Centre d'Ecologie
Fonctionnelle
& Evolutive

Adaptation to changing environments

Models of moving optimum

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Drivers of adaptive evolution

- When do organisms need to adapt by natural selection?

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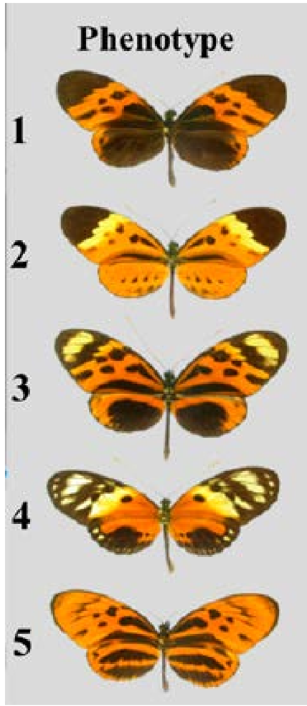
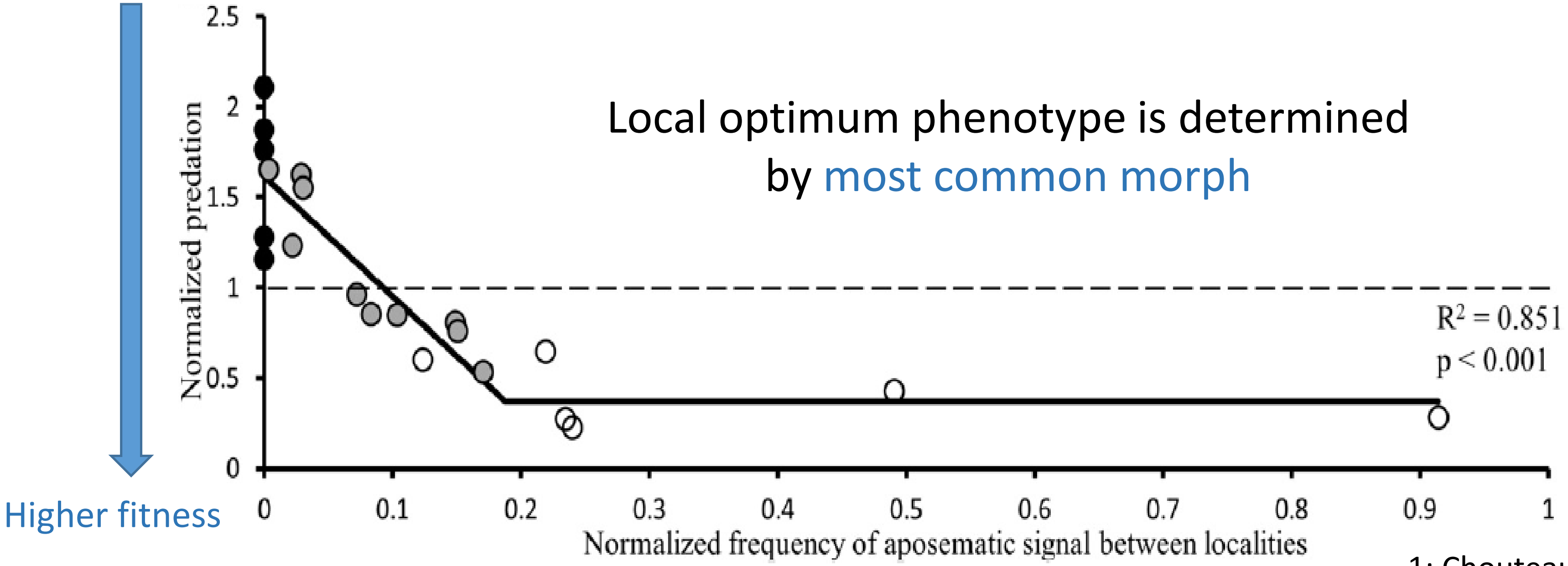
  - ➢ **Internal feedbacks**: Some aspect of the evolving population generates a **selective pressure on itself**.
    - Ecological: Resource competition causing negative frequency dependence, mimicry of warning signals causing positive FD[1]





Local optimum phenotype is determined by most common morph

1: Chouteau et al (2016 PNAS)

Drivers of adaptive evolution

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[2] Burt & Trivers (2008)

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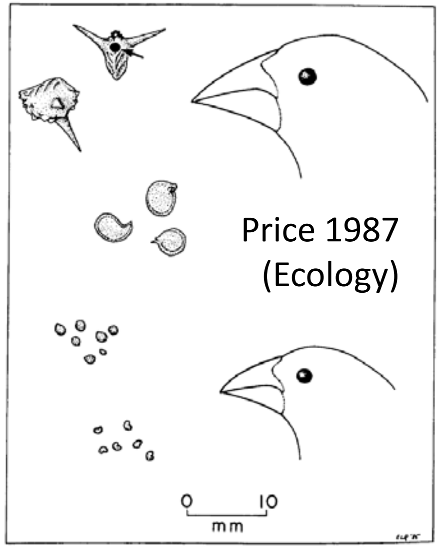
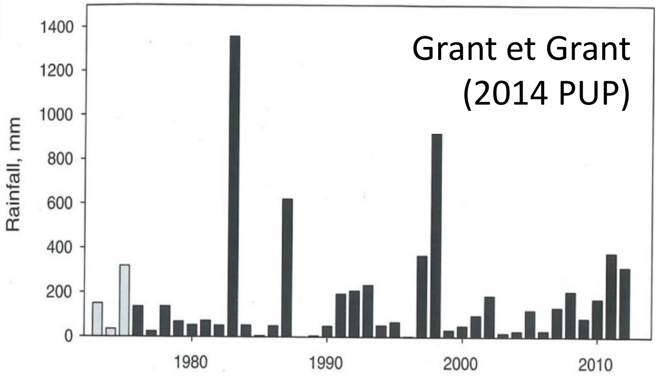
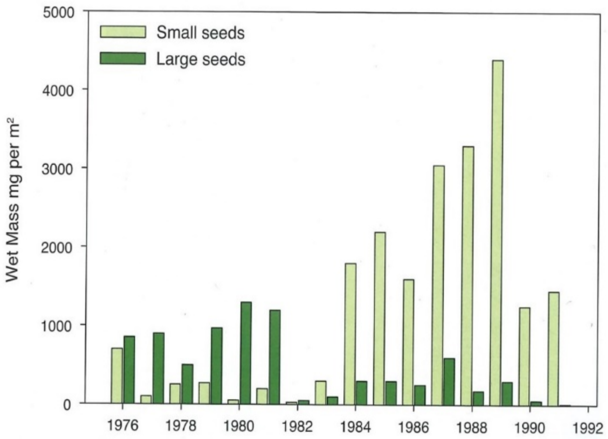
  - ➢ **External forcing**: A **changing environment** modifies which phenotype is optimal

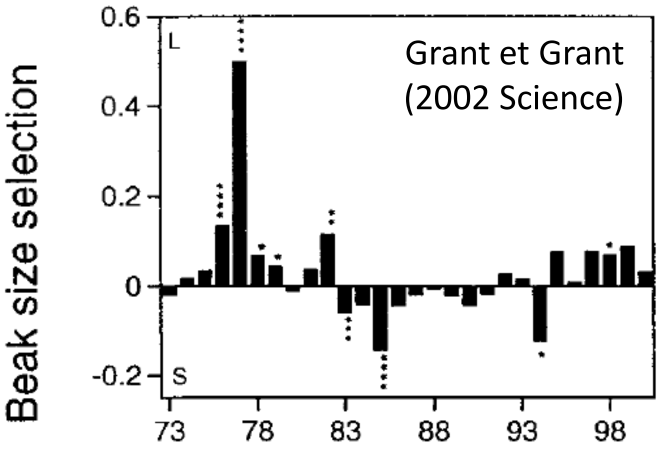


Price 1987 (Ecology)



Grant et Grant (2014 PUP)





Grant et Grant (2002 Science)

Drivers of adaptive evolution

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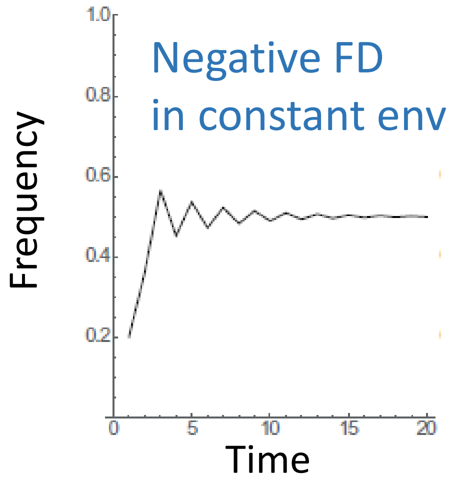
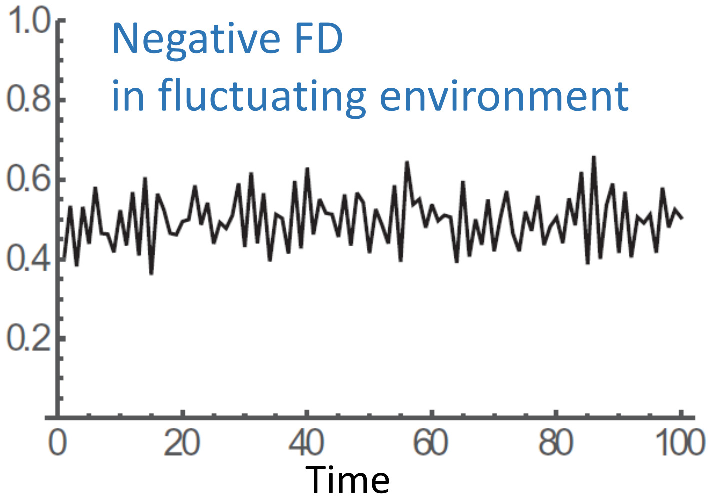
  - ➢ **External forcing**: A **changing environment** modifies which phenotype is optimal
- Even when internal feedbacks exist, long-term evolutionary dynamics may be sustained by environmental variation[3]

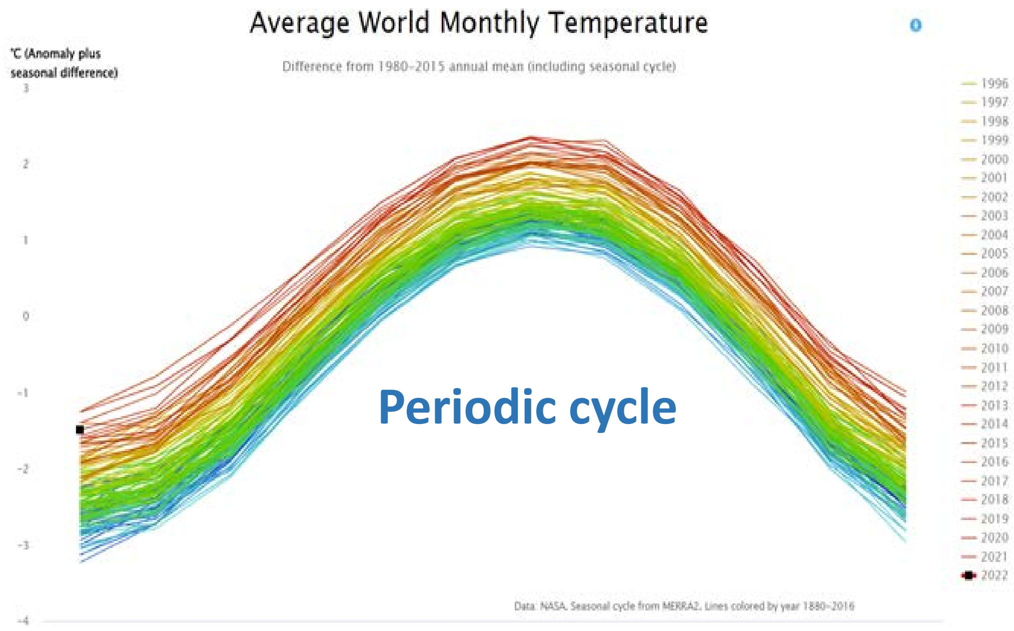




1: Chouteau et al (2016 PNAS)
2: Burt & Trivers (2008)
3: Chevin et al (2022 Evolution Letters)

Patterns of environmental change

- Natural systems are characterized by different types of environmental changes

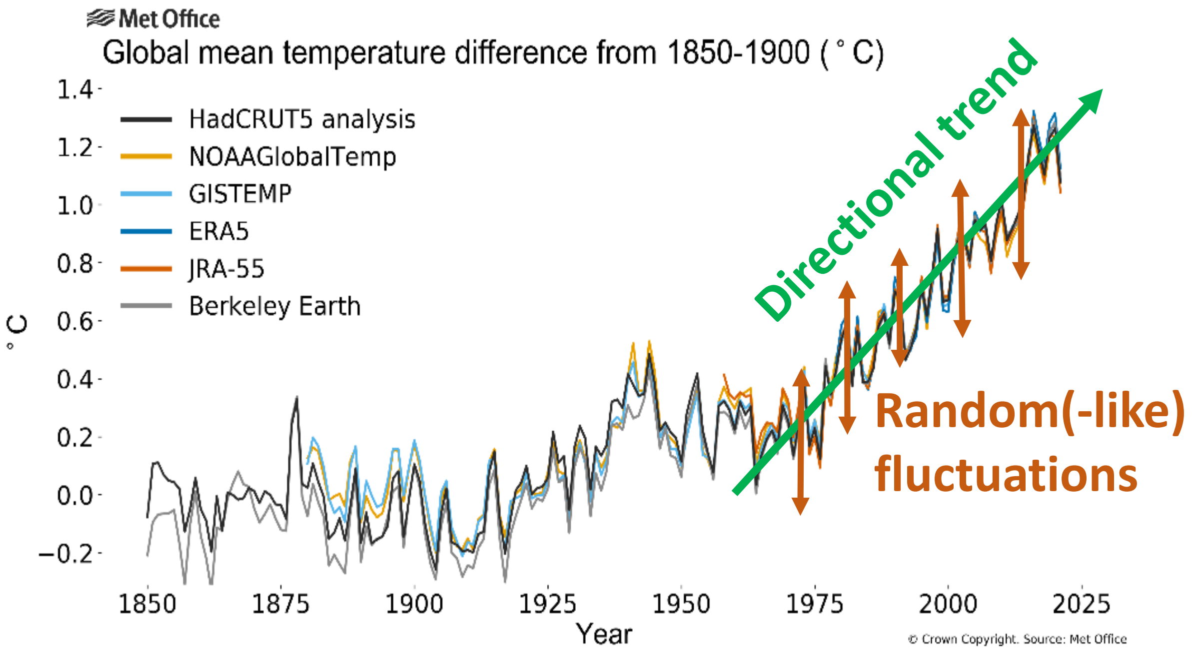


Average World Monthly Temperature

Difference from 1980-2015 annual mean (including seasonal cycle)

Periodic cycle

Data: NASA. Seasonal cycle from MERRA2. Lines colored by year 1880-2016



Met Office

Global mean temperature difference from 1850-1900 (°C)

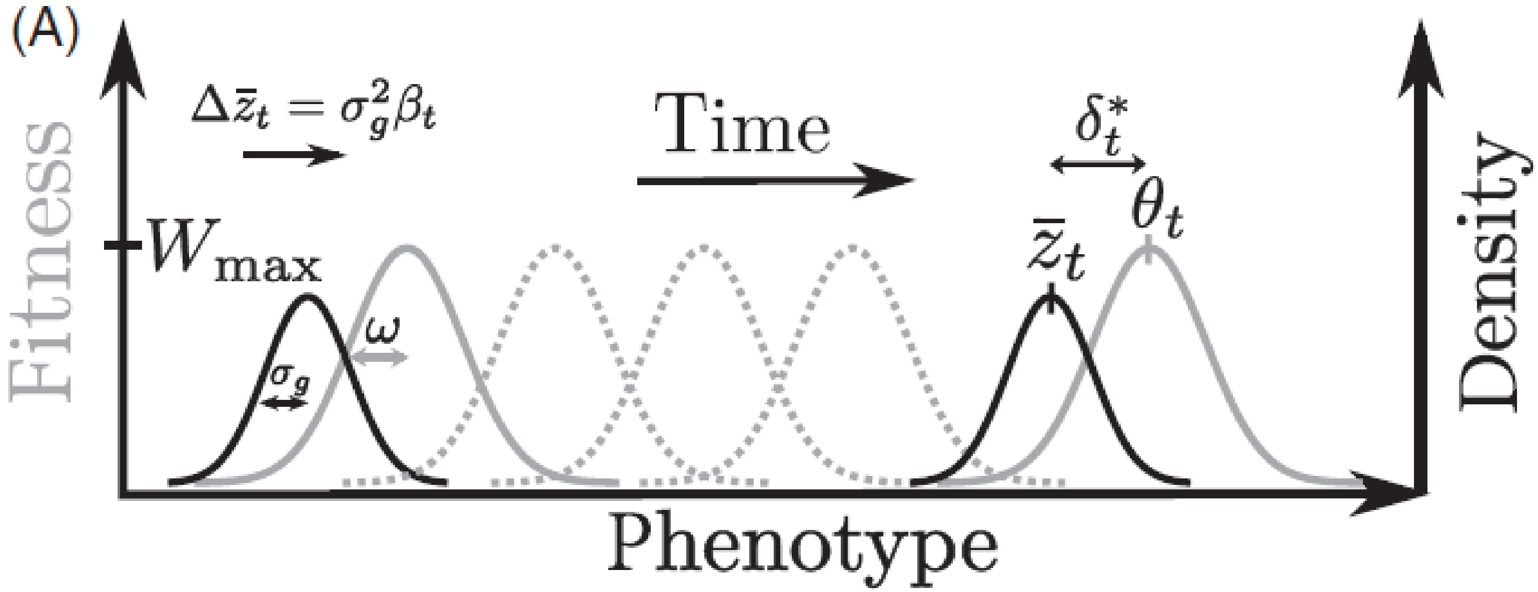
Directional trend

Random(-like) fluctuations

© Crown Copyright. Source: Met Office

Evidence for moving optimum

- In evolutionary theory, adaptation to changing environments often modeled as evolutionary tracking of a **moving optimum** for phenotypic traits[1].



- Makes logical sense, but **how well supported** emprically?

[1] Reviewed by Kopp & Matuszewski (2014 Evol Appl)

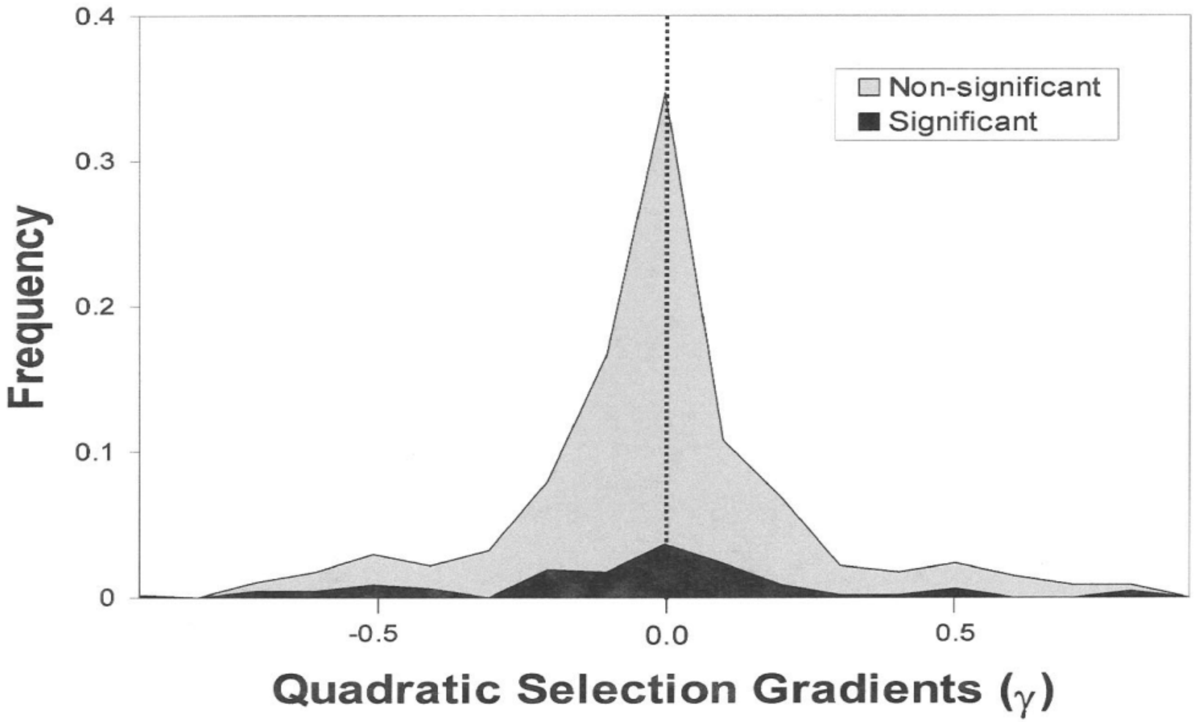
Evidence for moving optimum

- Direct evidence: (1) Phenotypic selection analysis.

