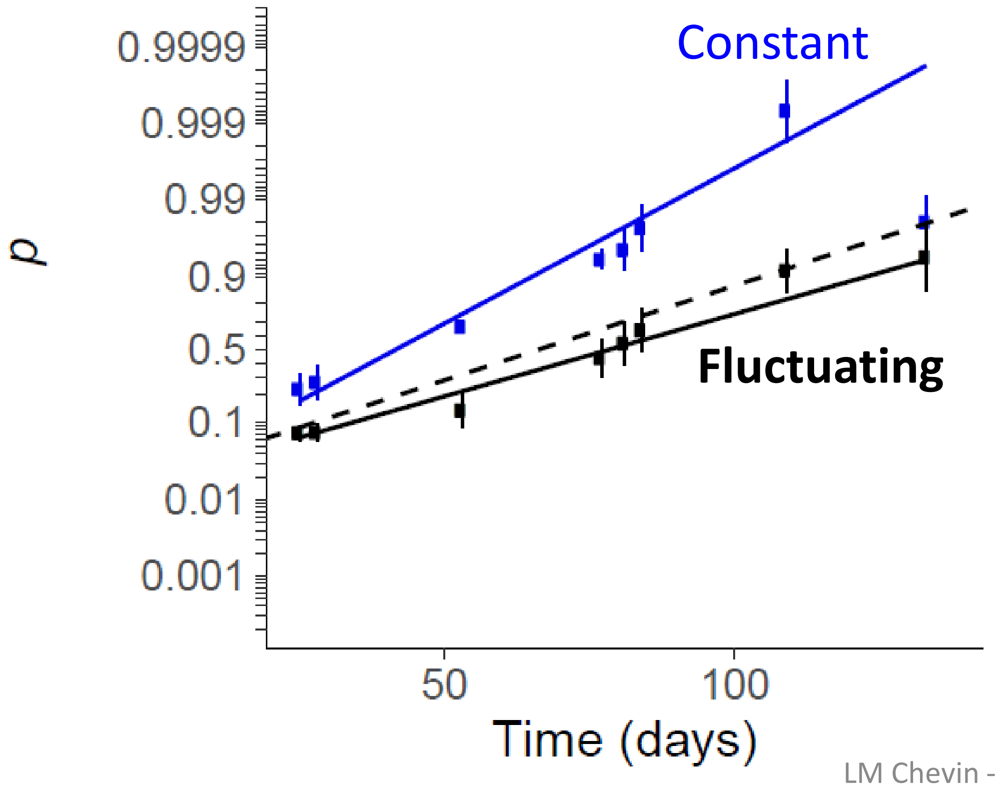
- Tracking frequency of one strain among two in a mixture,
  by amplicon sequencing of two loci at regular time points

- Analyzed by state-space model for logit(*p*)
  Equivalent to logistic GLMM with bivariate observations (2 loci).
  Random regression on time:
    - Mean slope = Mean selection coefficient
    - Variance of slopes = Drift + fluctuating selection (+block effects on selection?)

Rescan et al (2021 Plos Gen)

Effect of environmental variance on mean selection

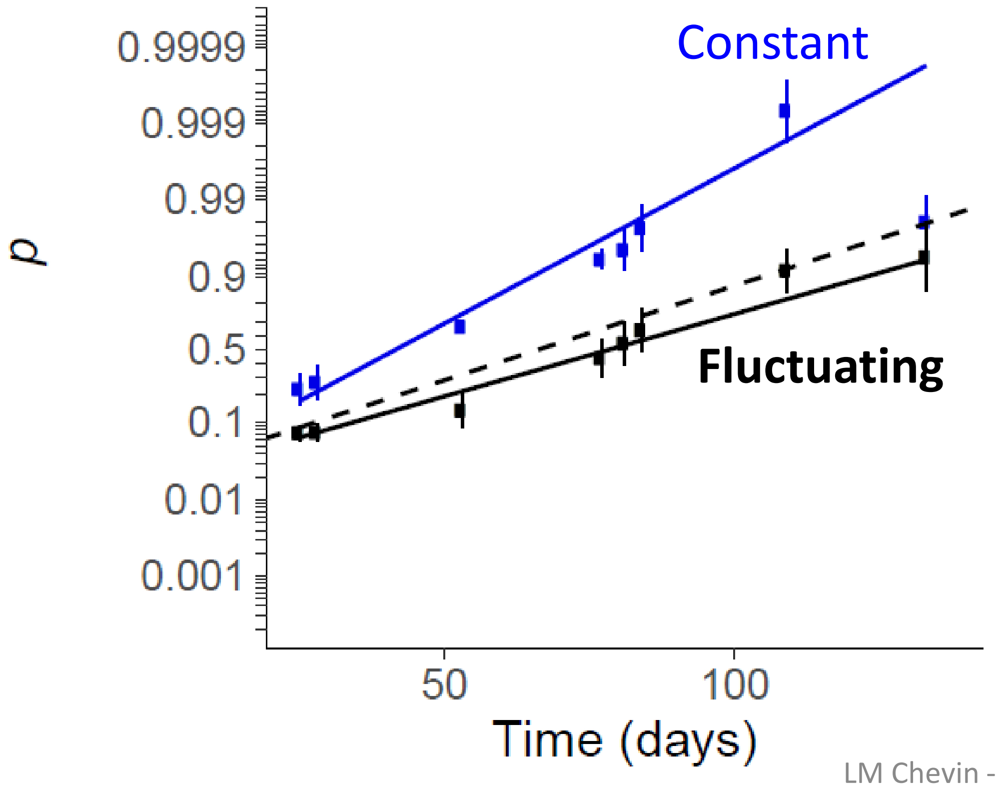
- **Environmental variance reduces the mean selection coefficient**