➢Quadratic selection gradient[1] $\gamma = \text{Cov}\left[(z-\bar{z})^2, \frac{W}{\overline{W}}\right]/\sigma_z^4$

Mean curvature of fitness landscape, $\gamma < 0$ generally interpreted as stabilizing selection

➢Meta-analysis found as many $\gamma > 0$ as $\gamma < 0$, interpreted as lack of evidence for stab. selection[2]



1: Lande & Arnold (1983 Evolution);
2: Kingsolver et al (2001 Am Nat)

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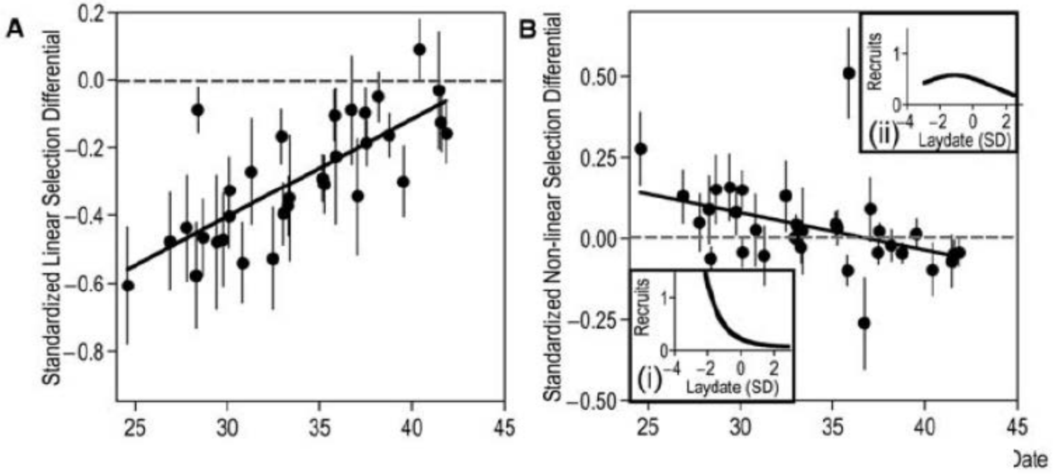
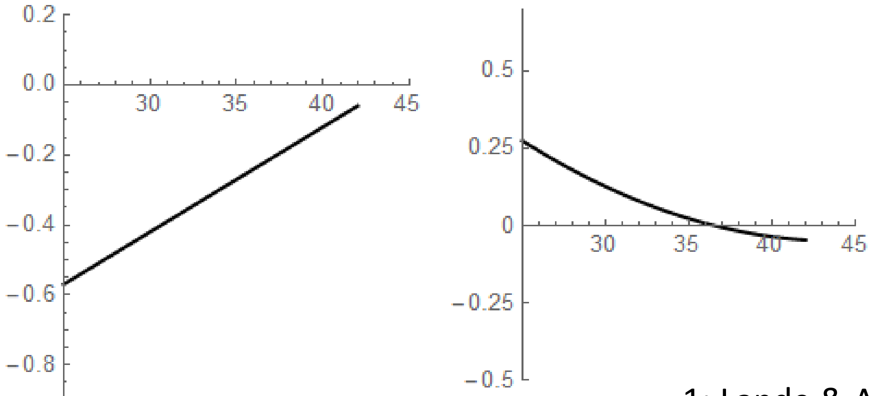
Measured directional and quadratic gradients
(Charmantier et al 2008 Science)



Assuming a moving optimum
with constant width



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➢ What appears in theoretical predictions for changes in mean and variance under selection is the strength of stabilizing selection $S = \frac{1}{V_s}$ not $\gamma = \frac{\beta^2 - S}{\sigma_z^4} = -S\,\frac{1 - S(z-\theta)^2}{\sigma_z^4}$
So why not estimate that directly?

➢ Can be done using log link in GLM [3] (eg Poisson regression, relevant for fecundity selection) or directly fitting the Gaussian peak in explicit framework (eg Stan)[4]

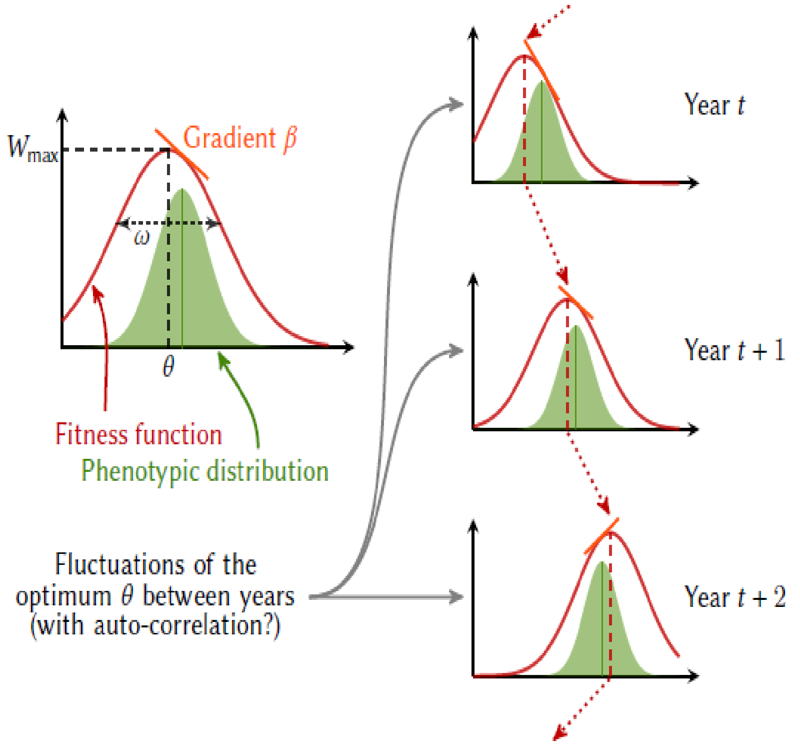
3: Chevin et al (2015 Evolution);
4: de Villemereuil et al (2020 PNAS)

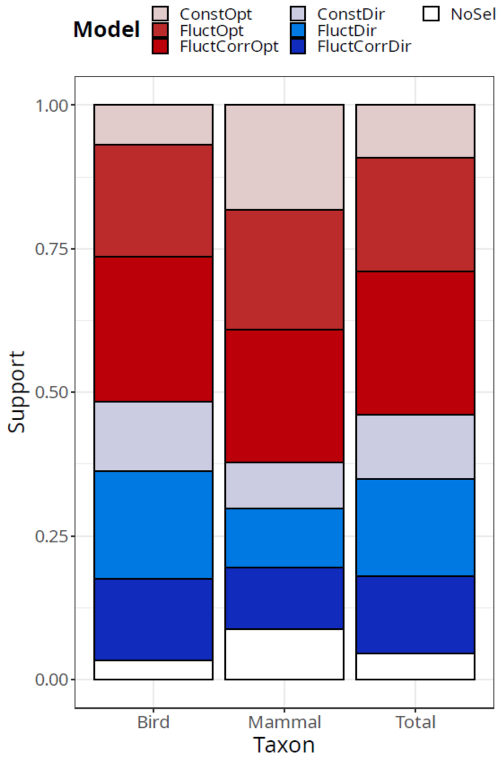
1: Lande & Arnold (1983 Evolution);
2: Kingsolver et al (2001 Am Nat)

Evidence for moving optimum

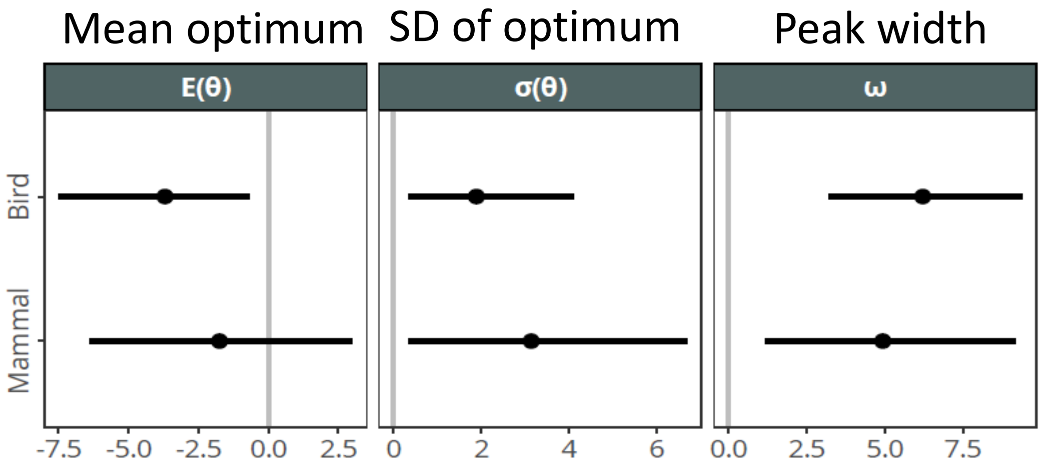
- Direct evidence: (1) Phenotypic selection analysis.

Estimating fluctuating selection as movements of Gaussian fitness peak for breeding time across birds and mammals in the wild[1] : 39 populations, 21 species, 9 to 63 yrs (average 33.2 years)





Models with optimum

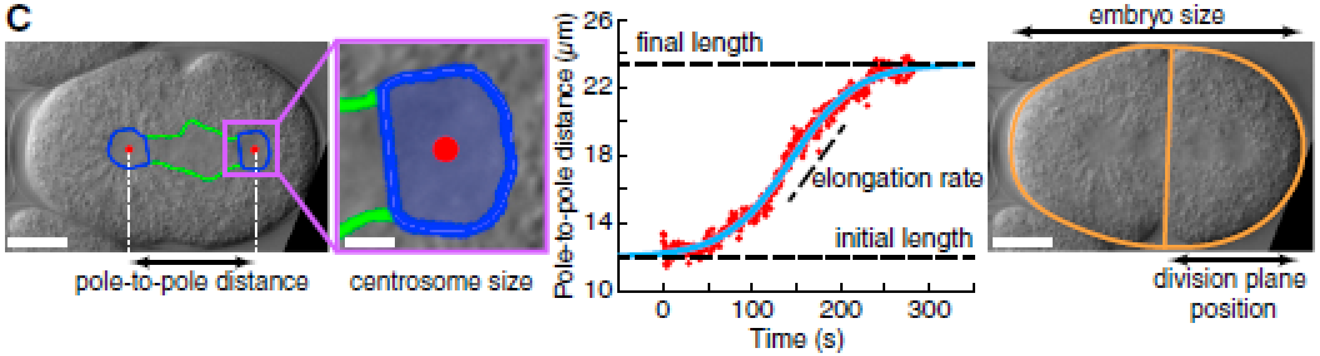


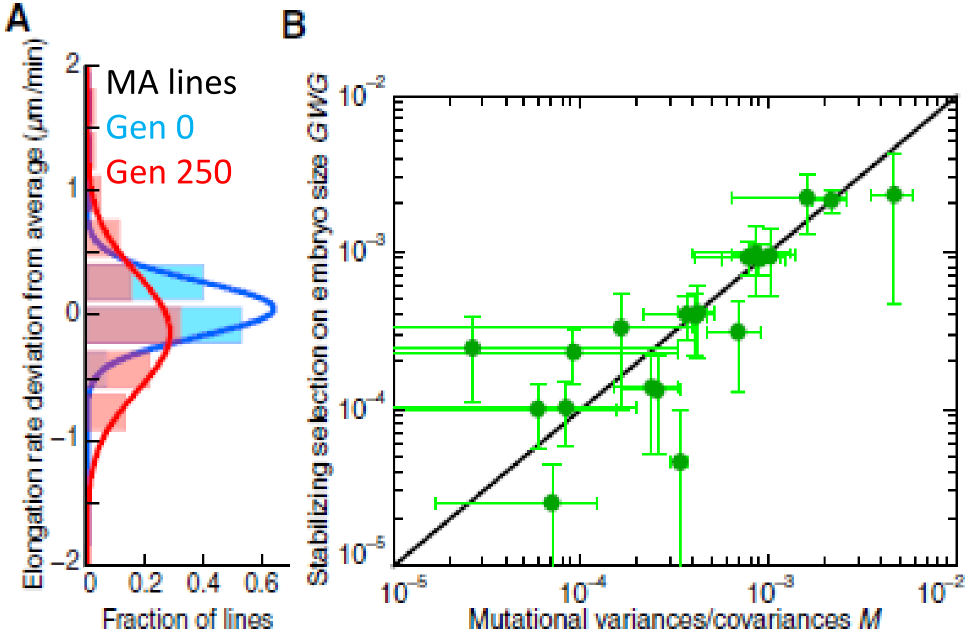
1: de Villemereuil et al (2020 PNAS)

Evidence for moving optimum

- <u>(Semi)-Direct evidence</u>: (2) <u>Comparison of mutational to standing genetic variance</u>

- High-throughput measurement of many spindle traits in *C. elegans* embryos





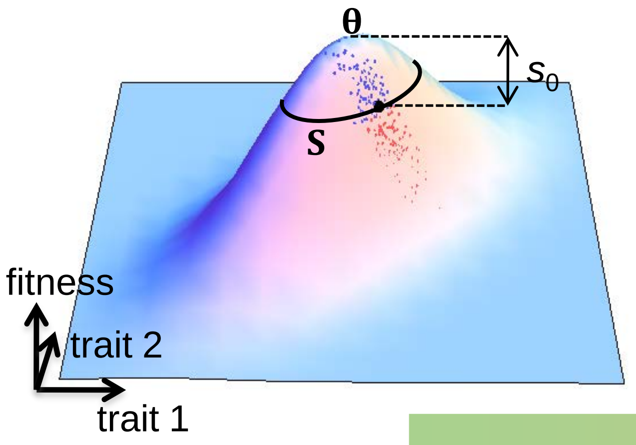
- Comparing MA lines to natural isolates: Standing variation of all traits (y-axis) well predicted by their mutational (co)variances (x-axis), but only **after accounting for stabilizing (& correlational) selection**

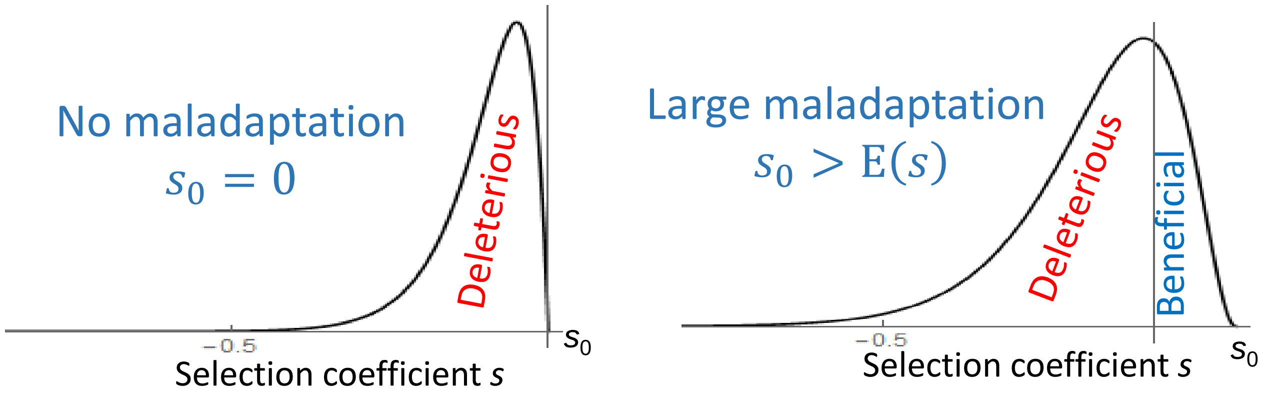
Farhadifar et al. (2015 Curr Biol)

Evidence for moving optimum

- Indirect evidence: (3) Distribution of fitness effects across environments

Theory (Martin & Lenormand 2006 Evolution):





No maladaptation

$s_0 = 0$

Large maladaptation

$s_0 > \mathrm{E}(s)$

Reverse
displaced
gamma

Increasing stress

- Larger variance of s
- Higher proportion of beneficials
- Same mean $\mathrm{E}(s) = -\mathrm{tr}(\mathbf{SM})/2$

Evidence for moving optimum

- Indirect evidence: (3) Distribution of fitness effects across environments

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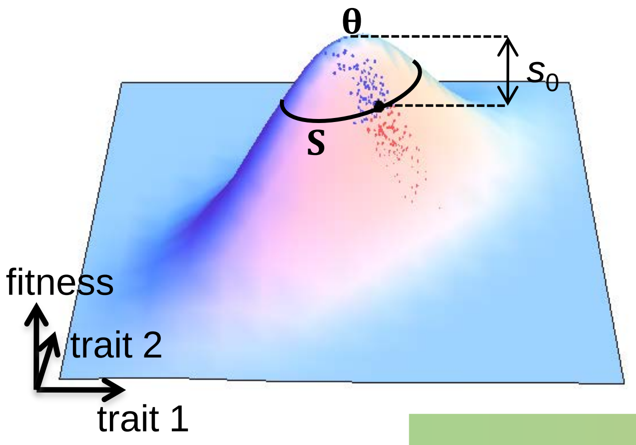
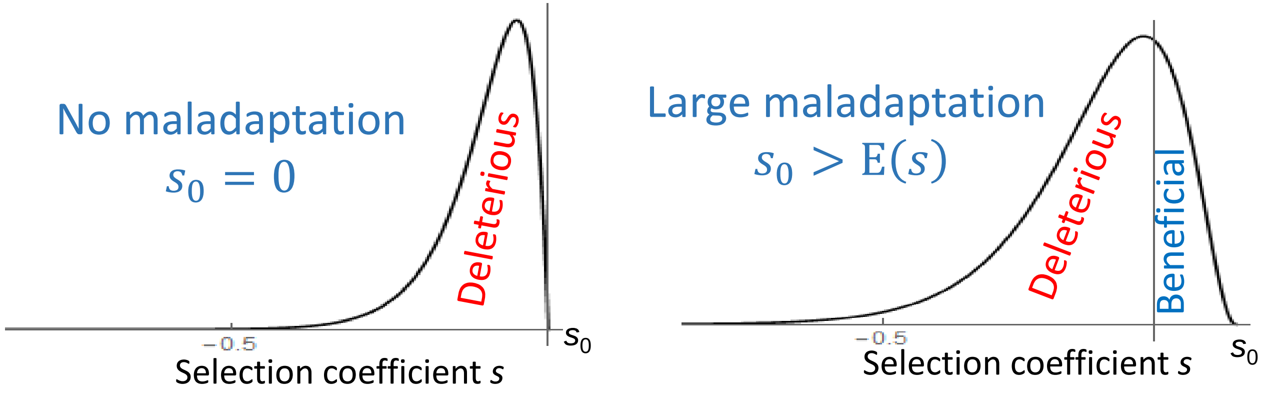




No maladaptation

$s_0 = 0$

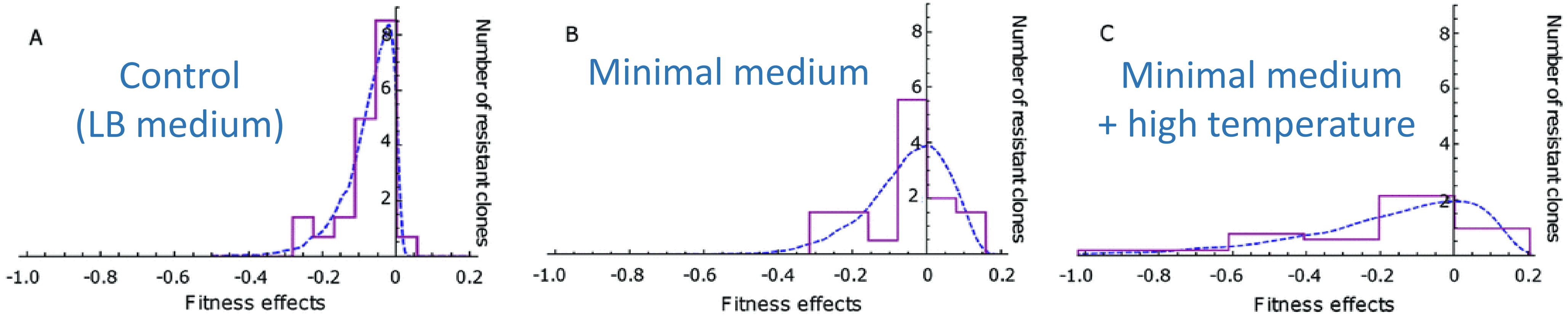
Large maladaptation

$s_0 > \mathrm{E}(s)$

Reverse displaced gamma

Increasing stress

Experiment 1 (Trindade et al 2012 Evolution): Confirmed + estimated all parameters from DFE predicted by FGM



Control (LB medium)