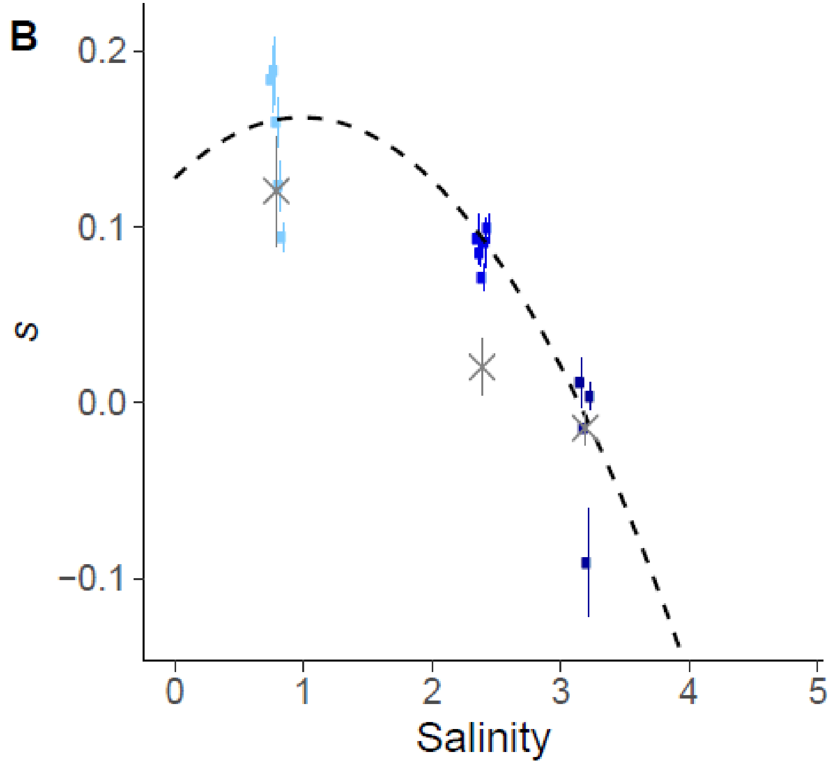


Rescan et al (2021 Plos Gen)

Effect of environmental variance on mean selection

- **Environmental variance reduces the mean selection coefficient**
- Consistent with **concave selection coefficient against environment** (Jensen's inequality), suggesting **strain difference in plasticity/tolerance breadth**



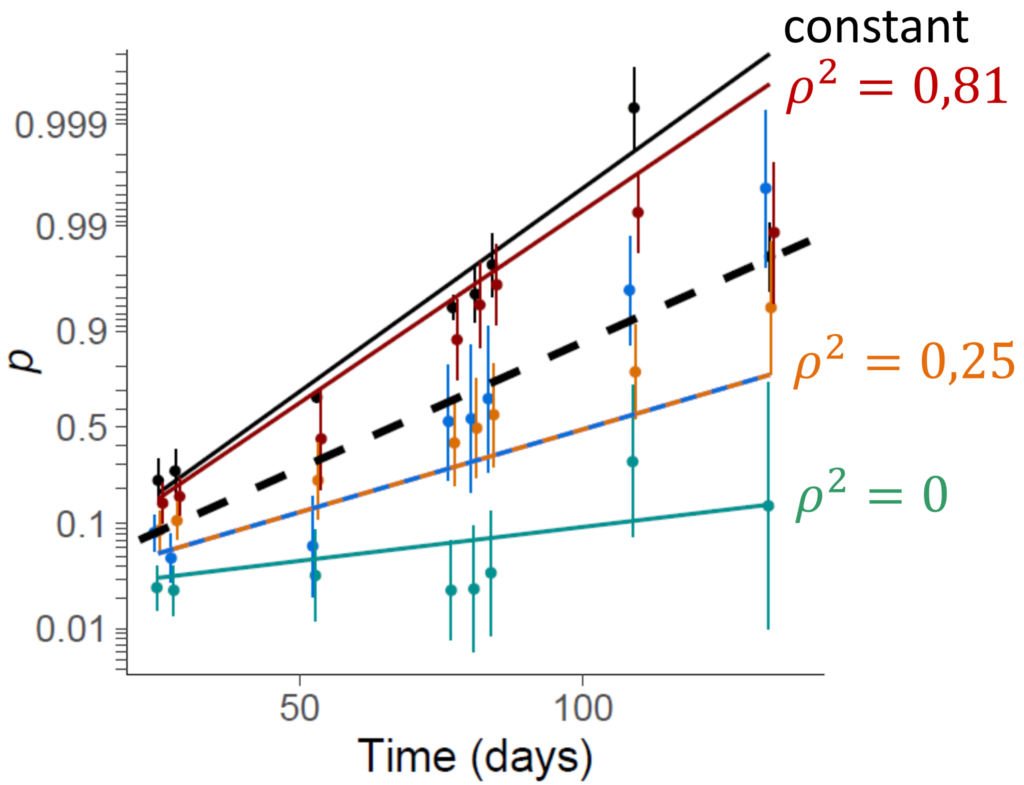


Rescan et al (2021 Plos Gen)

Effect of environmental autocorrelation

- Autocorrelation treatment **influences expected trajectory**
- Significantly higher selection coefficient in highly autocorrelated environment

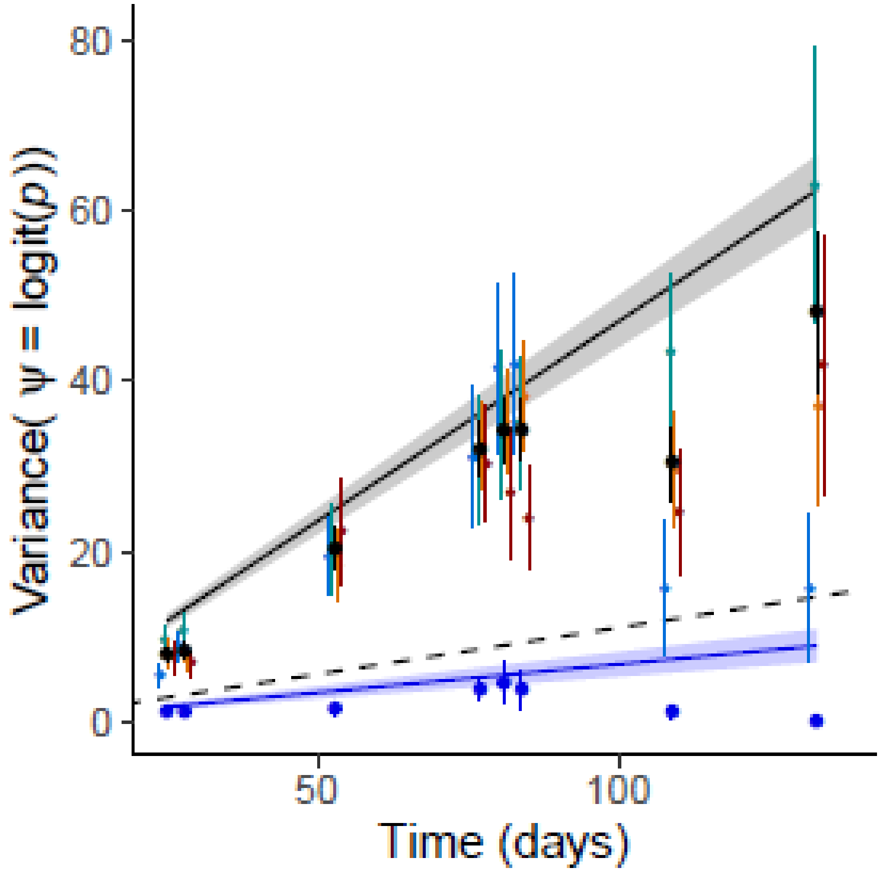
→ Points again to genetic differences in plasticity/tolerance breadth



Rescan et al (2021 Plos Gen)

Variance in frequency change

- **Faster increase in variance** over time in stochastic than constant environments
- But no detectable influence of the autocorrelation treatment on freq. variance
  However precision of variance estimate decreases over time because of extinctions

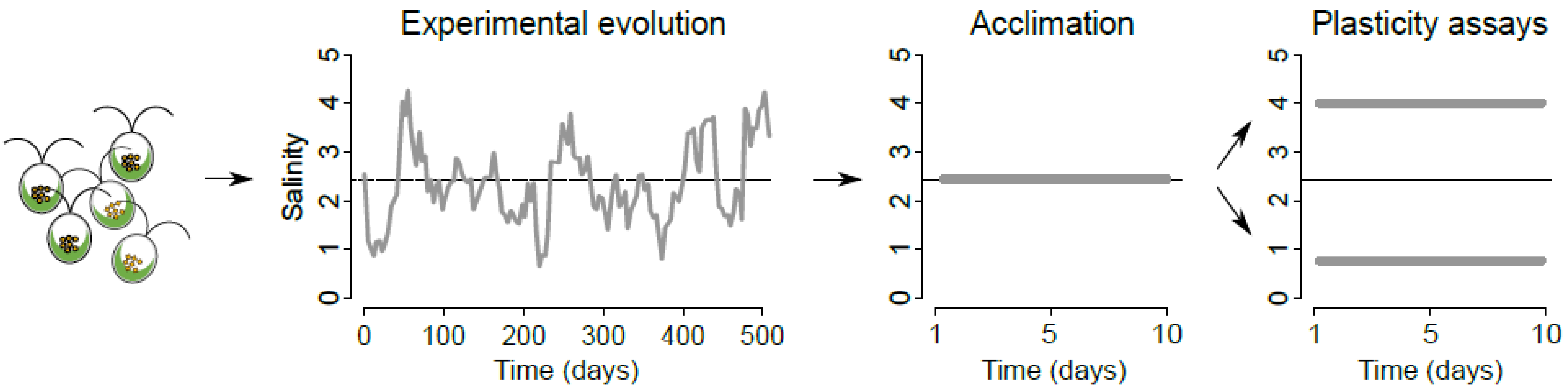


Fluctuating salinity

Constant salinity

Rescan et al (2021 Plos Gen)

Experimental evolution of plasticity



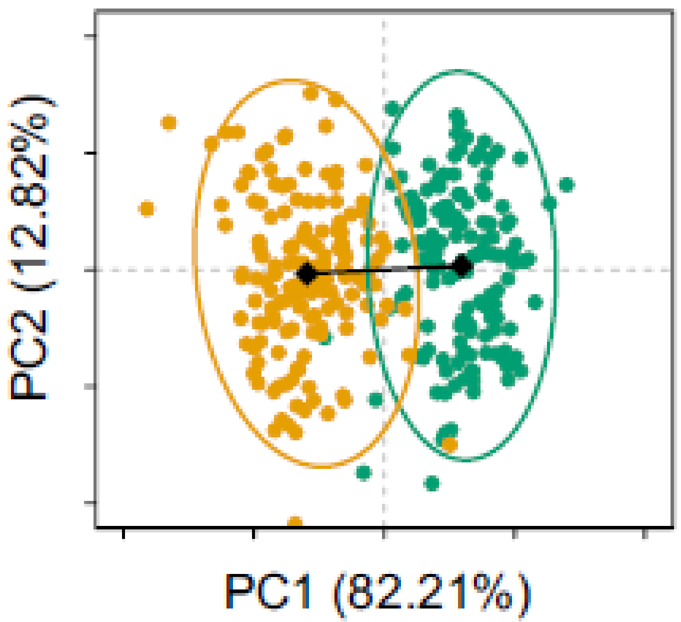
High-throughput morphological phenotyping:

- Size (FSC)
- Complexity/Granularity (SSC)
- Chlorophyll content (red fluorescence)

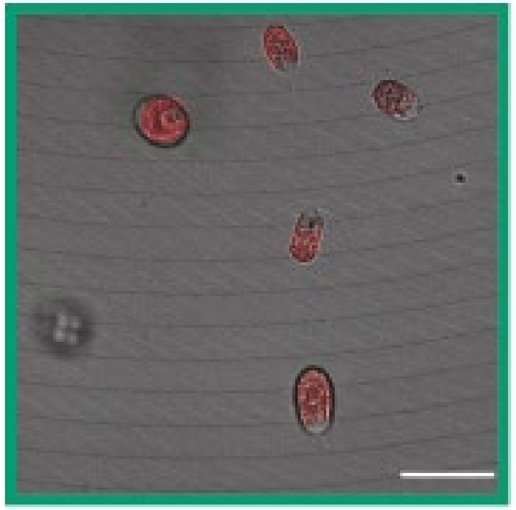
Leung et al (2020 Ecol Lett)

Experimental evolution of plasticity

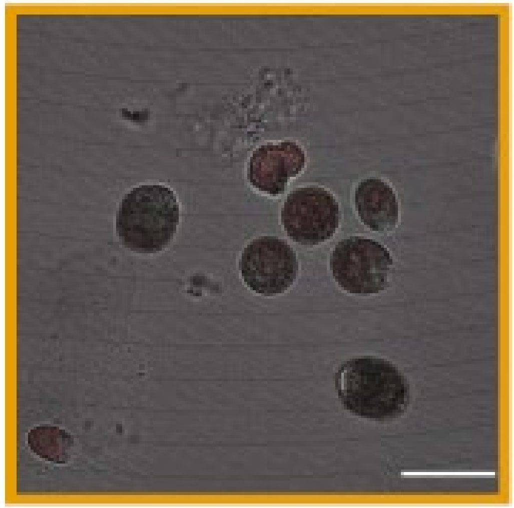
- Plastic responses to salinity



Low salinity



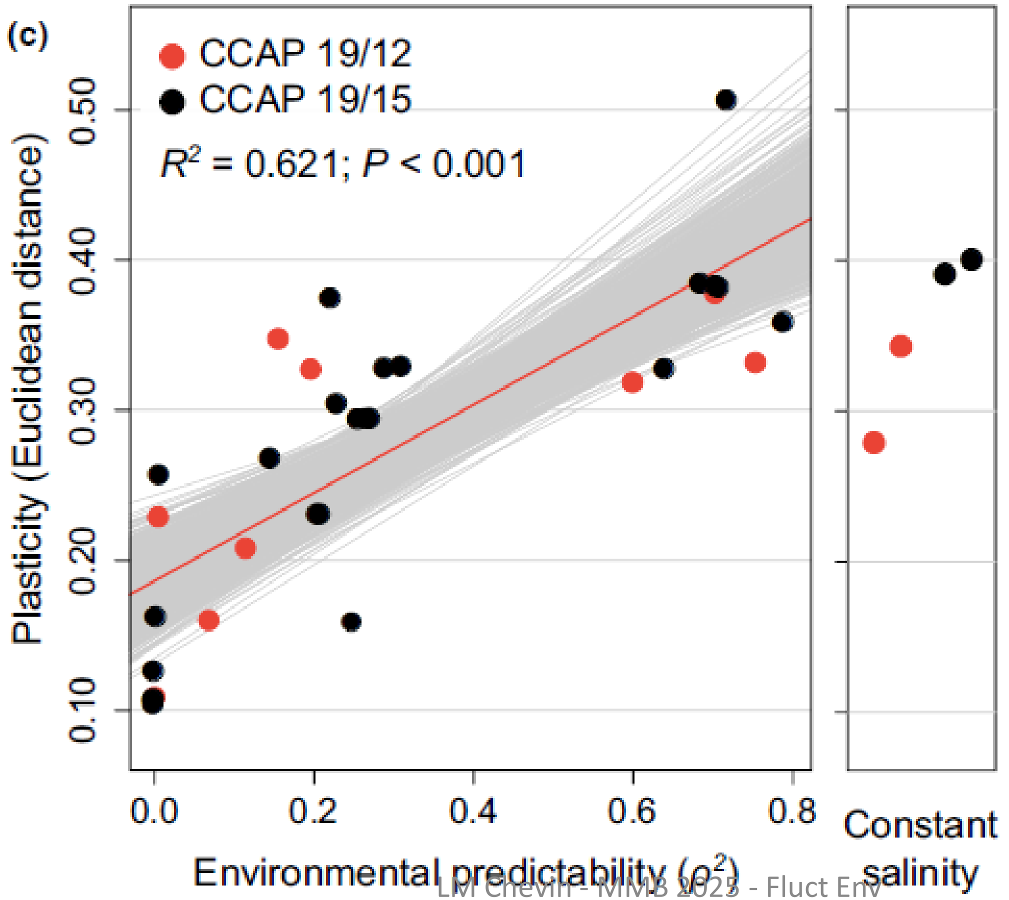
High salinity



Leung et al (2020 Ecol Lett)