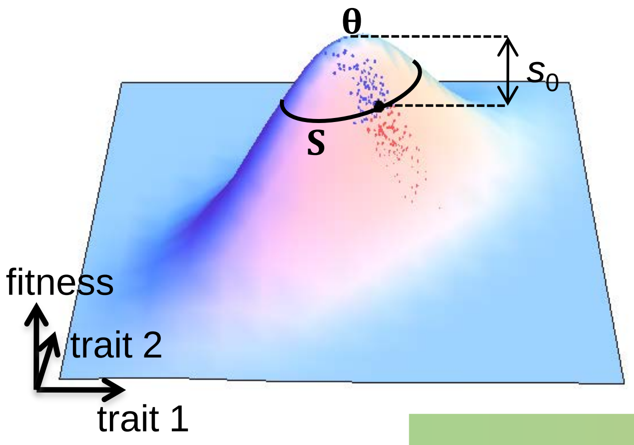
Minimal medium

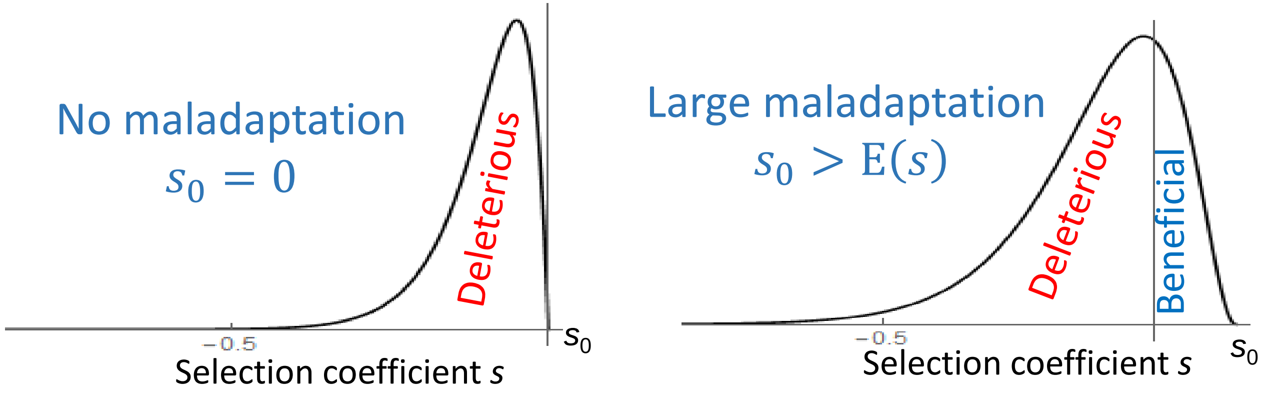
Minimal medium + high temperature

Evidence for moving optimum

- Indirect evidence: (3) Distribution of fitness effects across environments

Theory (Martin & Lenormand 2006 Evolution):

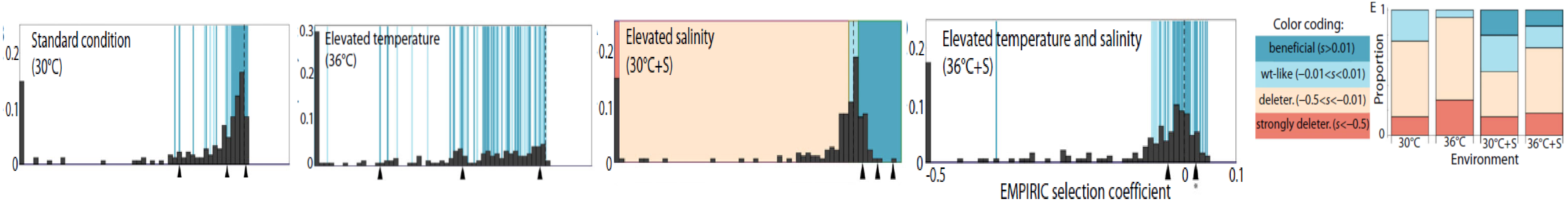




Reverse displaced gamma

Increasing stress

Experiment 2 (Hietpas et al 2013 Evolution): Confirmed + estimated s_0 from FGM

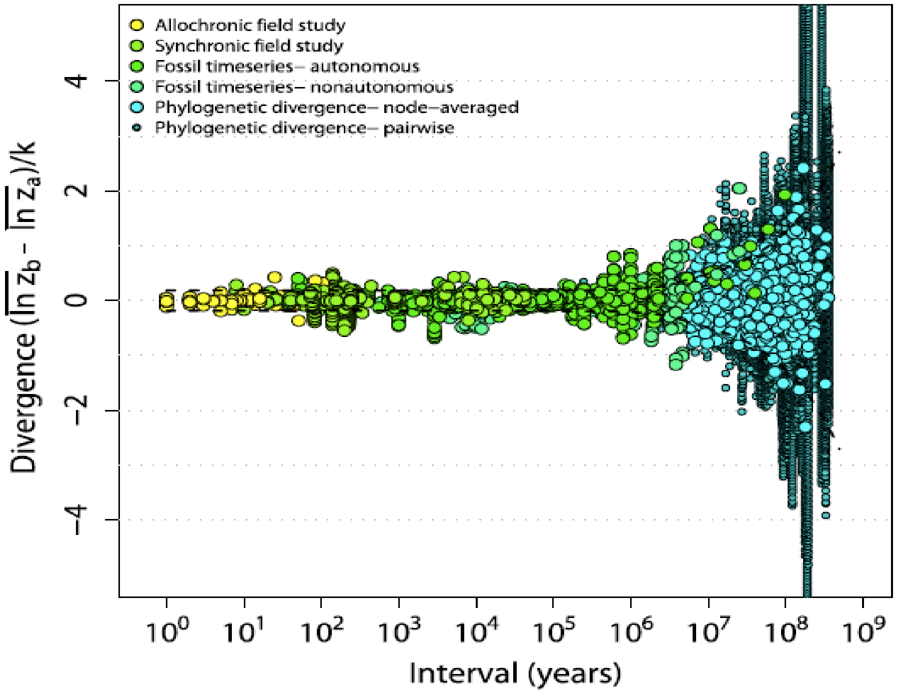


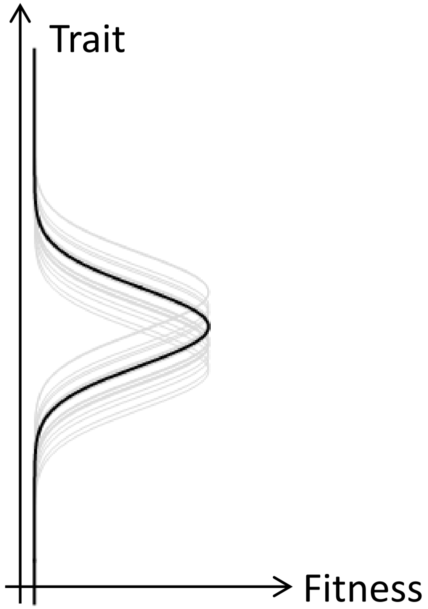
Evidence for moving optimum

- Indirect evidence: (4) Paradox of stasis

➢ **Rates of evolution** across timescales[1]:
Fast over short times, stasis in the long run, then burst after 10^6 yrs.

➢ Compared to evolutionary QG theory[1]: Not consistent with drift,
but consistent with **stationary fluctuations of an optimum phenotype + rare strong shifts**.



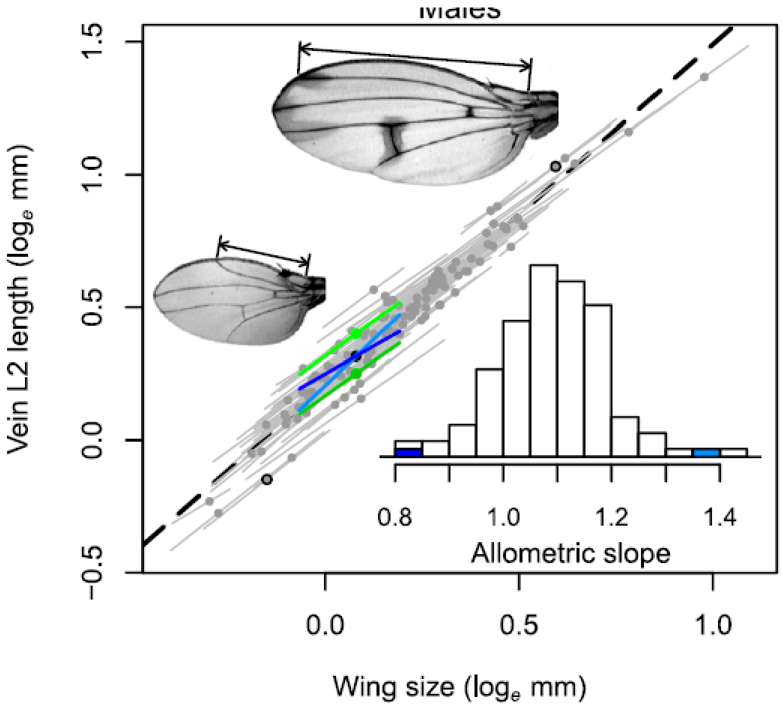


1: Estes & Arnold (2007 Am Nat);
Uyeda et al (2012 PNAS)

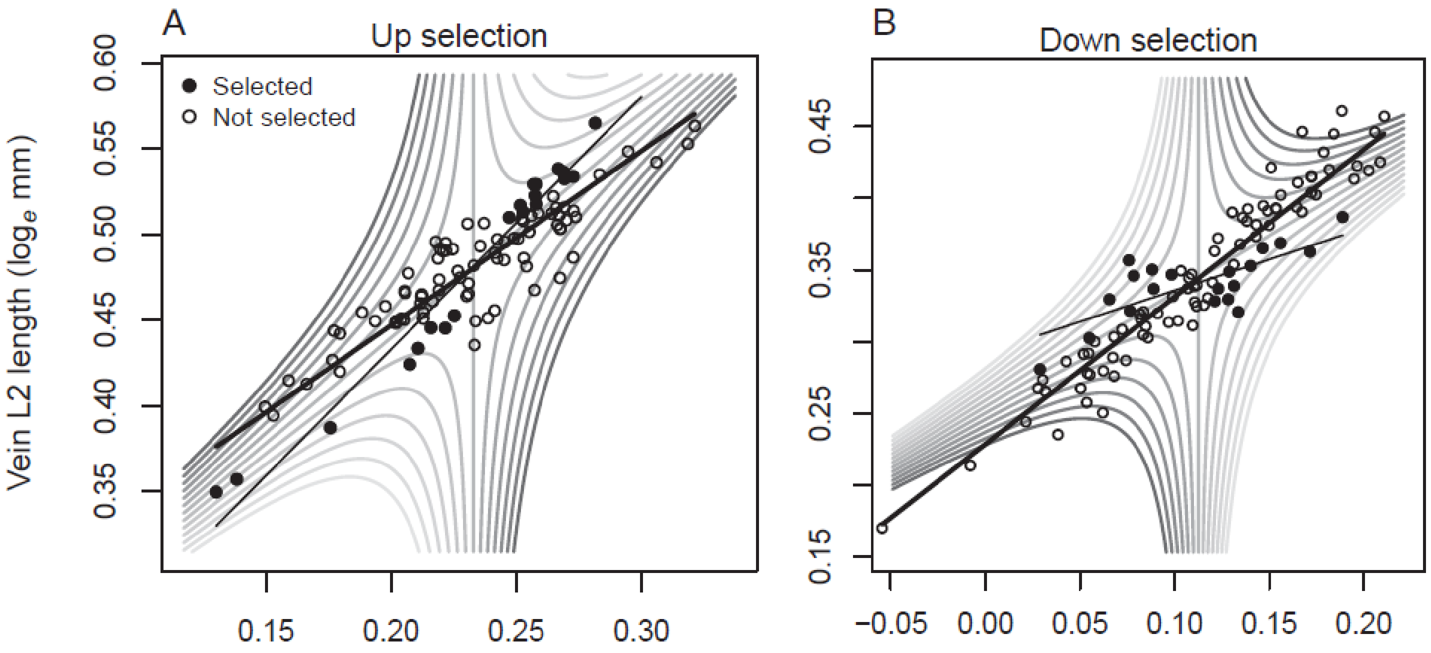
Evidence for moving optimum

- Indirect evidence: (5) Reversion of selection responses

Strongly conserved allometric relationship (111 species)



+ and - selection on allometric intercept and slope (using correlational disruptive selection)

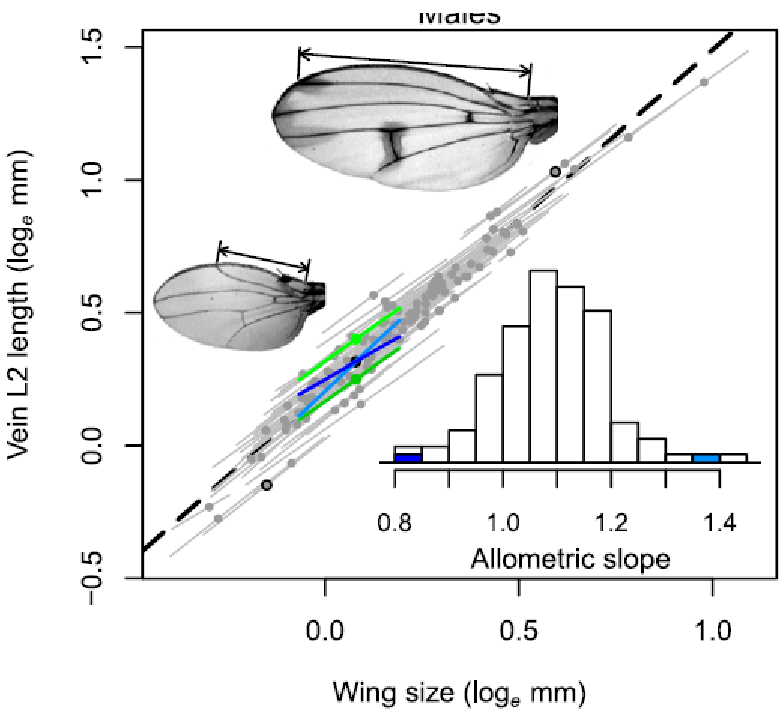


1: Bolstad et al (2015 PNAS)

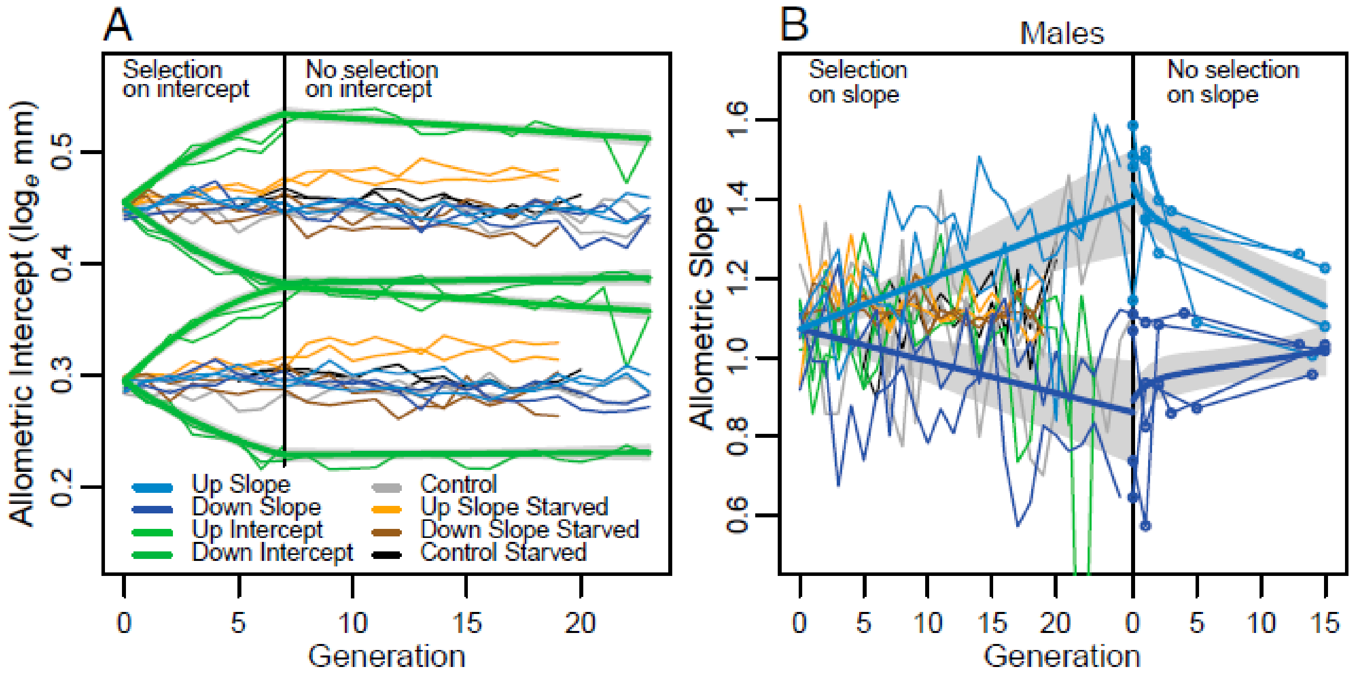
Evidence for moving optimum

- <u>Indirect evidence</u>: (5) <u>Reversion of selection responses</u>

Strongly conserved allometric relationship (111 species)



Rapid response, but **reverts after selection is relaxed**



Could be due to break up of LD,
but here could only account for 15-20% of response

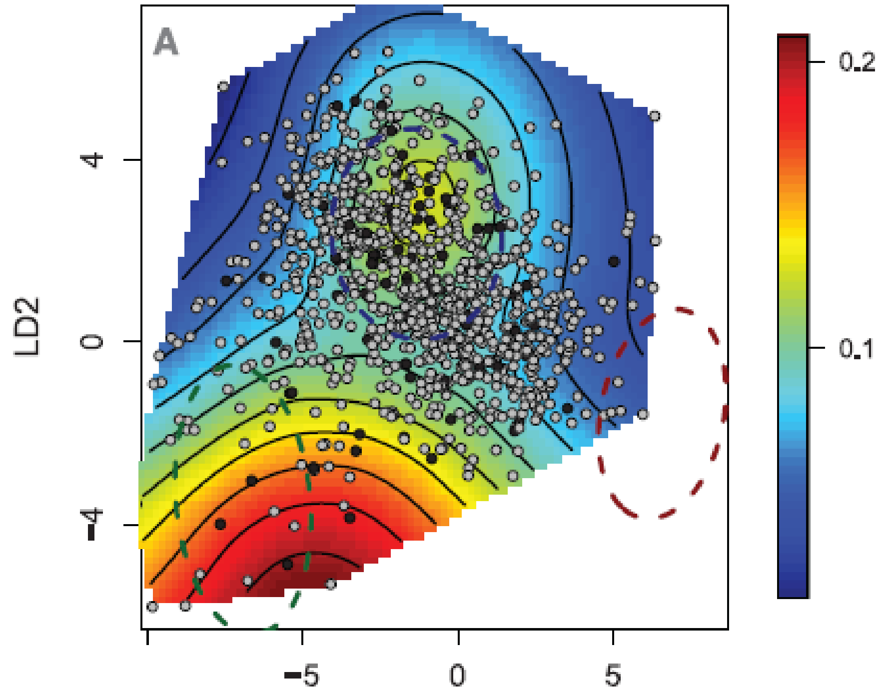
1: Bolstad et al (2015 PNAS)

Evidence for moving optimum

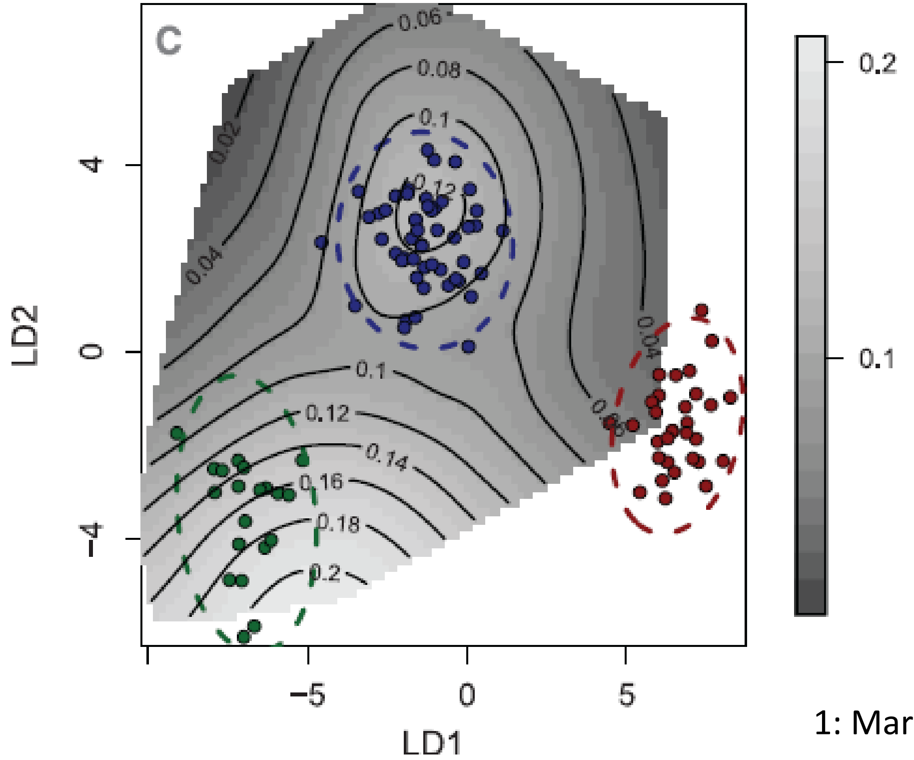
- <u>Indirect evidence</u>: (6) <u>Ecological speciation</u>

➢F2 hybrids between forming species, in nascent adaptive radiation in *pupfishes*

Recombinants reveal underlying fitness landscape



Original species **lie on fitness peaks**



1: Martin & Wainwright (2013 Science)

Evidence for moving optimum

Combining these converging lines of evidence:

(1) (Fluctuating) phenotypic selection analysis
(2) Comparison of mutational to standing genetic variance
(3) Distribution of fitness effects across environments
(4) Paradox of stasis
(5) Reversion of selection responses
(6) Ecological speciation
\+ others (eg fitness cost of artificial selection in natural environments[1], …)

Stabilizing selection seems overall well supported.