Experimental evolution of plasticity

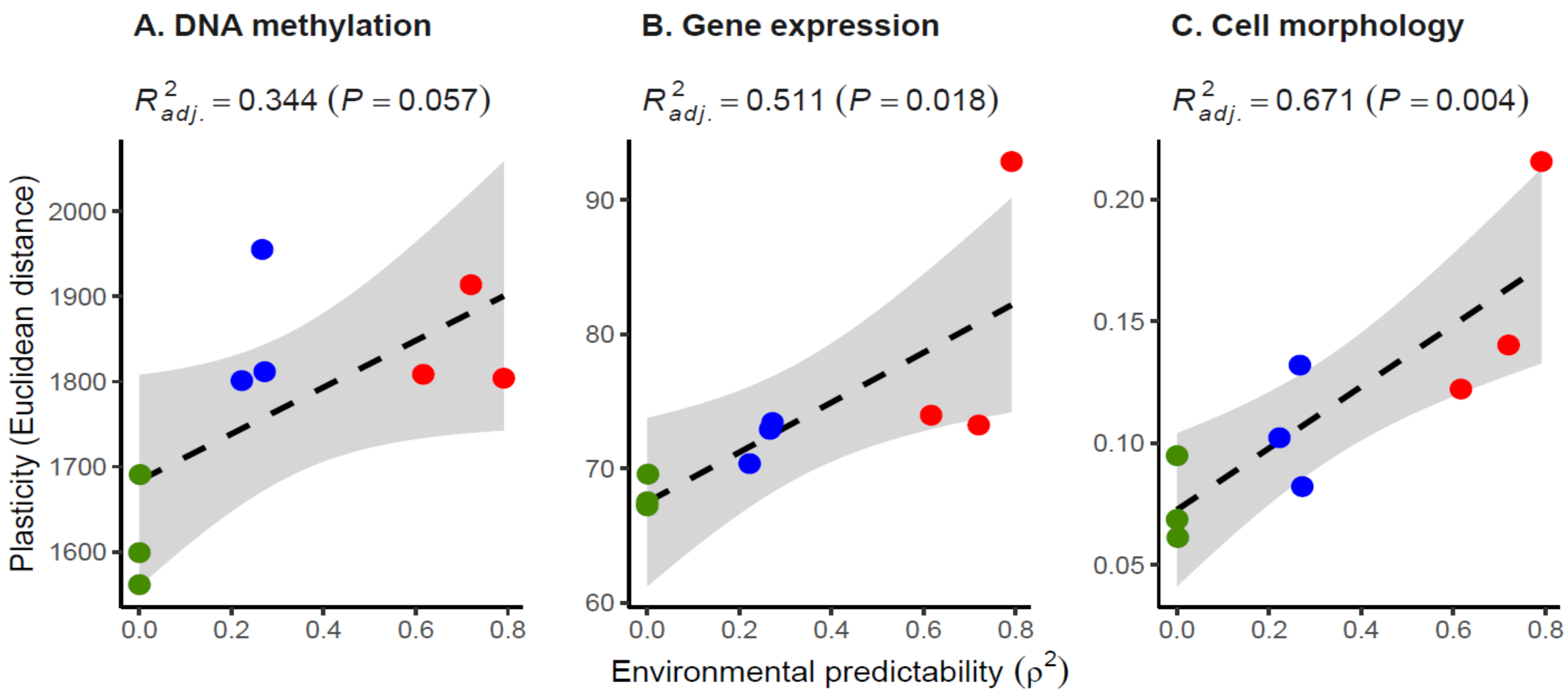
- **Reduced plasticity** evolved in lines that experienced **less predictable environments**[1], consistent with classical theoretical predictions[2]



1: Leung et al (2020 Ecol Lett)
2: Levins (1963 Am Nat); Moran (1992 Am Nat); Scheiner & Gavrilets (1993 JEB)

Experimental evolution of plasticity

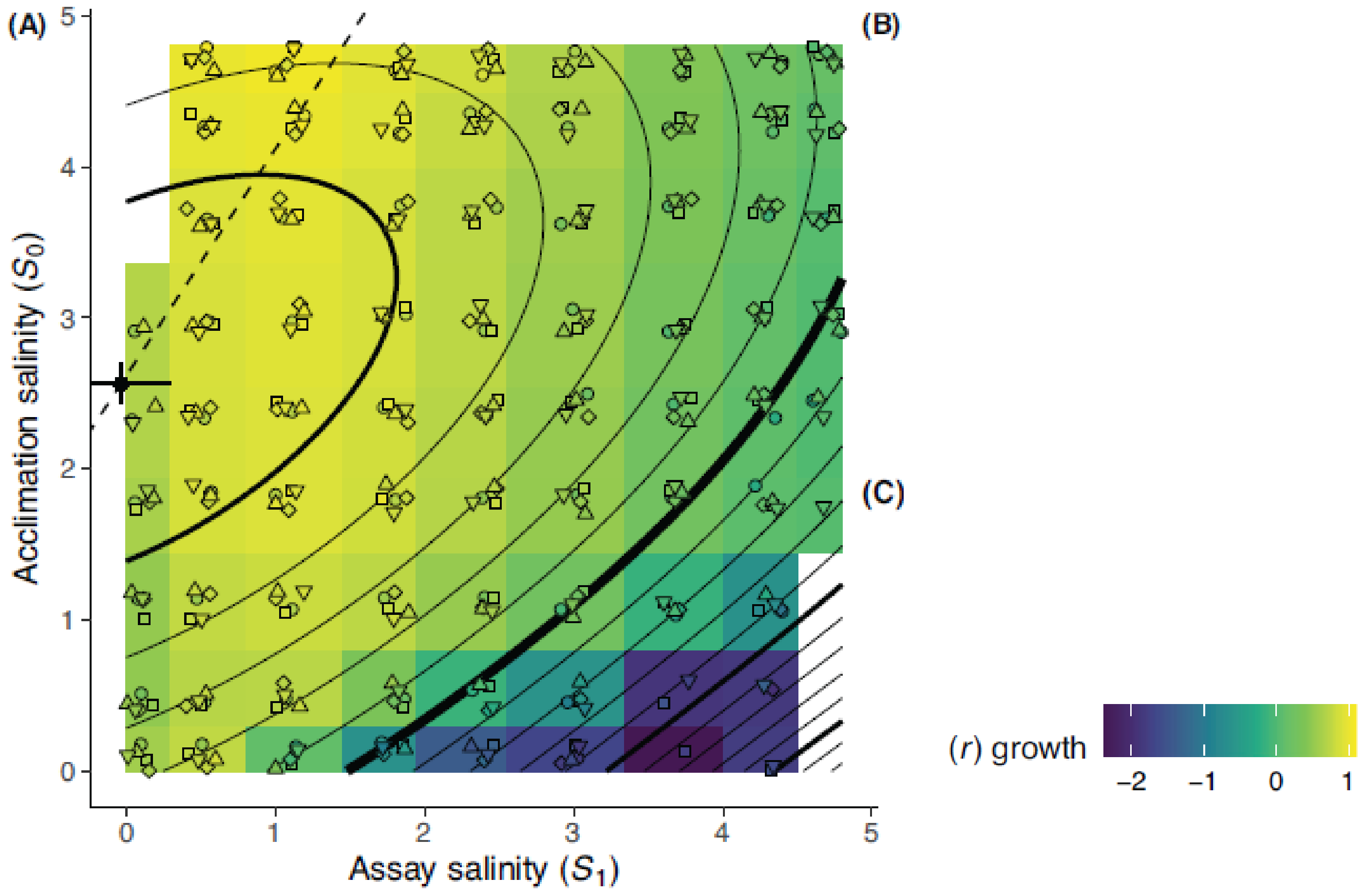
- **Gene expression & DNA methylation** are also plastic wrt salinity[1]
- Consistent evolution of plasticity in response to environmental predictability[2]



1: Leung et al (2022 Mol Ecol)
2: Leung et al (2023 PLoS Biol)

Experimental evolution of tolerance curves

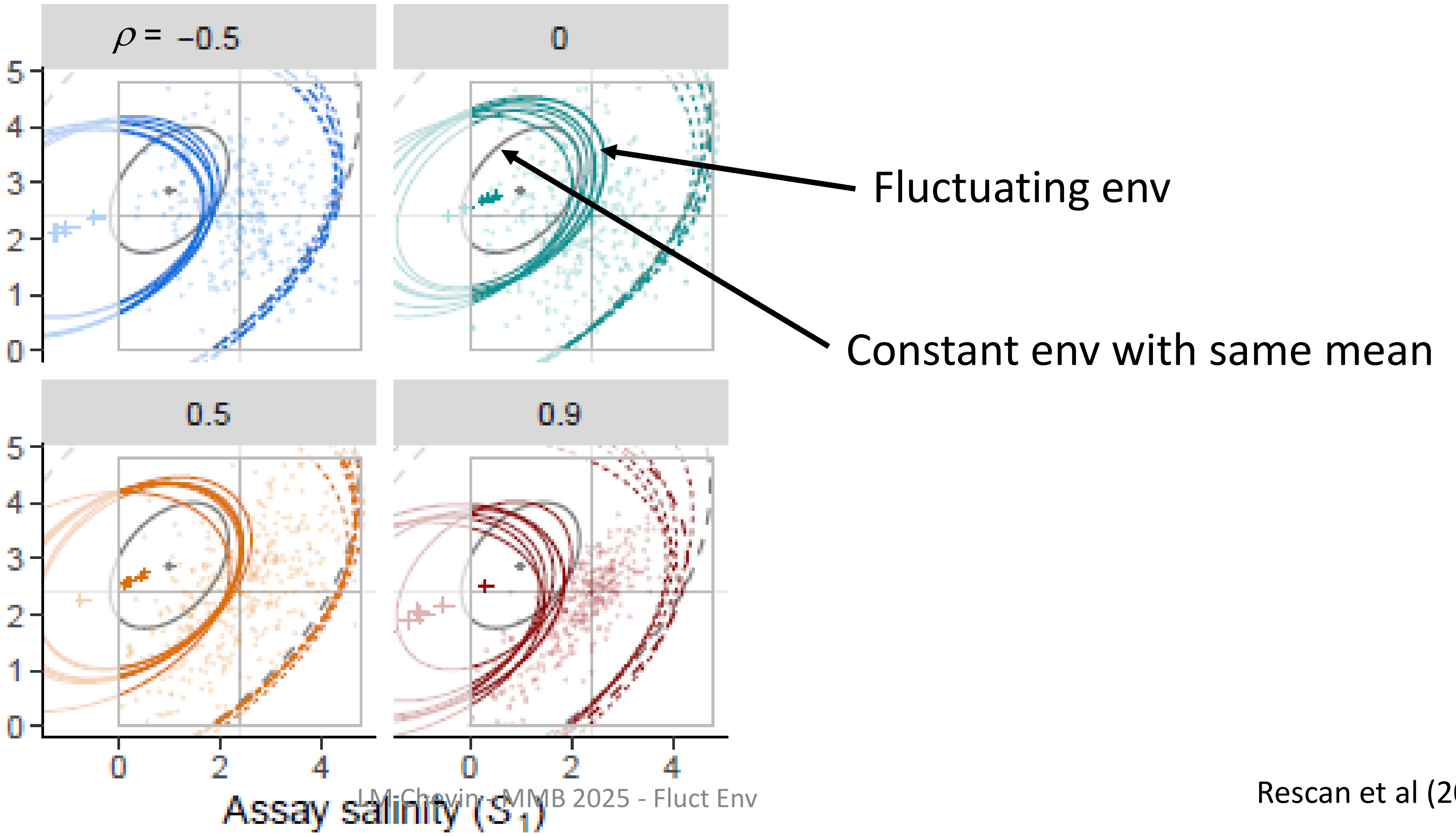
- Growth rate against current and previous salinity in assays after ~500 gen