However specific shape of fitness peak may deviate from that usually assumed, especially far from optimum.

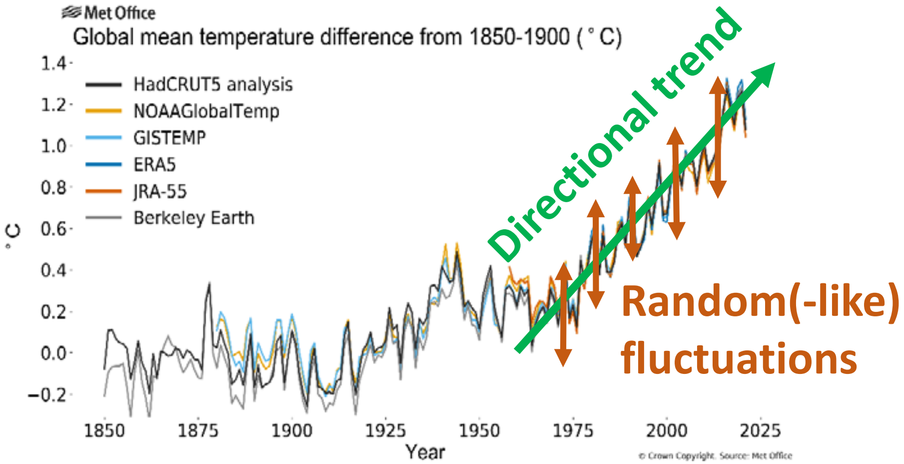
1: McGinnity et al (2003 Proc B)

Goal and overview of the lecture

How can moving optimum models help understand and predict adaptation to changing environments?

Foreword: Moving optimum model

1. Adaptation to directional environmental change
2. Adaptation to cycling environments
3. Adaptation to stochastic environmental fluctuations



Directional trend

Random(-like) fluctuations

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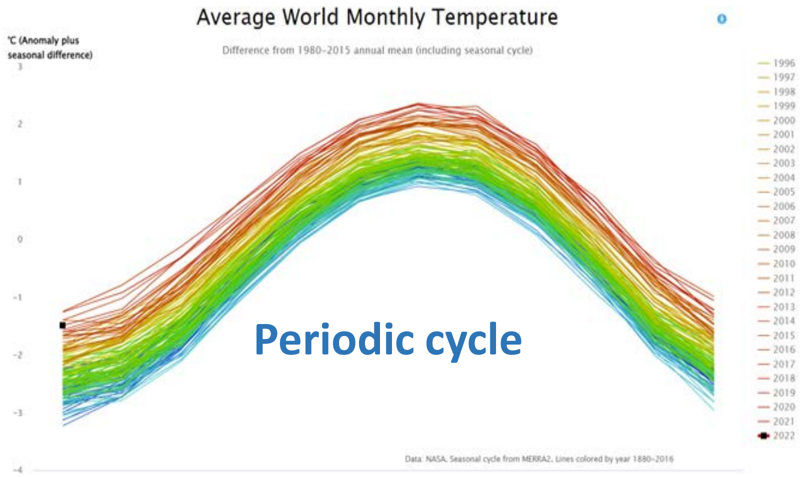
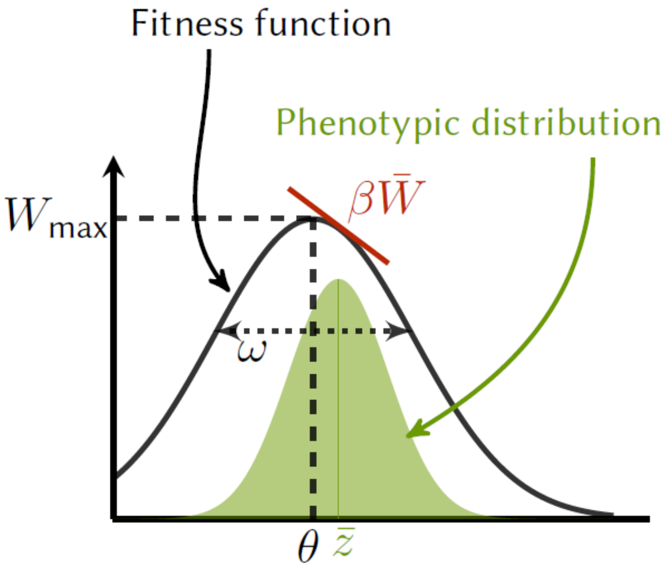


Periodic cycle

Data: NASA. Seasonal cycle from MERRA2. Lines colored by year 1880-2016



Gaussian fitness peak

- Any phenotype-fitness map with an optimum can be approximated as Gaussian (2nd order Taylor series on log sale)

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

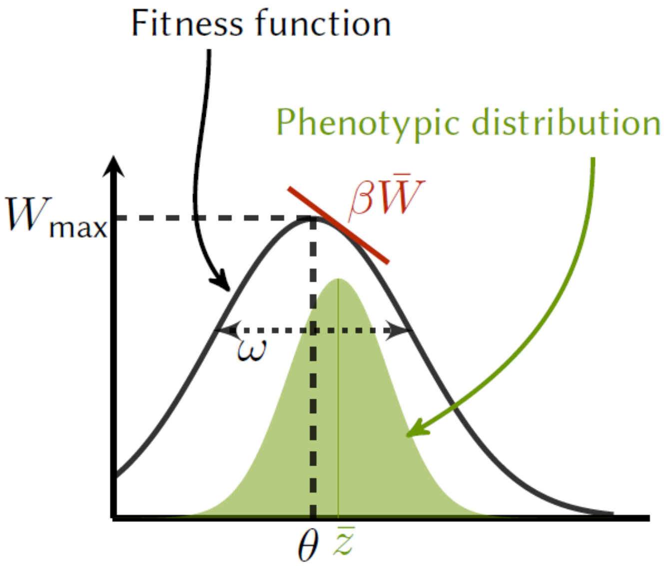
Optimum phenotype θ, width of fitness peak ω

- If trait z is a normally distributed (polygenic+residual variation), then **mean fitness is also Gaussian with respect to mean phenotype**

$$\bar{W} = \int_{-\infty}^{\infty} p(z)W(z)dz \propto \exp\left(-\frac{S(\bar{z}-\theta)^2}{2}\right)$$

$S = \frac{1}{V_s} = \frac{1}{(\omega^2+\sigma_z^2)}$ is the strength of stabilizing selection

Latter (1970 Genetics)



Gaussian fitness peak

- The **mean mismatch with optimum $x = \bar{z} - \theta$** drives evolutionary dynamics

➢ Change in frequency p of a mutation with effect α on the trait in haploid population:

$$\Delta\ln\left(\frac{p}{1-p}\right) = \ln\left(\frac{W(\bar{z}+\alpha)}{W(\bar{z})}\right) = -\frac{S}{2}[(x\ +\alpha)^2 - x^2] = -\frac{S}{2}[\alpha^2 + 2\alpha x]$$

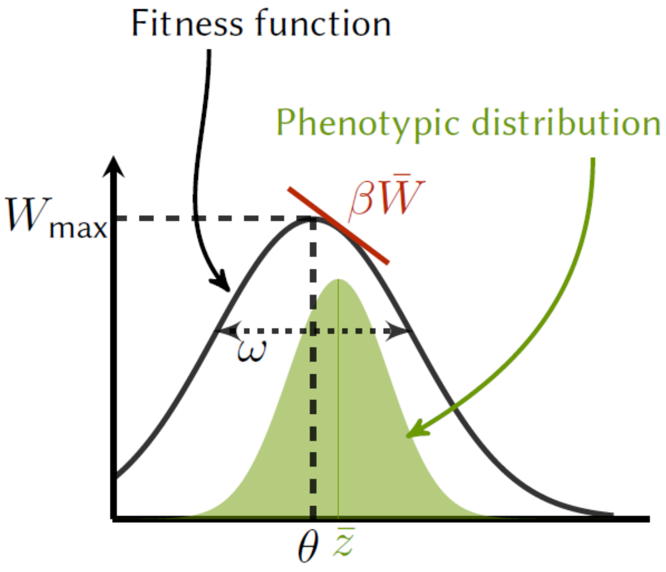
→ **linear in mismatch**.

➢ For a normally distributed trait, directional gradient (selection on mean phenotype) is[1]:

$$\beta = \frac{\partial \ln \bar{W}}{\partial \bar{z}} = -Sx$$

→ **linear in mismatch**

Lande (1976 Evolution)



Gaussian fitness peak

- Response to selection also depends on additive genetic variance:
  $\Delta\bar{z} = G\beta = -GS\boldsymbol{x}$ → Linear restoring force reducing deviations from optimum $\boldsymbol{x}$

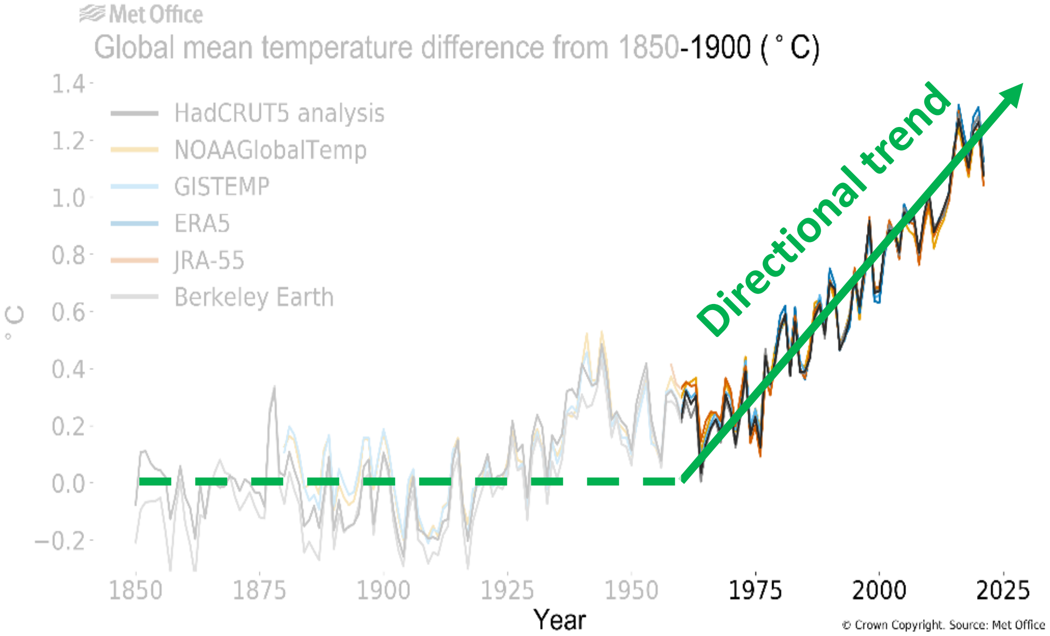
➢ For a given deviation $\boldsymbol{x}$, faster evolution if larger **adaptive potential SG**, i.e. narrow fitness peak x large additive genetic variance.

➢ When genetic variance can be approximated as constant, simple dynamical system allowing analytical progress under relevant types of environmental change.

Lande (1976 Evolution)

Directional environmental change

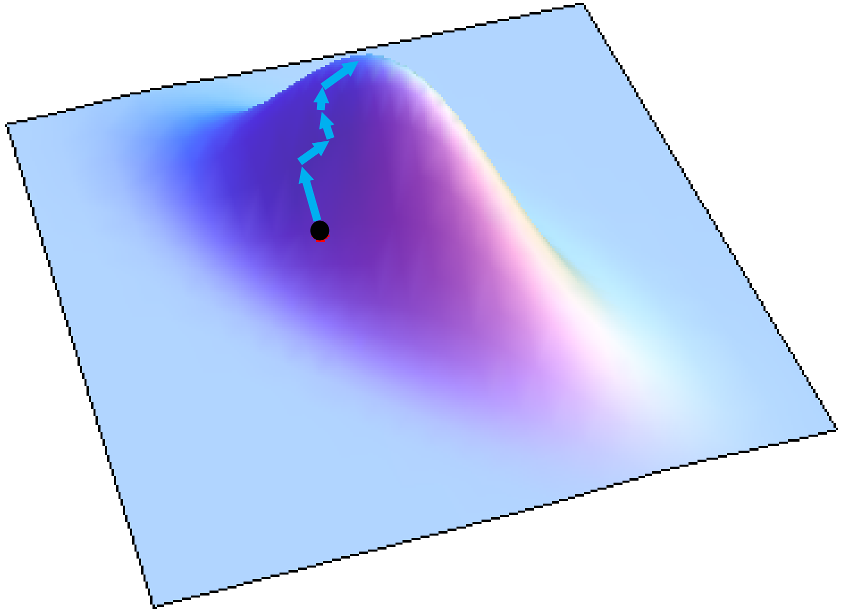
- Abrupt directional change (environmental shift) addressed in previous lectures (in adaptive walk[1] and polygenic[2] regimes)
- More gradual tendencies (e.g. global warming) can be modeled as **steady change at constant speed *v***, preceded by a constant environment



1: Orr (1998 Evolution)
2: Lande (1976), Hayward & Sella (2022)

Directional environmental change

- Low mutation regime (origin-fixation process):
  Adaptive walk by sequential fixation in otherwise monomorphic population.
- Reminder: Under sudden shift, populations start far from optimum
  → large effect mutations can fix in early steps[1]



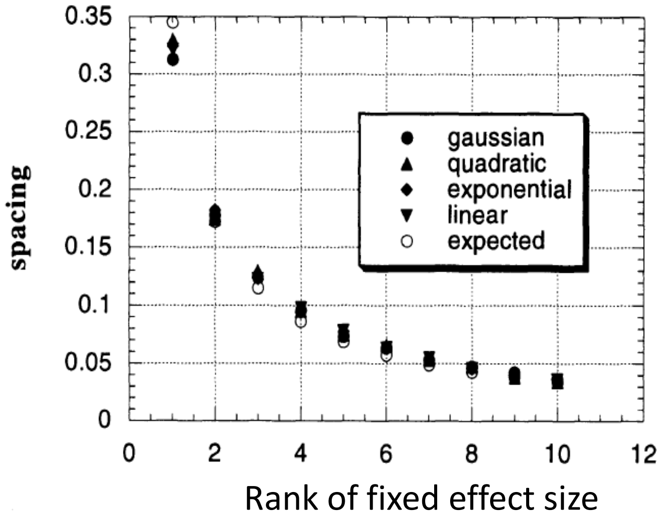
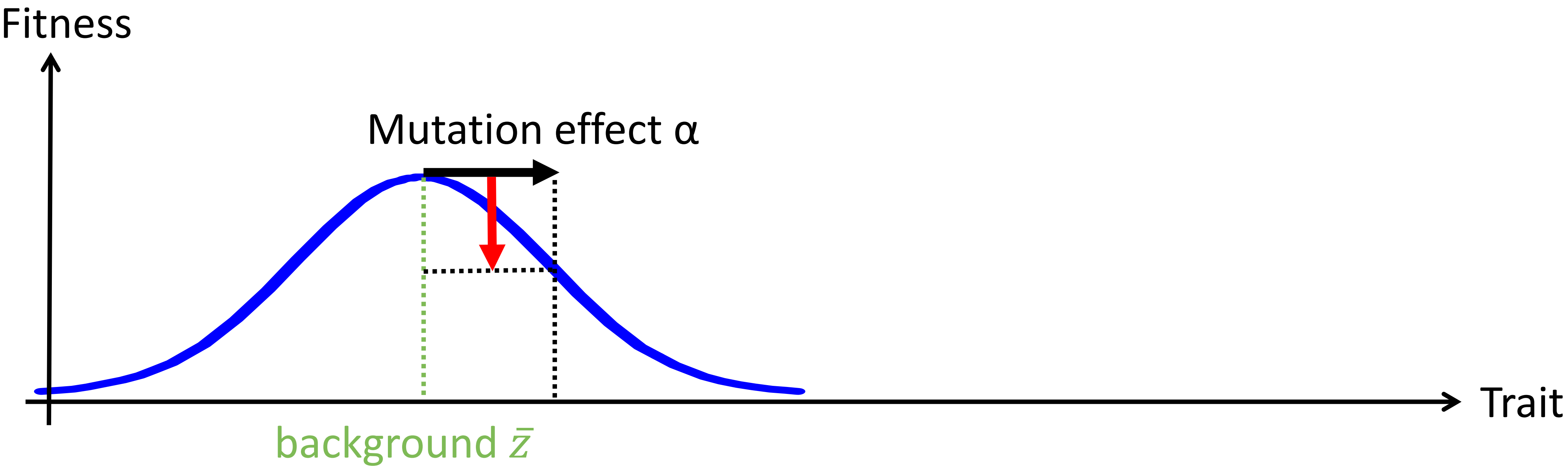


FIG. 8. Spacings between largest and next-to-largest, etc. factors fixed during adaptation.