Rescan et al (2022 Evol Lett)

Experimental evolution of tolerance curves

- **Broader tolerance to current and past salinity** evolved in fluctuating salinity. Little (but significant) effect of predictability



Rescan et al (2022 Evol Lett)

Conclusion

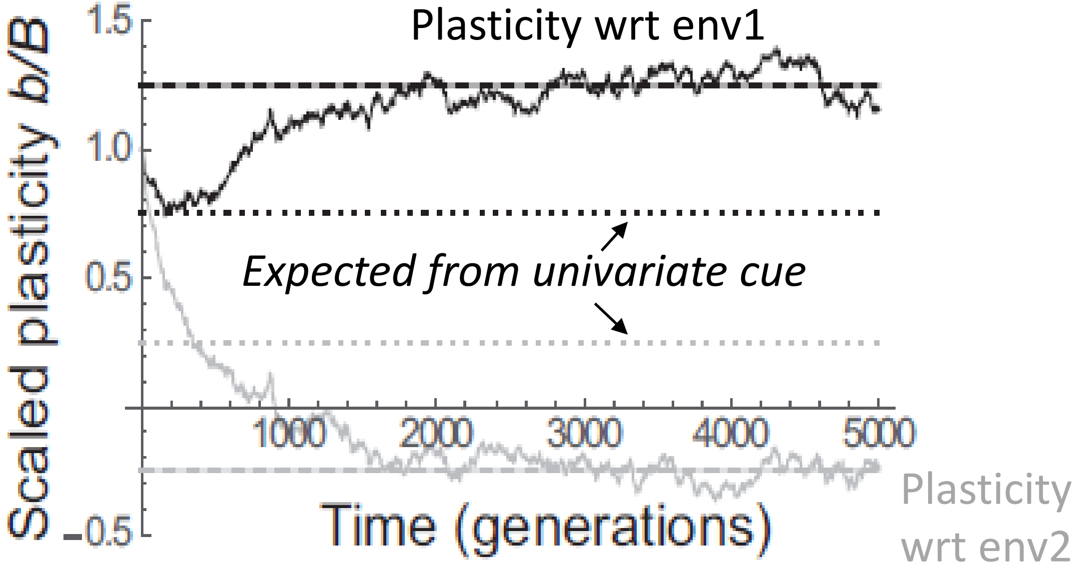
- Models of fluctuating optimum phenotypes are reasonably consistent with nature, and yield analytical insights about different levels of population biology:
  - Gene frequency changes
  - Evolution of quantitative traits
  - (Evolution of) phenotypic plasticity
  - Population dynamics and extinction risk…
- These predictions can be compared to the results of experiments with controled fluctuation patterns, as a bridge between theory and nature.
- Can help understand adaptation, but only a starting point: reality is more complex! Multiple peaks, species interactions, frequency dependence (flattening fitness peaks…), spatial variation, etc…

Thanks!

Questions?

Plasticity and environmental predictability

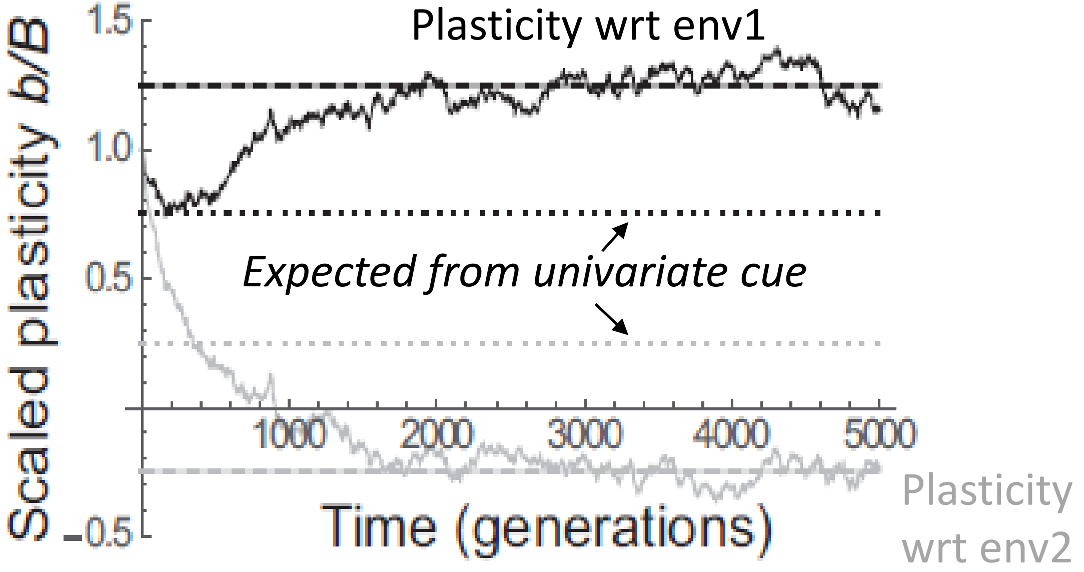
- **In complex environments**, phenotypes respond to multivariate cues.
- Equilibrium plasticity wrt specific environmental variables can be in excess, or opposite, to changes of optimum[1]. Seems maladaptive, but plastic response to full multivariate cue is still adaptive.

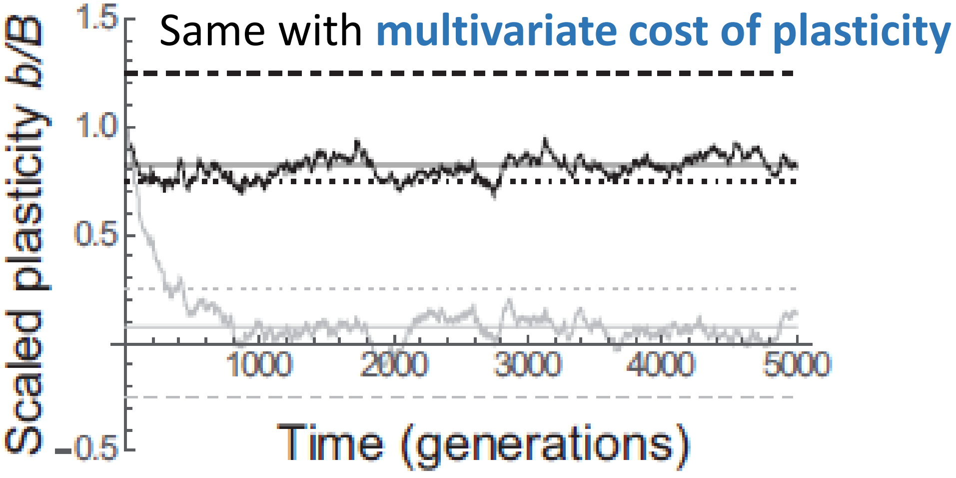


1: Chevin & Lande (2015 Evolution)

Plasticity and environmental predictability

- **In complex environments**, phenotypes respond to multivariate cues.
- Equilibrium plasticity wrt specific environmental variables can be in excess, or opposite, to changes of optimum[1]. Seems maladaptive, but plastic response to full multivariate cue is still adaptive.
- Multivariate costs of plasticity can make plasticity closer to slope of optimum wrt single cues

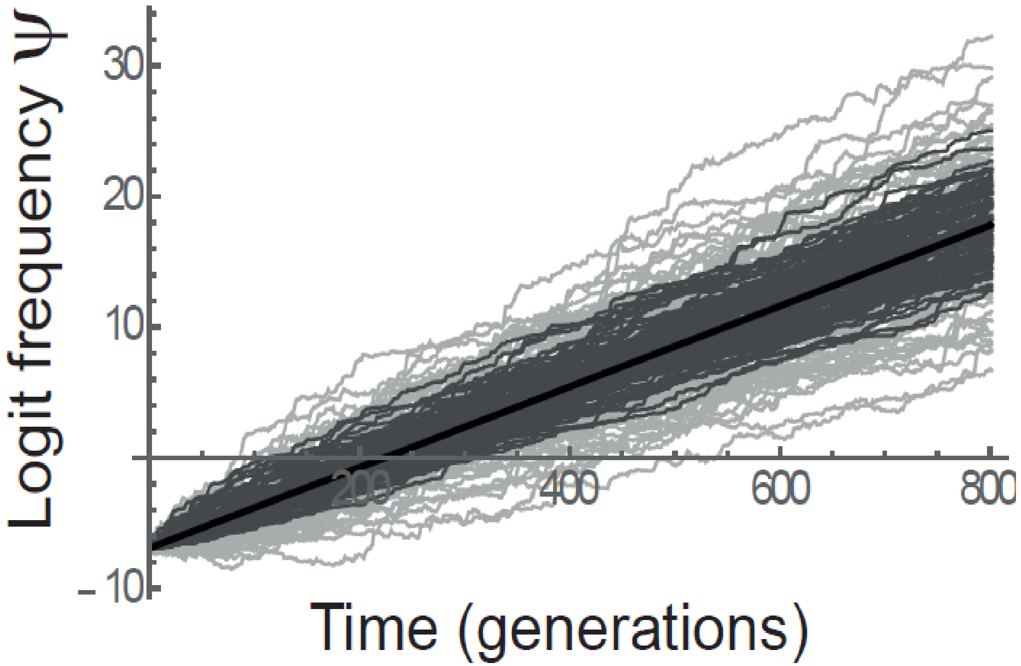




1: Chevin & Lande (2015 Evolution)

Selection at QTL for plasticity

- Plasticity QTL, with environment-dependent effect on trait: $\alpha = a_\alpha + b_\alpha \varepsilon$
- Mutations with different effects on plasticity can have the same expected selection coefficient, but different stochastic variances.



Hyper-optimal plasticity (overshoots optimum)

Sub-optimal plasticity (undershoots optimum)

Chevin (2019 Genetics)