[1] 1: Orr (1998 Evolution)

Directional environmental change

- Low mutation regime (origin-fixation process):
  Adaptive walk by sequential fixation in otherwise monomorphic population.
- Under **gradual trend**, **selection coefficients change as optimum moves**
  → A mutation first needs to **become beneficial**



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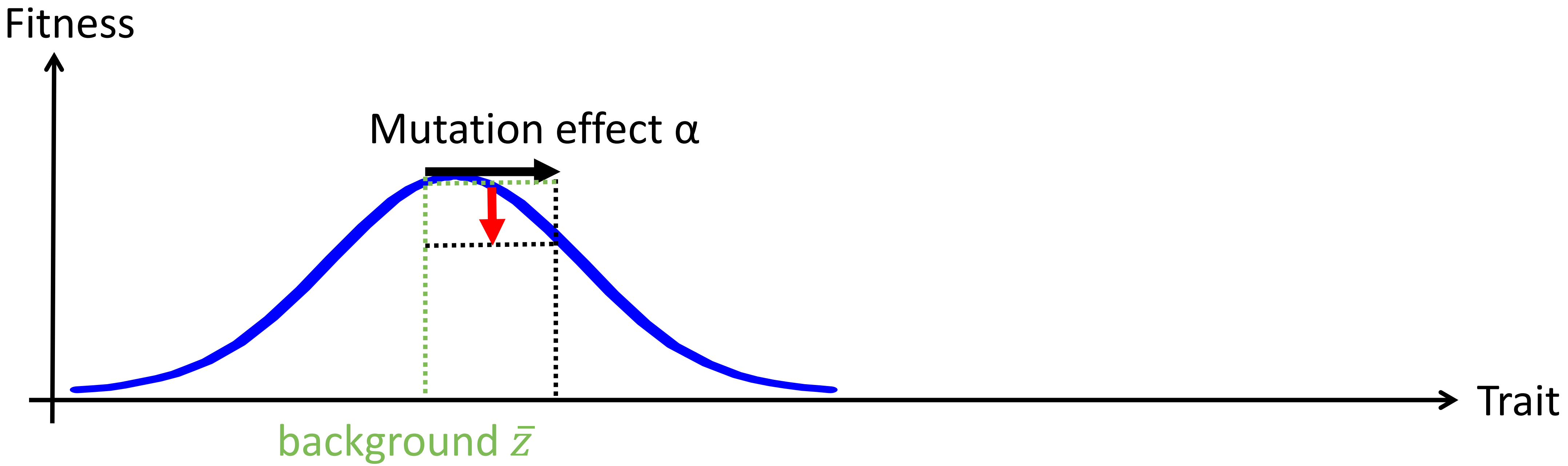

Directional environmental change

- Low mutation regime (origin-fixation process):
  Adaptive walk by sequential fixation in otherwise monomorphic population.
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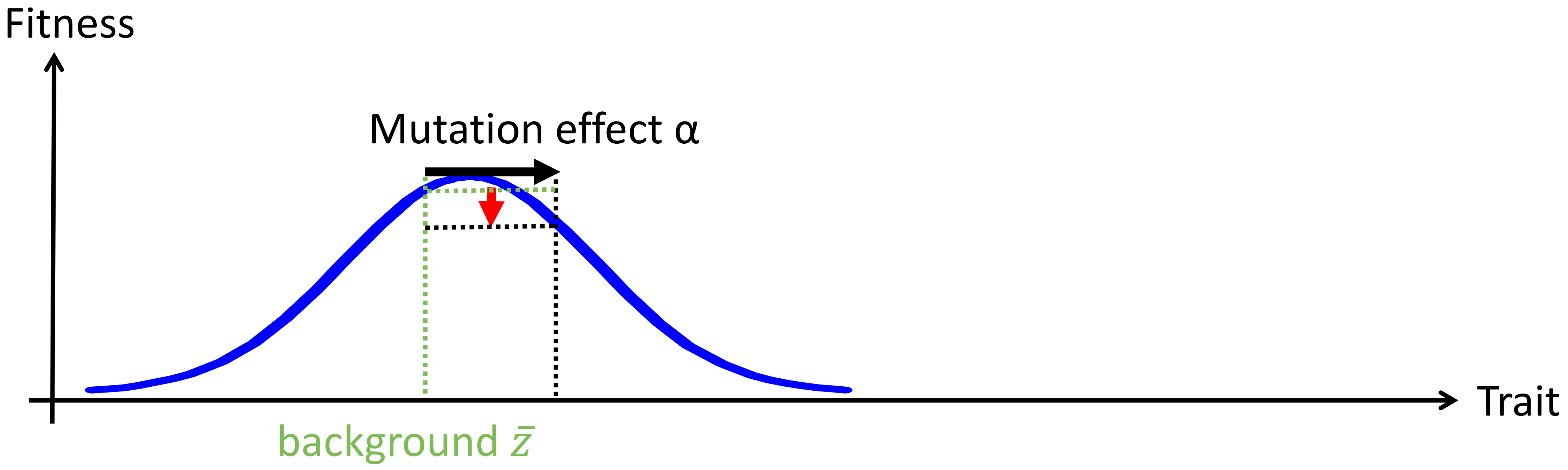

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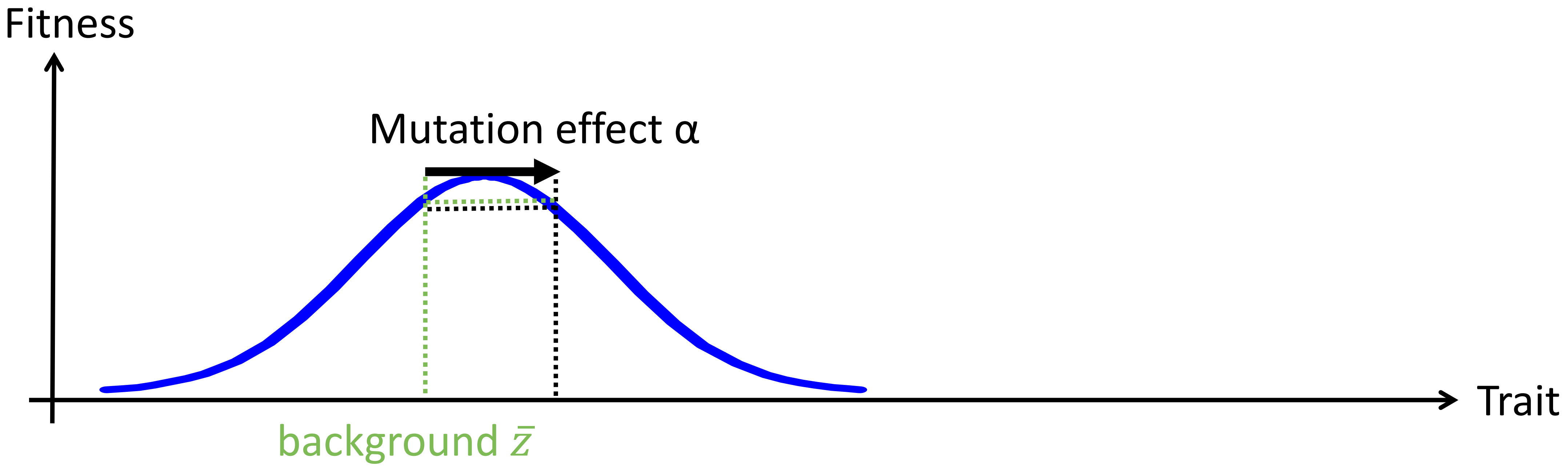

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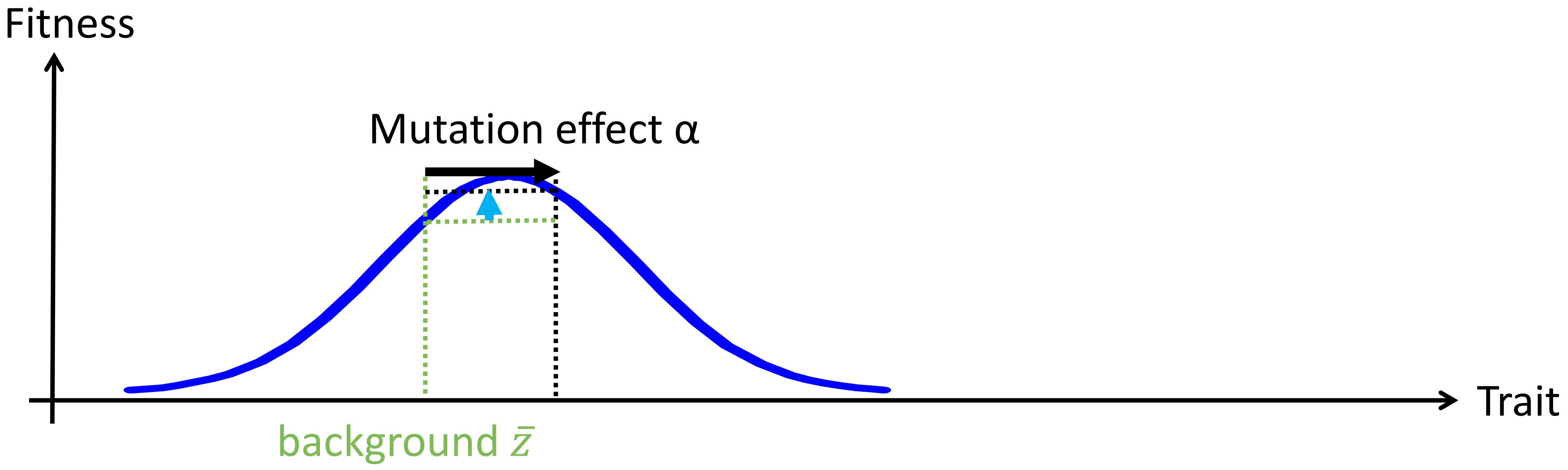

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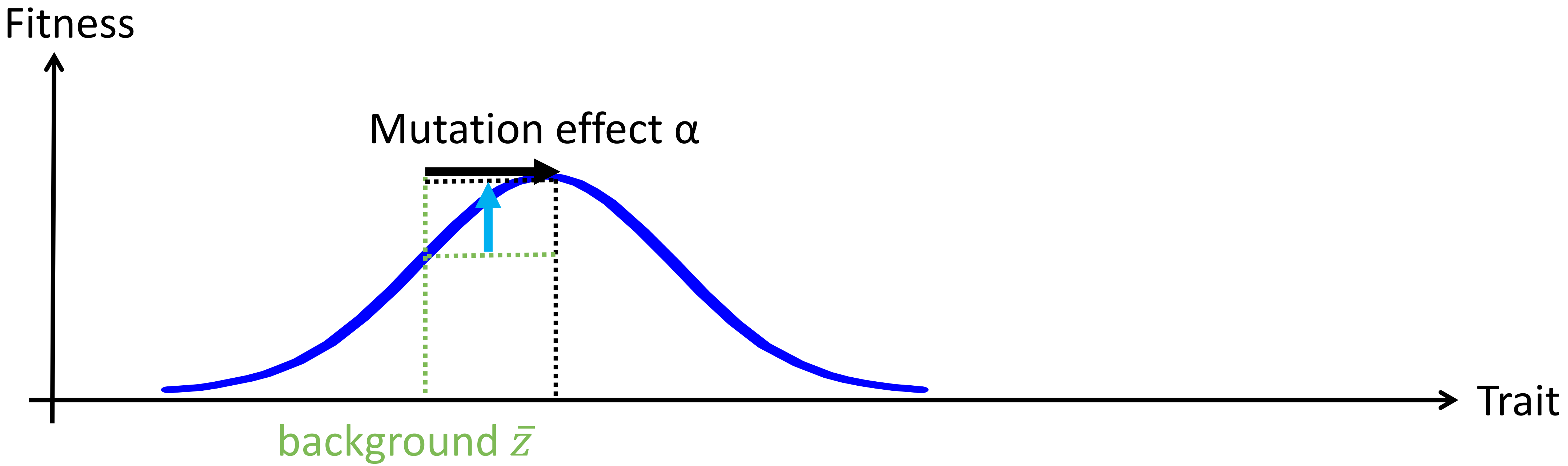

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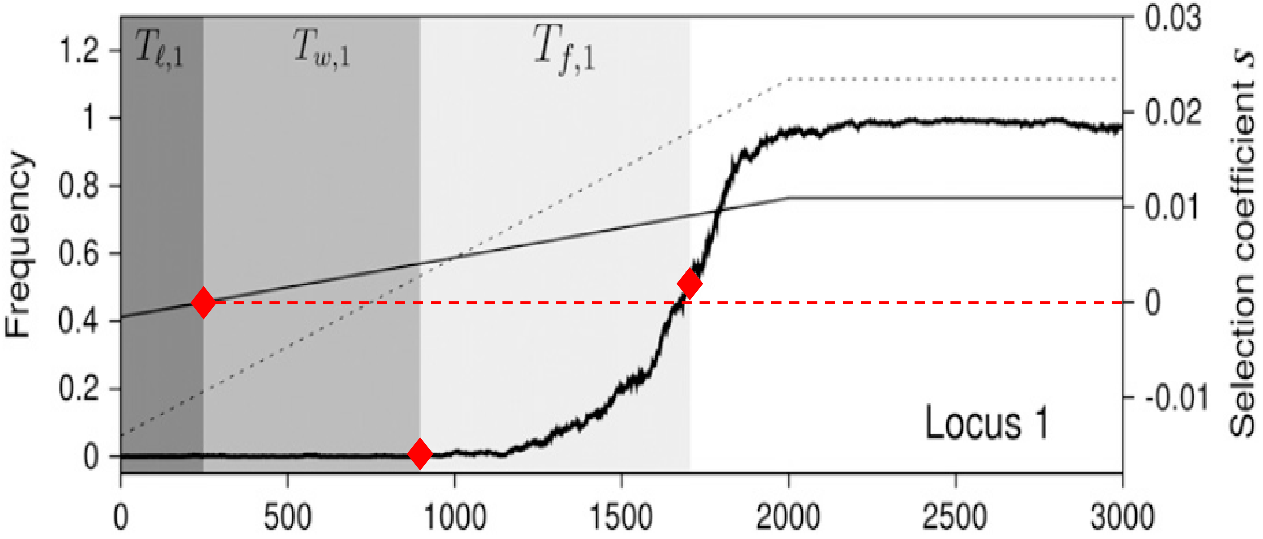

1: Kopp & Hermisson (2007, 2009a,b Genetics)

Directional environmental change

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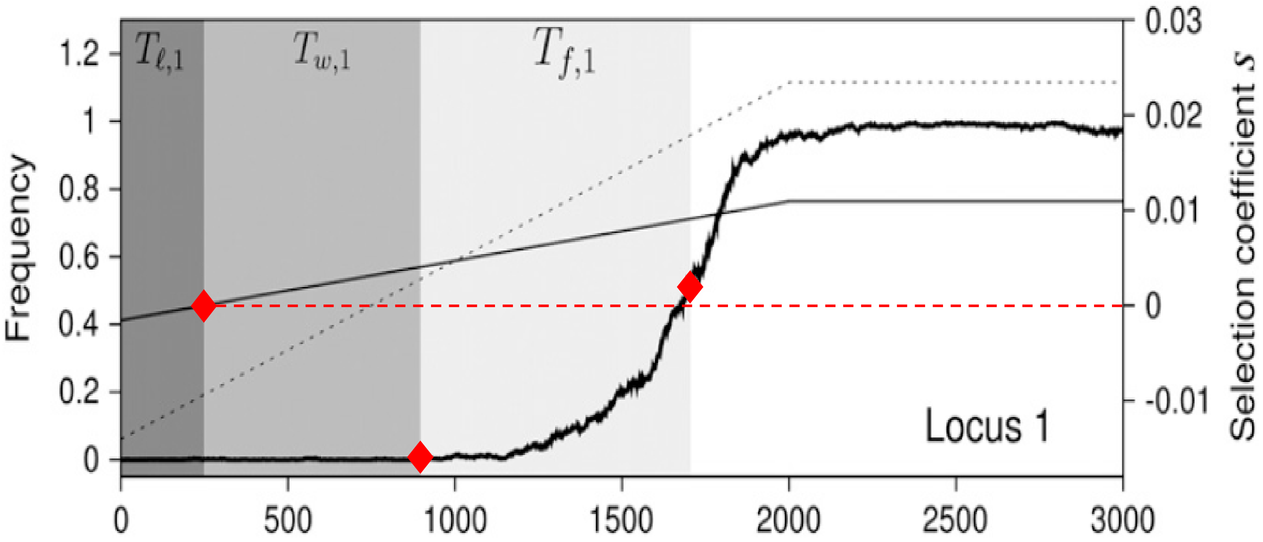
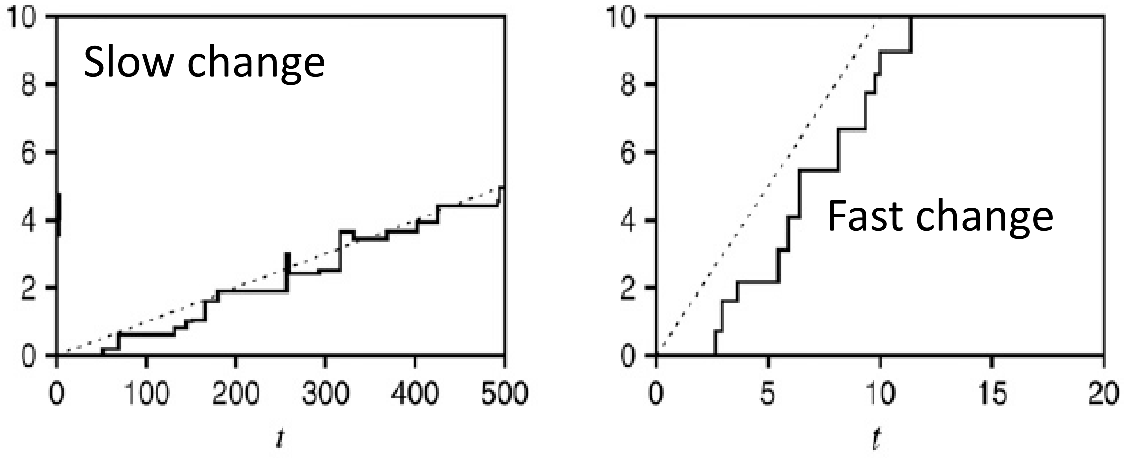
  then **escape drift** (T_w), then **reach high frequency** (T_f)[1].
- Slower environmental changes are dominated by T_ℓ, **favoring small steps because they become beneficial earlier**





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Directional environmental change

- Low mutation regime (origin-fixation process):
  Adaptive walk by sequential fixation in otherwise monomorphic population.
- Under **gradual trend**, **selection coefficients change as optimum moves**
- A **single composite parameter** determines the genetics of adaptation[1]:

$$\gamma = \frac{v}{NUS\sigma_\alpha^3}$$

v: Speed of environmental change } Ecology

N: population size
U: genomic mutation rate
S: Strength of stabilizing selection
σ_α : SD of mutation phenotypic effects } Adaptive potential

➢ **Large γ**: Environment changes fast relative the adaptive potential.
Adaptation is **genetically limited**, mutations of large effects can fix (cf Orr 1998)

➢ **Small γ**: Environment changes slowly relative the adaptive potential.
Adaptation is **environmentally limited**, mutations of small effects mostly fix

---

[1] Kopp & Hermisson (2007, 2009a,b Genetics)

Directional environmental change

- <u>Highly polymorphic regime:</u>
- Distance to optimum $x = \bar{z} - \theta$ initially increases as phenotype lags behind optimum.
- This increases the strength of directional selection and response.

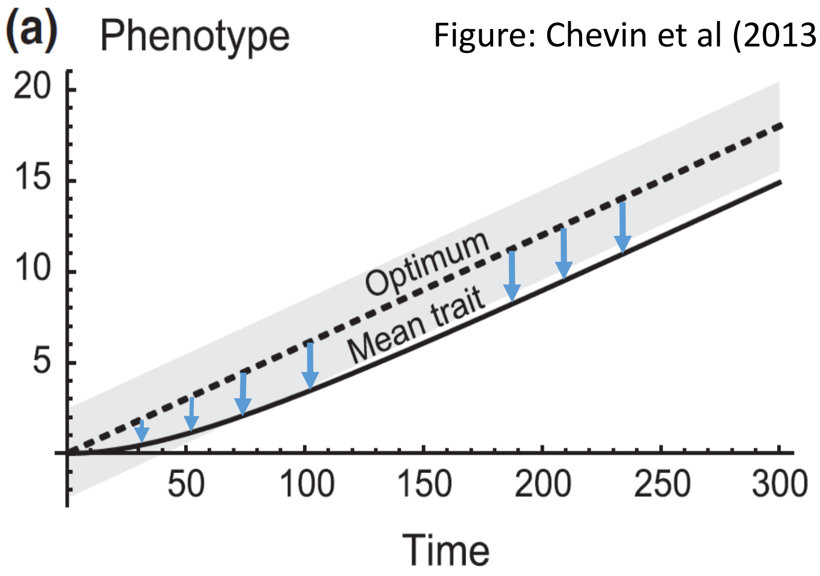
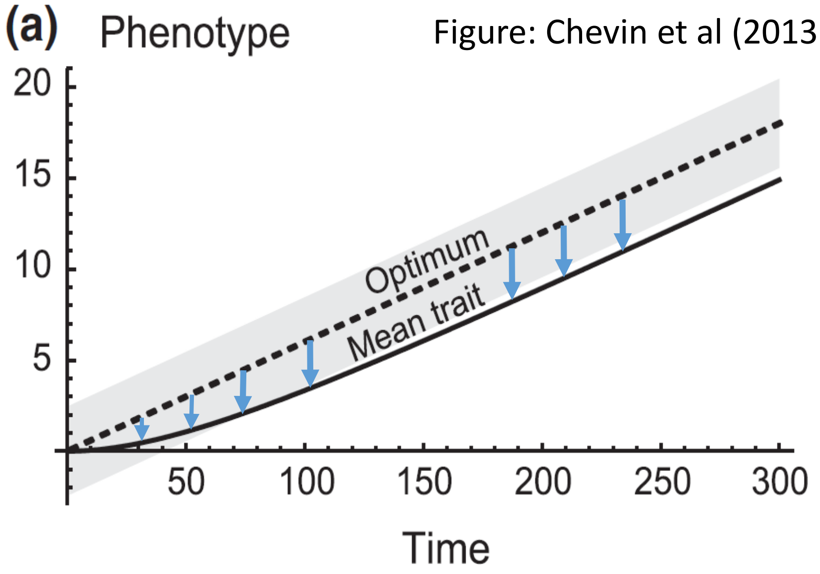


Figure: Chevin et al (2013)

1: Pease et al 1989; Lynch et al 1991; Lynch & Lande 1993

Directional environmental change

- <u>Highly polymorphic regime:</u>
- Distance to optimum $x = \bar{z} - \theta$ initially increases as phenotype lags behind optimum.
- This increases the strength of directional selection and response.
- Lag eventually equilibrates, with mean phenotype evolving at same speed as optimum: $\Delta\bar{z} = -GSx_{\mathrm{eq}} = v$
- Equilibrium lag is thus $x_{\mathrm{eq}} = -\frac{v}{SG}$ → larger with fast environmental change and low adaptive potential



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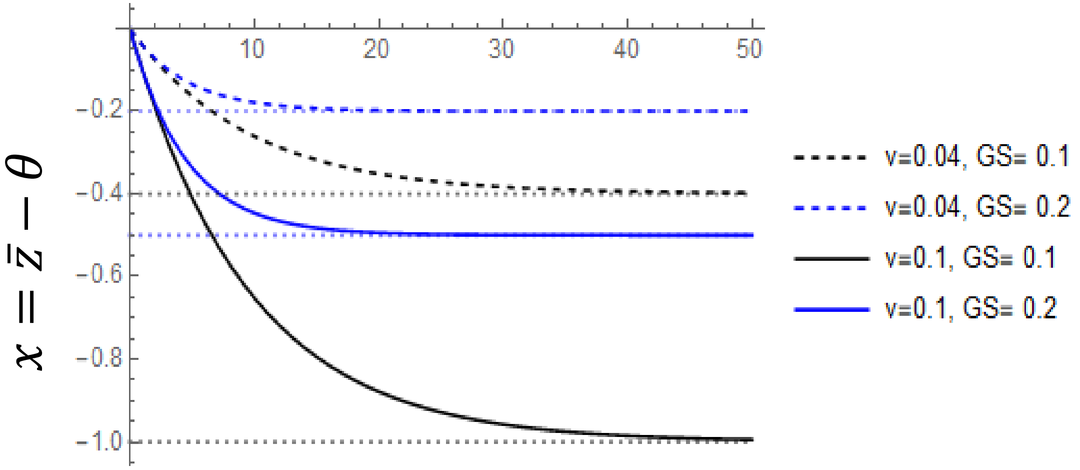

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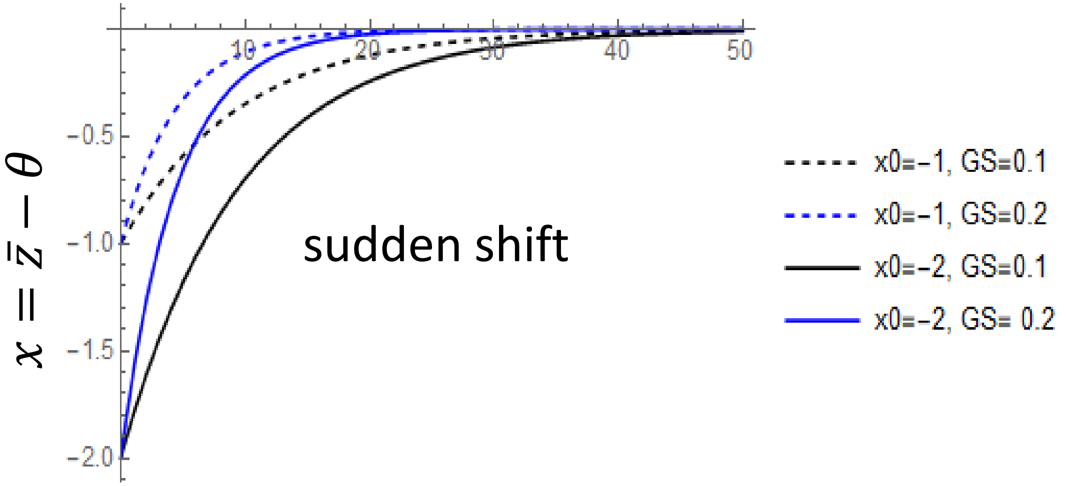
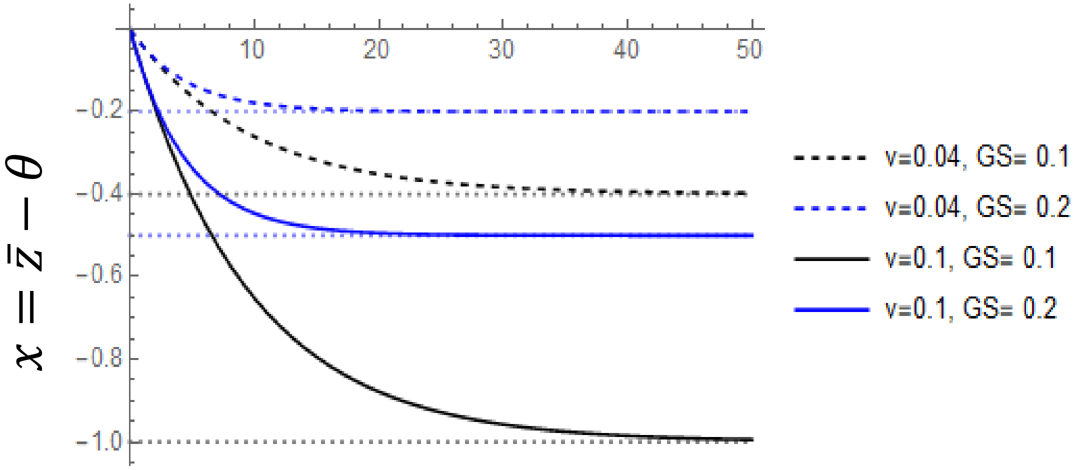
  → larger with fast environmental change and low adaptive potential
- Reciprocal dynamics to sudden shift





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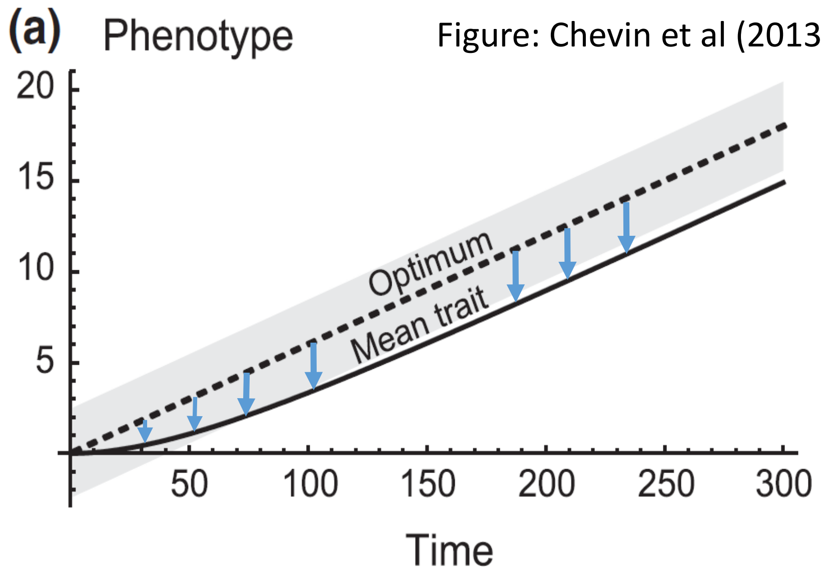
- Analog to adaptive walk regime: $\gamma = \frac{v}{NUS\sigma_\alpha^3}$



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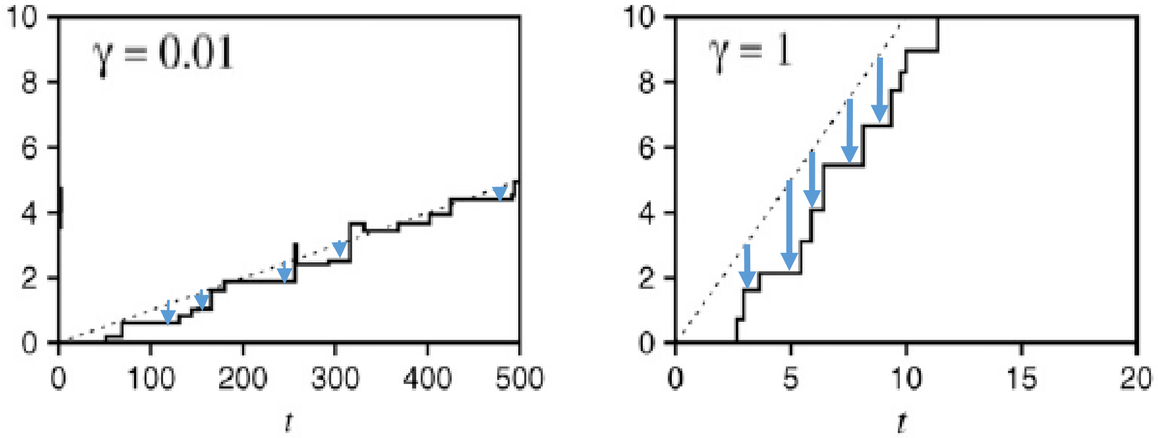


1: Pease et al 1989; Lynch et al 1991; Lynch & Lande 1993

Directional environmental change

- <u>Highly polymorphic regime:</u>
- Maximum reduction in population growth rate caused by maladaptation:

  Lag load $L = \frac{S}{2} x_{\mathrm{eq}}^2 = \frac{v^2}{2SG^2}$
- The **critical rate of environmental change** at which $r_{max} - L = 0$ is $v_c = \sqrt{2 r_{max} S G}$
- Narrower fitness peak (larger S) causes larger fitness drop for a given mismatch x, but also faster evolutionary reduction of x. The latter dominates, increasing v_c.
- But may be violated with other fitness function[2]

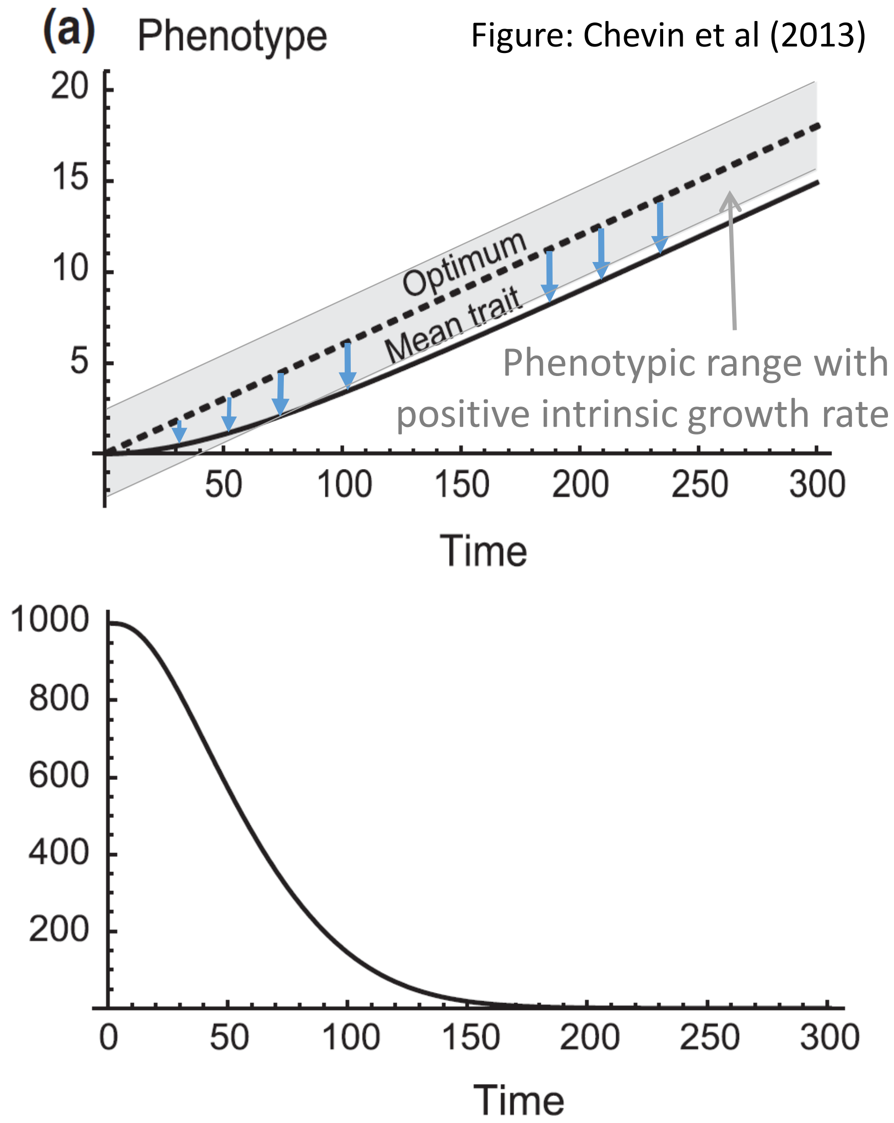


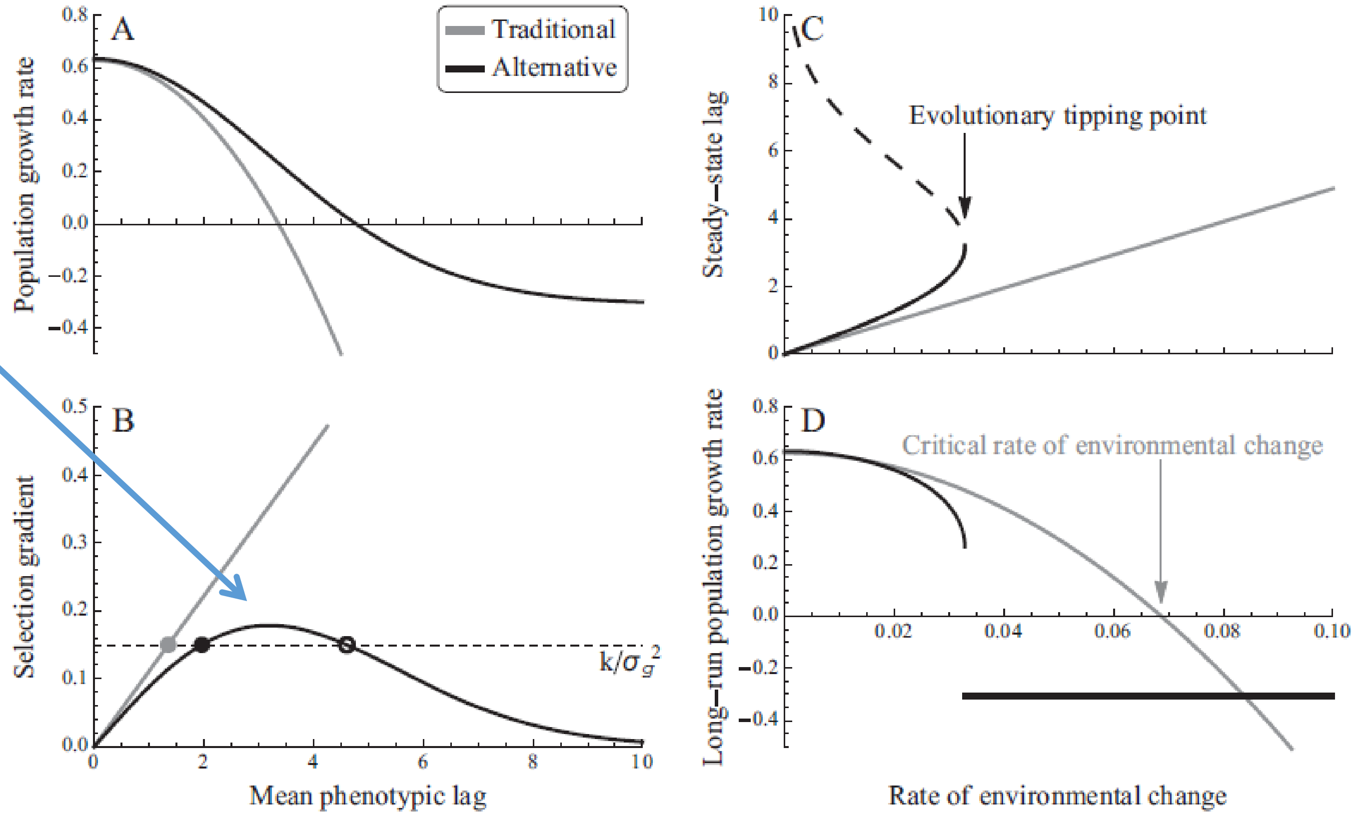
Figure: Chevin et al (2013)

1: Pease et al 1989; Lynch et al 1991; Lynch & Lande 1993

2: Osmond et al (2017); Klausmeier et al (2020)

Directional environmental change

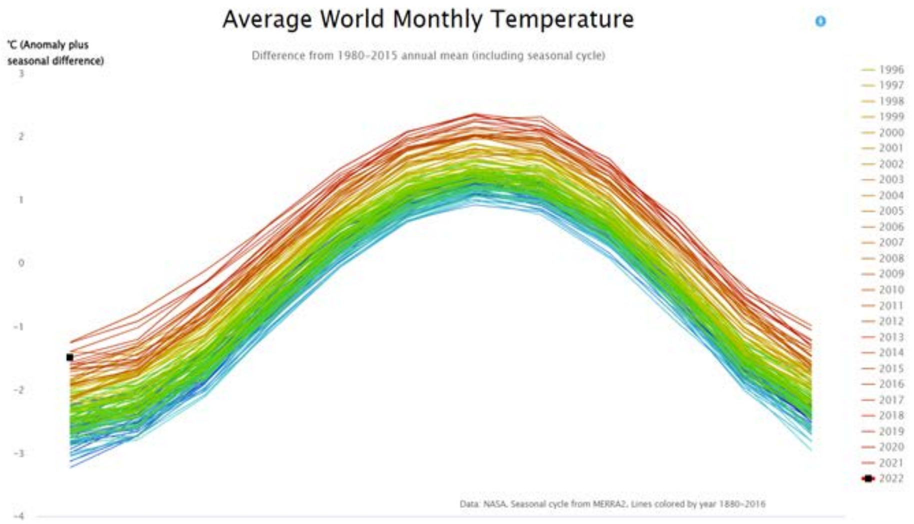
- Fitness function where strength of selection β does not increase monotonically with maladaptation
- Maximum selection gradient = **Tipping point** for rate of evolution
- Larger lags lead to ever-increasing maladaptation: Extinction vortex
- Even transient increase in lag may be impossible to recover from: hysteresis



Osmond et al (2017); Klausmeier et al (2020)

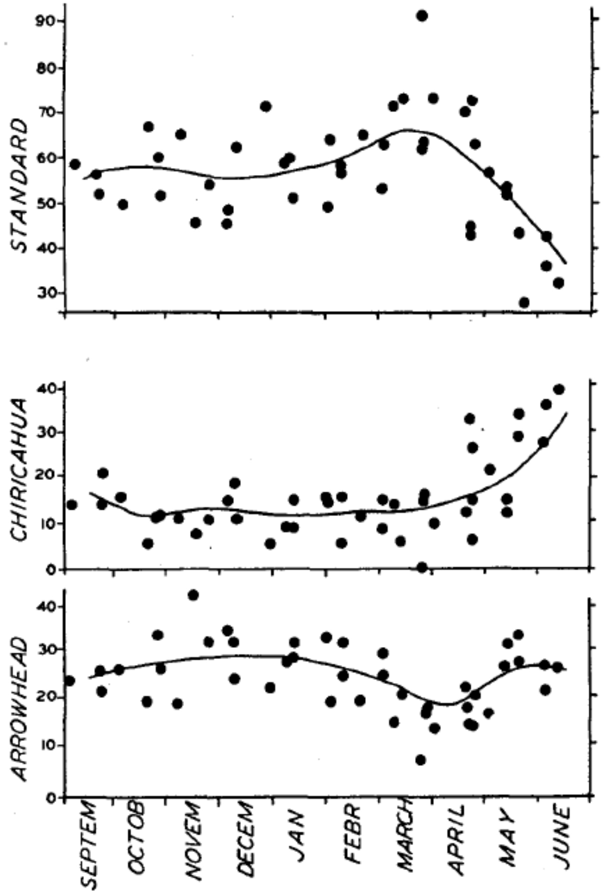
Cycling environment

- Seasonality occurs on evolutionary timescales for short lived species.
- Such organisms usually have large population sizes, thus high adaptive potential.
- Other cycles occur with larger periods (El Niño, North Atlantic oscillation…), and could be tracked by more long-lived organisms

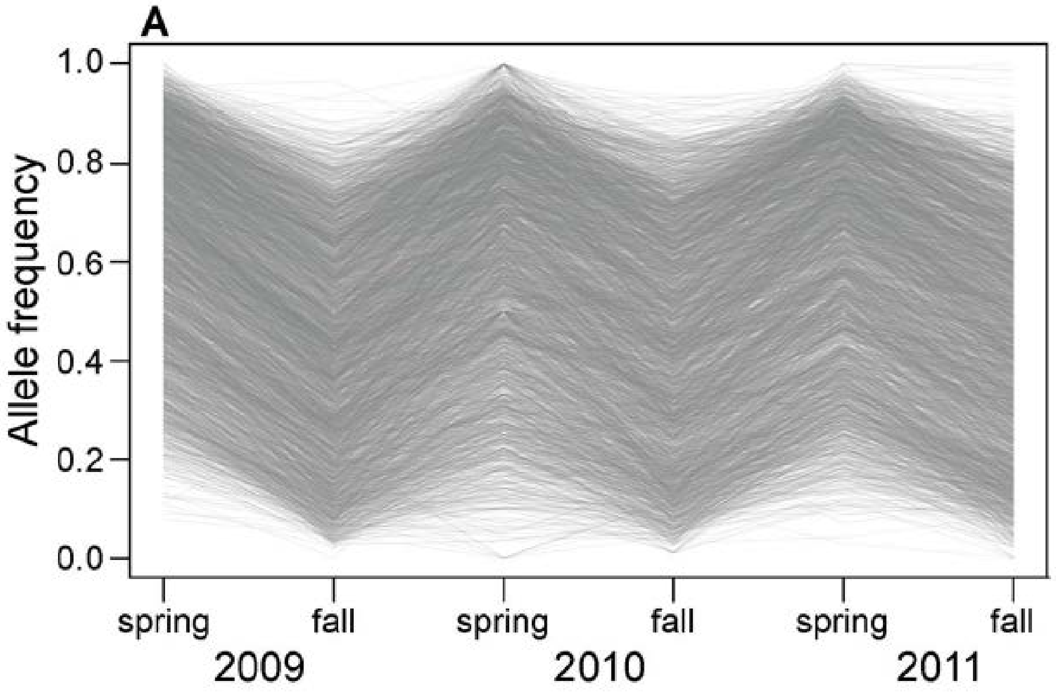


Cycling environment

Chromosomal inversions *in Drososophila*
(Dobzhanksy 1943 Genetics)



1750 SNPs throughout genome
(Bergland et al 2017 PLoS Genetics)

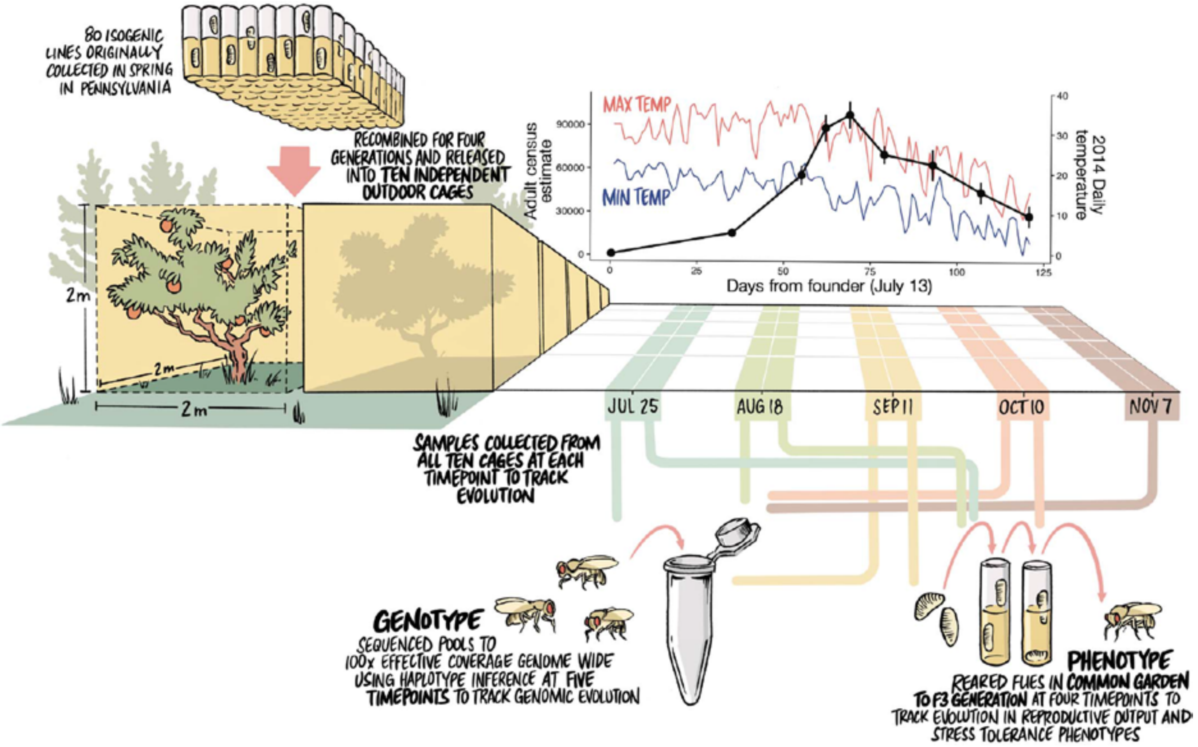


Cycling environment

Direct observation of adaptive tracking on ecological time scales in *Drosophila*

Science **375**, 1246 (2022)

Seth M. Rudman[1,2]*†, Sharon I. Greenblum[3,4]*†, Subhash Rajpurohit[1,5]†, Nicolas J. Betancourt[1], Jinjoo Hanna[1], Susanne Tilk[3], Tuya Yokoyama[3], Dmitri A. Petrov[3], Paul Schmidt[1]*



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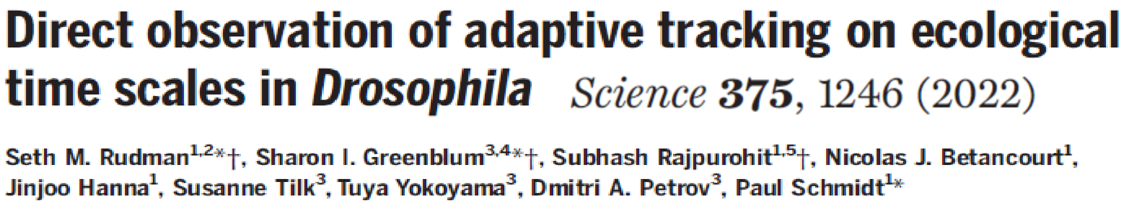

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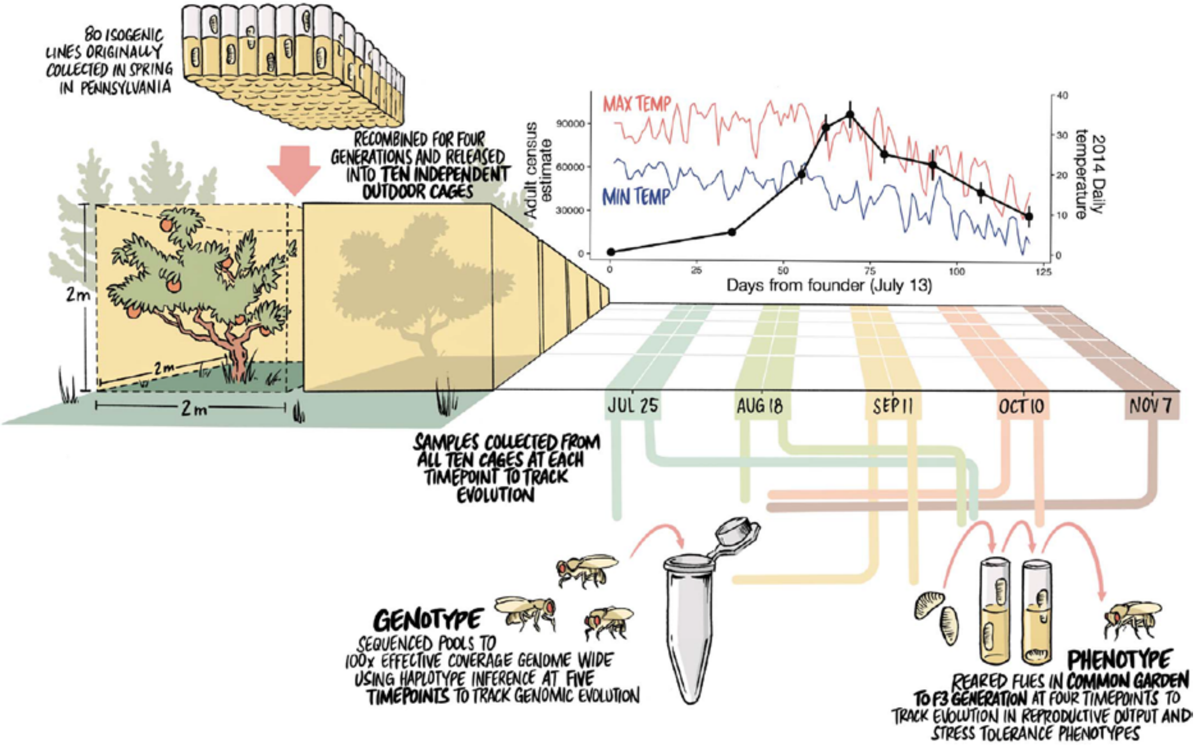
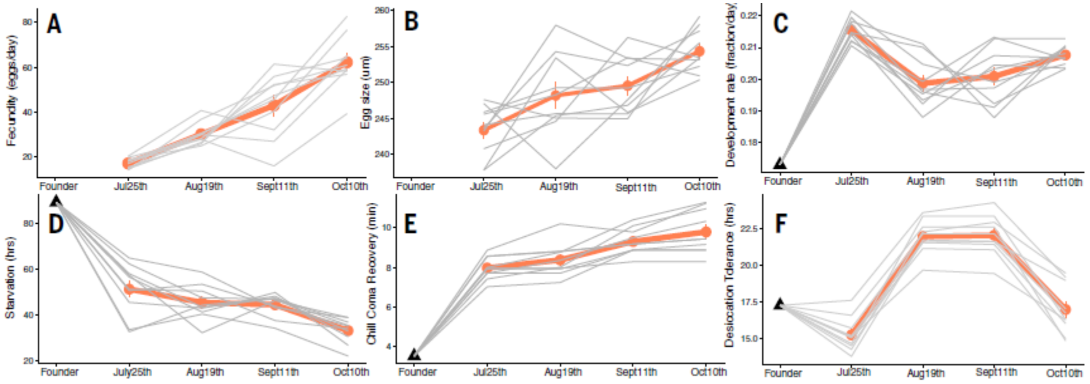
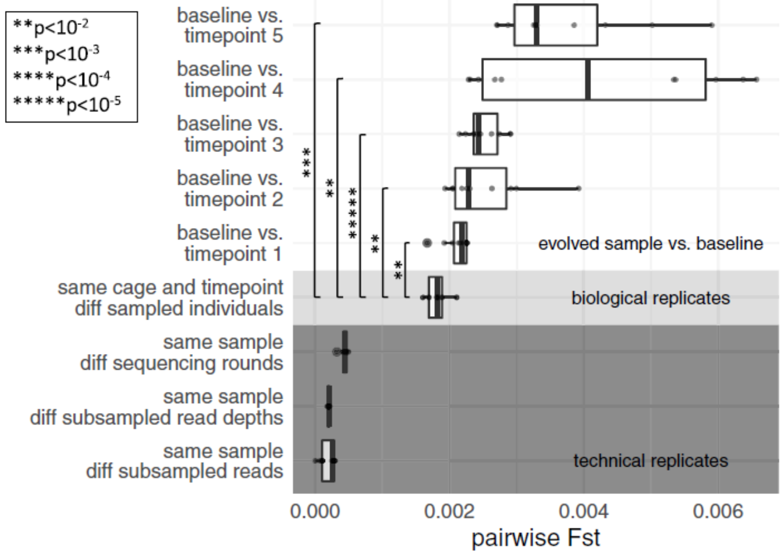


Parallel phenotypic changes



Largely repetable genetic differentiation over time



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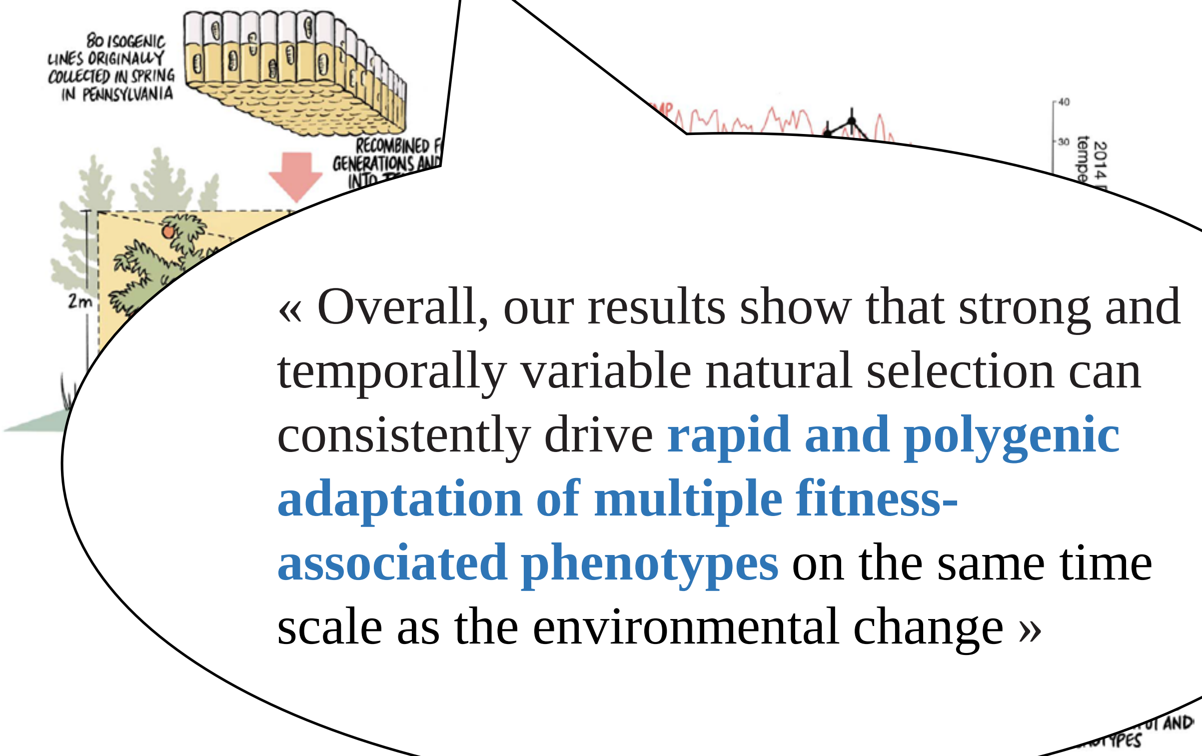
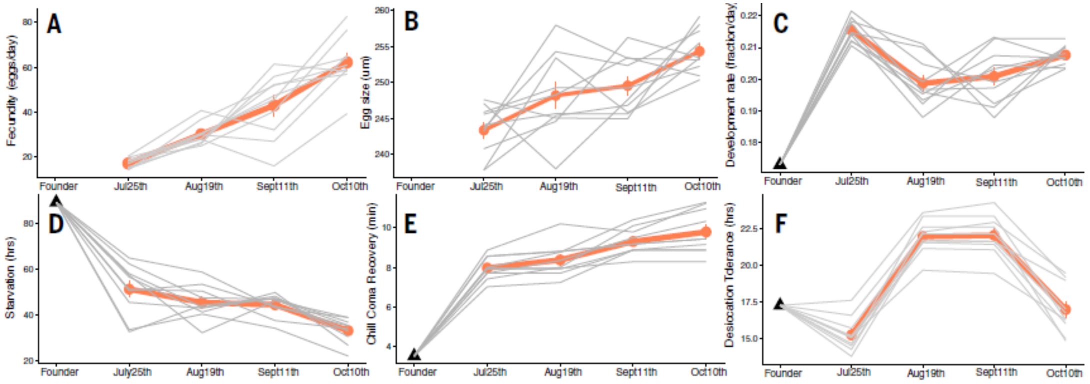


« Overall, our results show that strong and temporally variable natural selection can consistently drive **rapid and polygenic adaptation of multiple fitness-associated phenotypes** on the same time scale as the environmental change »

Parallel phenotypic changes



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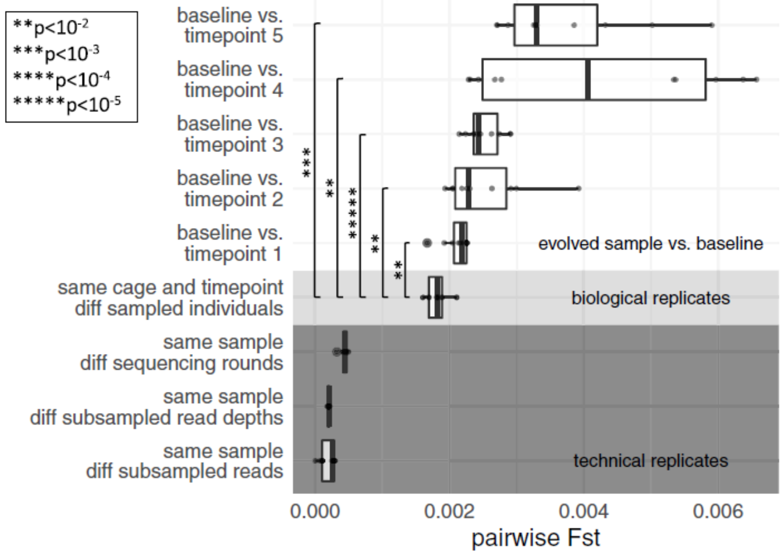


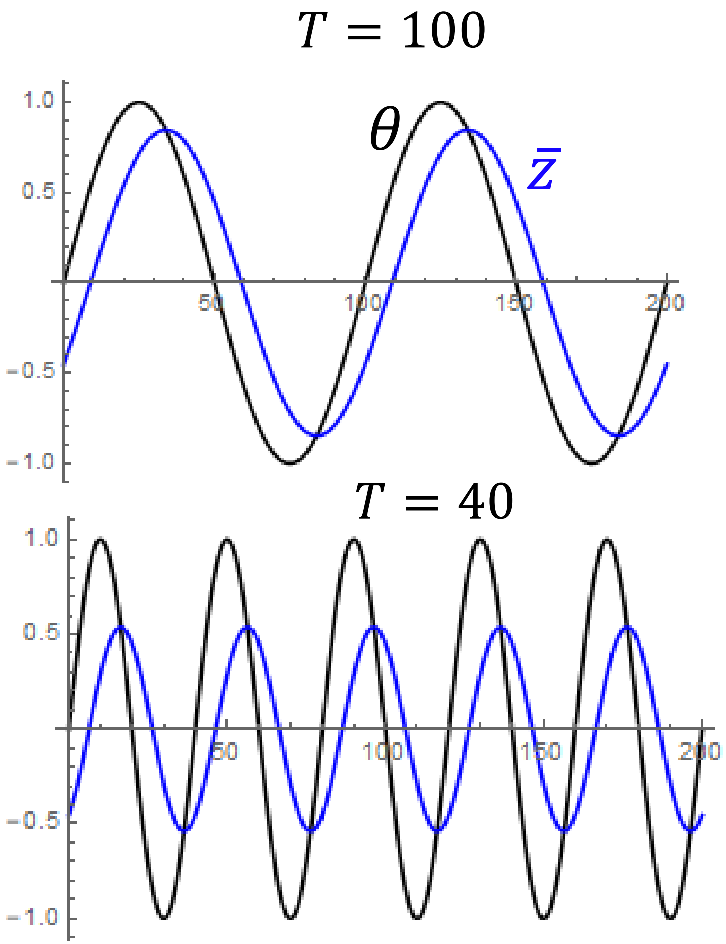
Cycling environment

- **Model**[1]: $\theta = A\sin\left(\frac{2\pi t}{T}\right)$, amplitude A and period T
- **Polygenic trait** with constant G
- After $\sim\frac{1}{SG}$ generations, mean phenotype settles into sine wave with same period as optimum, but:

 - amplitude multiplied by $\zeta = \frac{SGT}{\sqrt{(SGT)^2+(2\pi)^2}} \leq 1$

- phase shifted (delayed) by $\varphi = -\mathrm{arcTan}\left(\frac{2\pi}{SGT}\right)$

- **Higher adaptive potential SG** and **slower oscillations** (larger T) lead to closer adaptive tracking of optimum ($\zeta \to 1$ and $\varphi \to 0$)



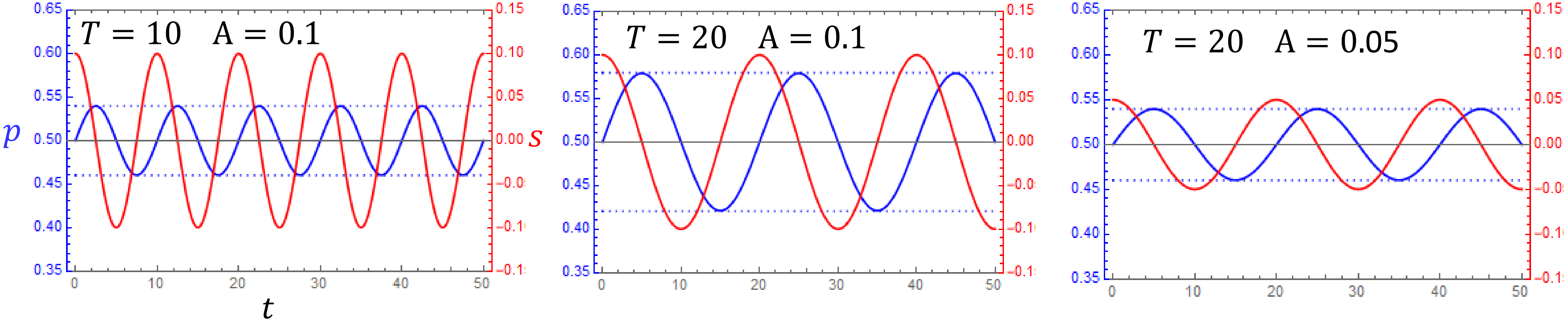
Lynch et al 1991; Lande & Shannon 1996

Cycling environment

- **Single locus** with selection coefficient $s = A \sin\left(\frac{2\pi t}{T}\right)$

➢ Quarter-period lag between frequency p and s ($\max(p)$ when $s = 0$)

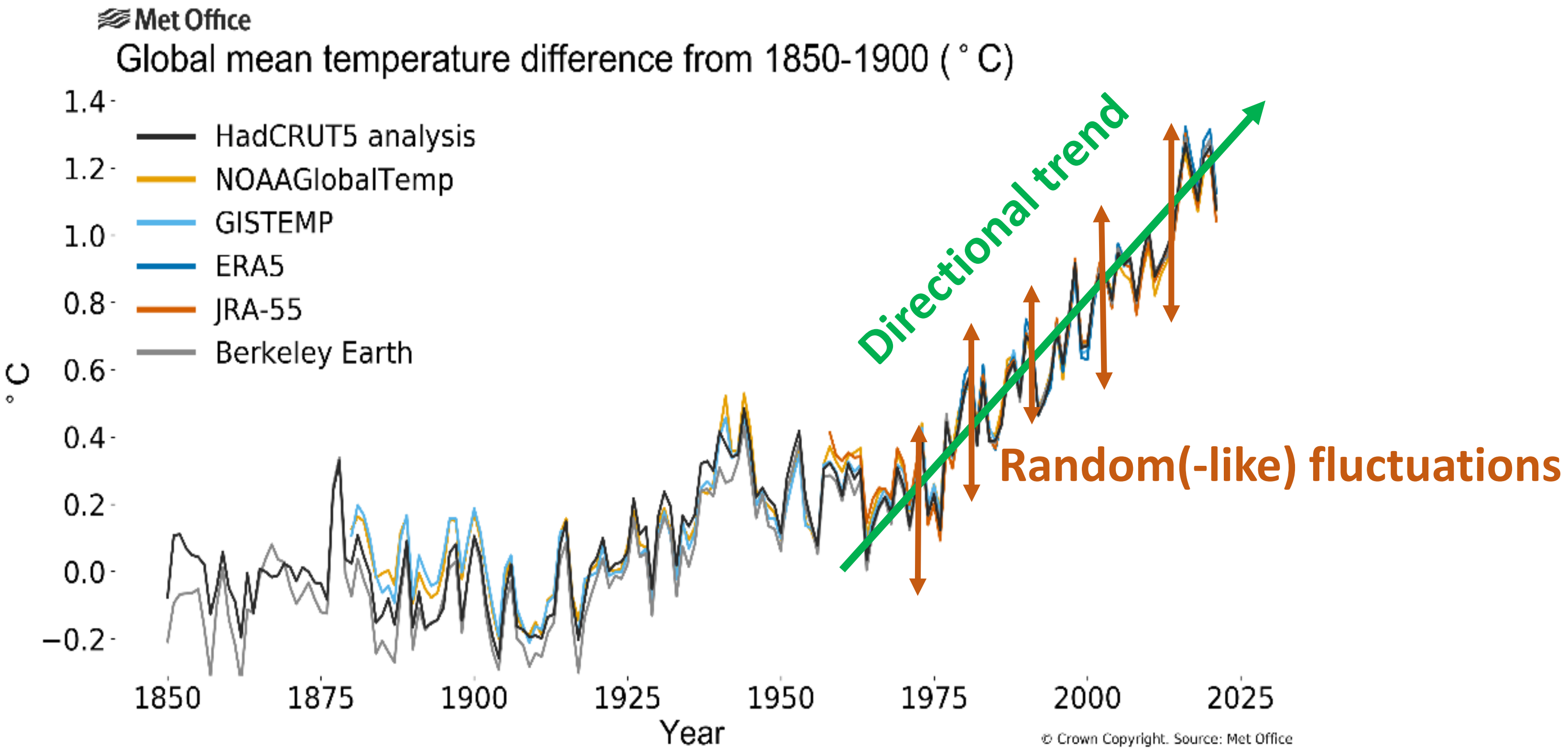
➢ Amplitude of p is $A_p \approx A\frac{T}{8\pi}$ → larger under larger period and maximum s



Adapted from Chevin et al (2022)

Randomly fluctuating environment

- Most environments exhibit residual noise, after removing any trend



Randomly fluctuating environment

- Most environments exhibit residual noise, after removing any trend

- These fluctuations may well have deterministic causes, but if the latter are

    (i) unknown

    (ii) external to the system (and potentially complex)

    (iii) beyond reach of measurement precision,

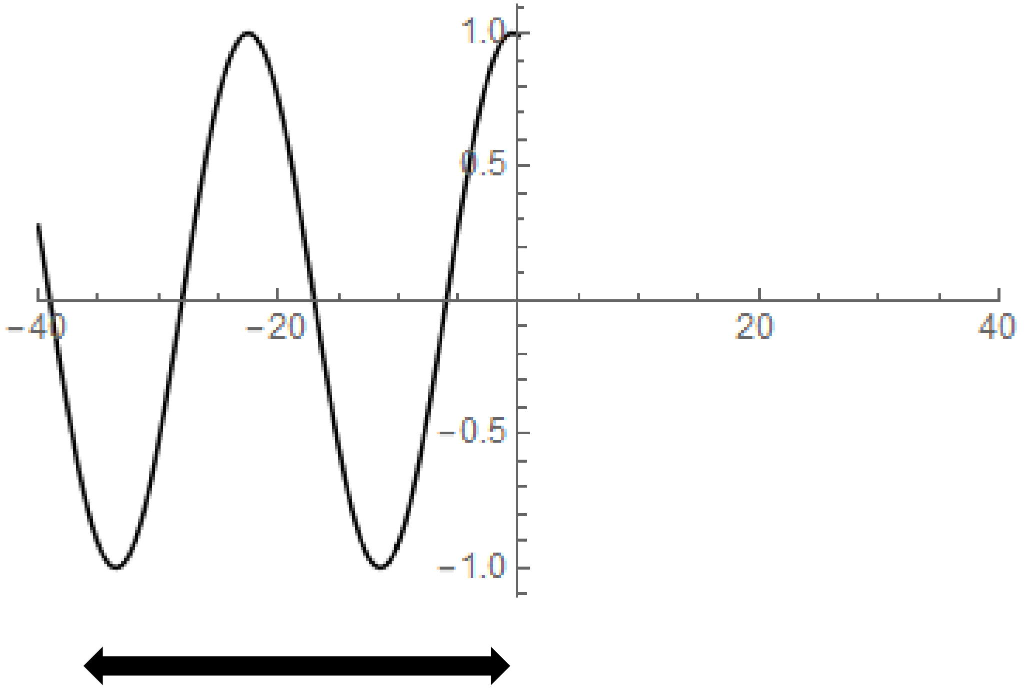
then fluctuations are **effectively random**, both to scientists analyzing them and to organisms experiencing them.

→ Treated as **stochastic processes** = random variable with time dependence

Prediction in stochastic environment

- **Randomness matters when making predictions**

Deterministic time series:



Measured

Prediction in stochastic environment

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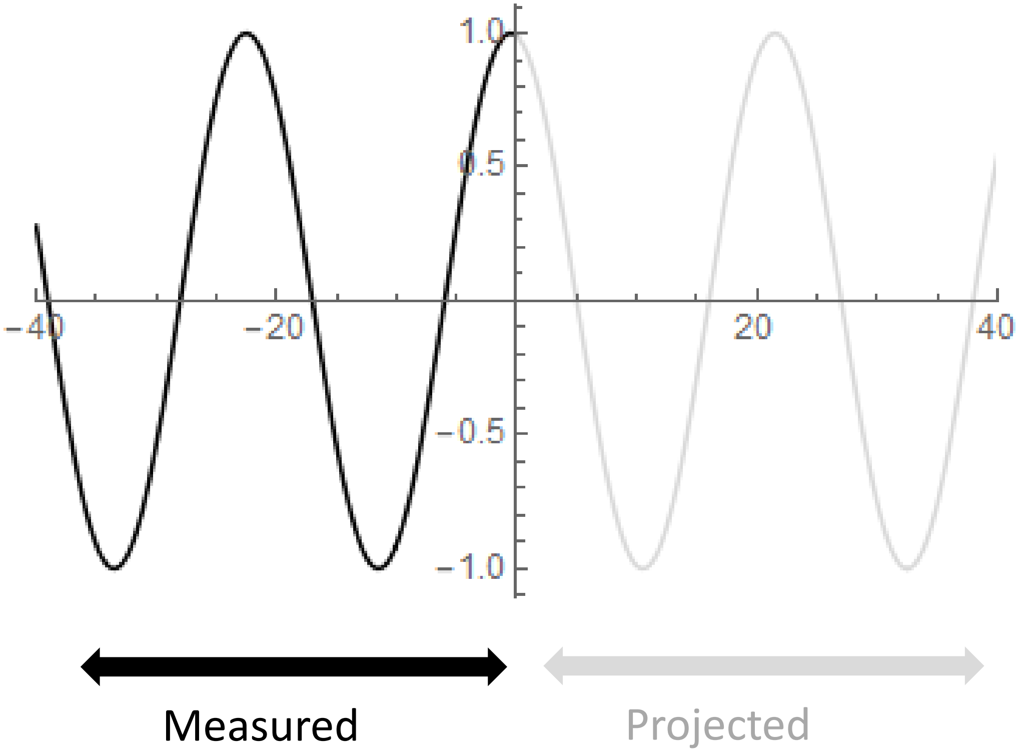
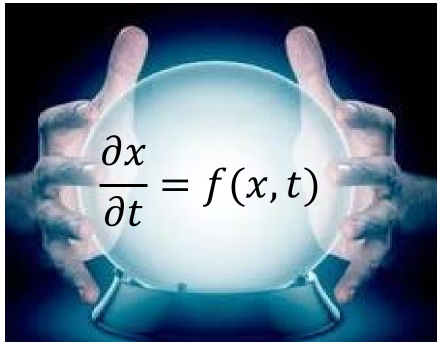


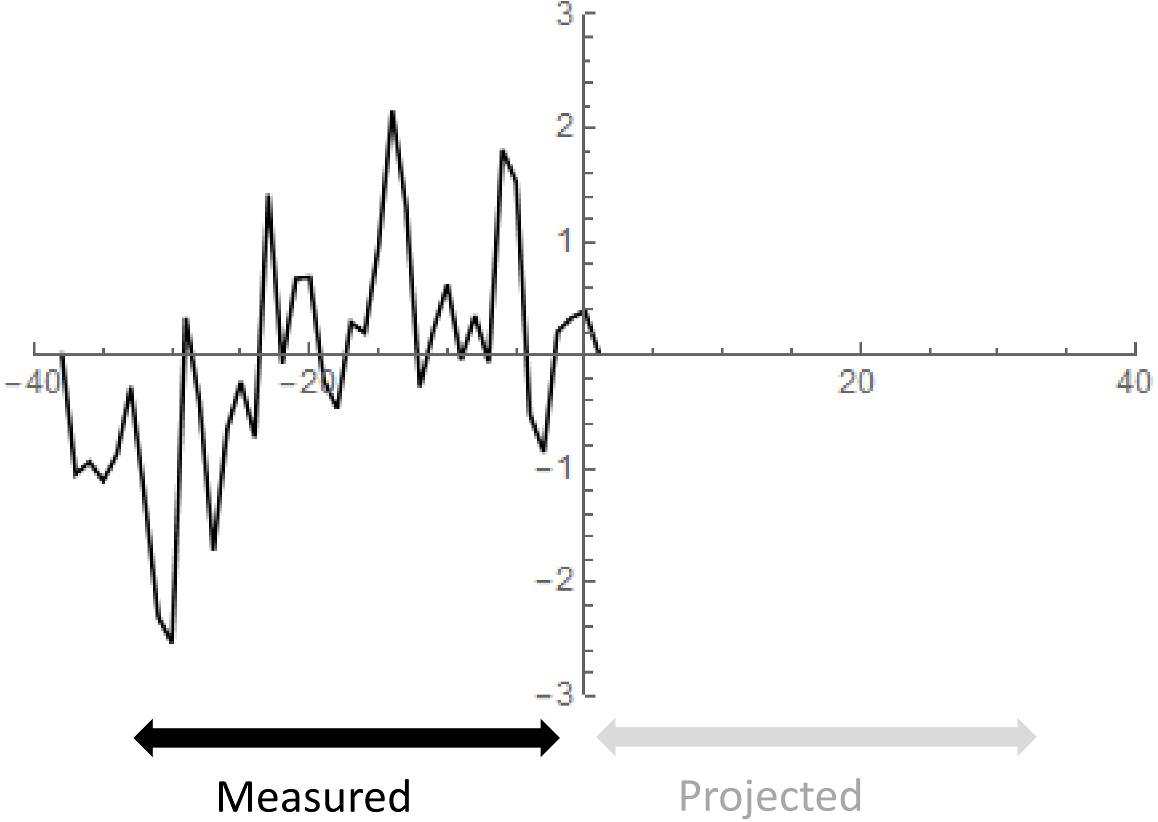


The future is certain provided accurate measurement of the past, and perfect knowledge of causal factors.

Prediction in stochastic environment

- **Randomness matters when making predictions**

Stochastic time series:



Prediction in stochastic environment

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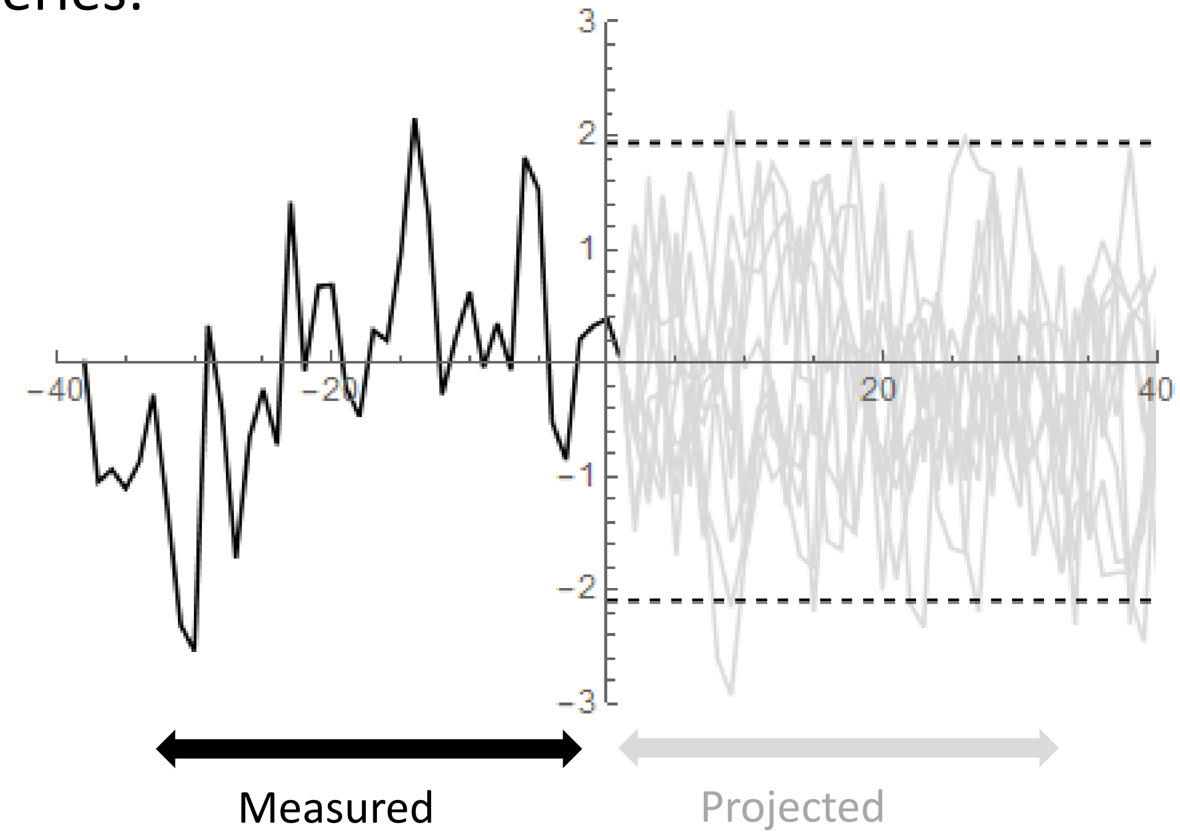
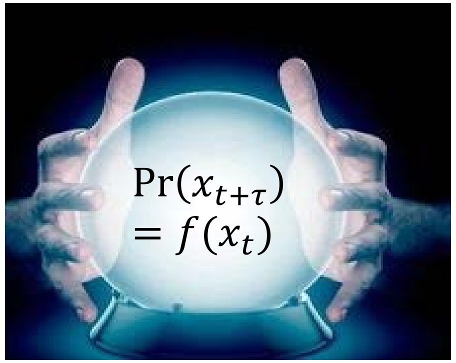


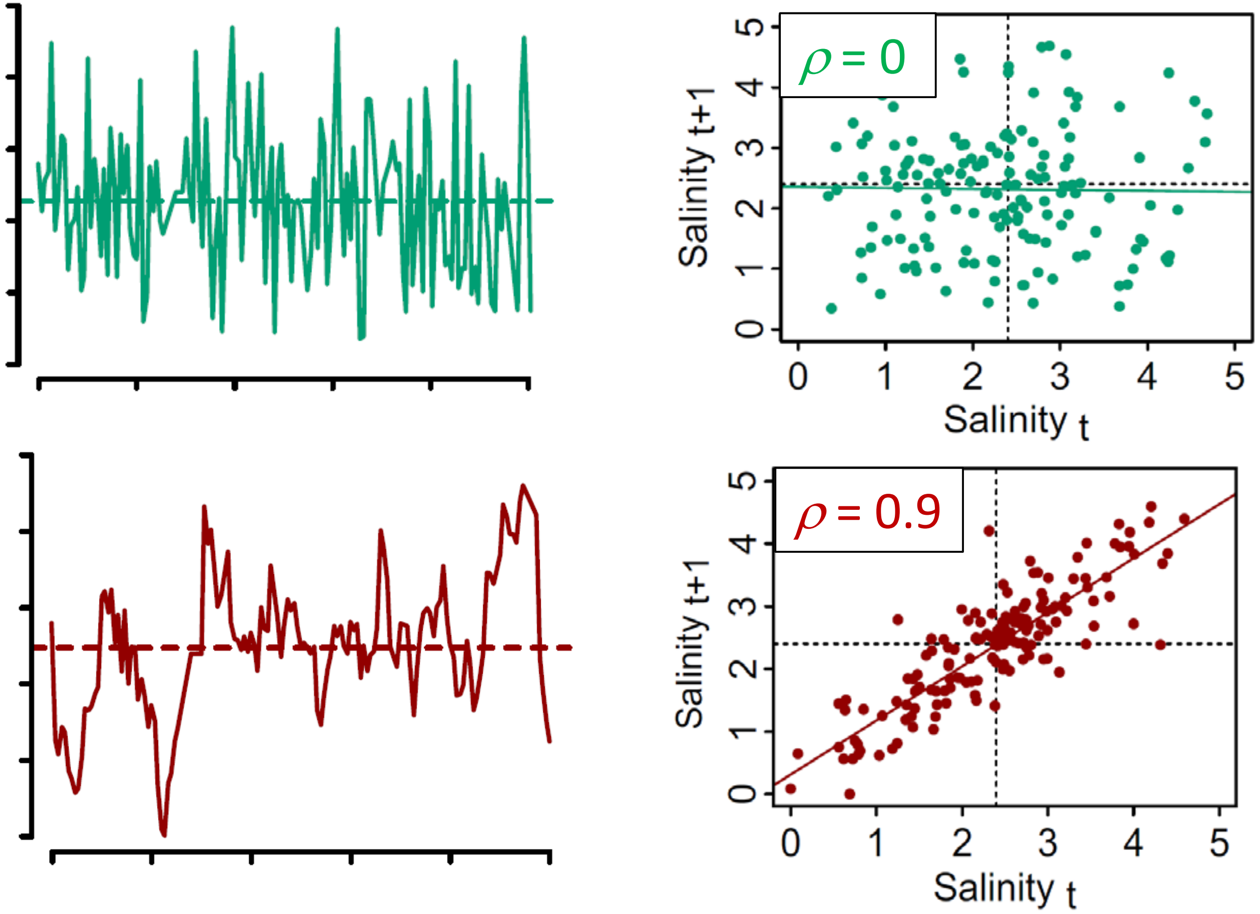


The future is probabilistic even with perfect measurement

Variance of the process matters, not just expectation

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 responses to fluctuating optimum

- Selection on **mutation with phenotypic effect α** in background phenotype m, in haploid population[1].

Denoting $\psi = \ln\left(\frac{p}{q}\right)$, ie the logit frequency,

$$\Delta\psi = \ln W_{m+\alpha} - \ln W_m = -\frac{s\alpha}{2}[\alpha + 2(m-\theta)]$$

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

Additive in mismatch → **If optimum θ follows a Gaussian process, so does ψ**.

If changes in background mean phenotype m can be neglected,
then ψ simply integrates all past optimas, with equal weight on all times

[1] Kimura (1954 Genetics), Gillespie (1991), Chevin (2019 Genetics)

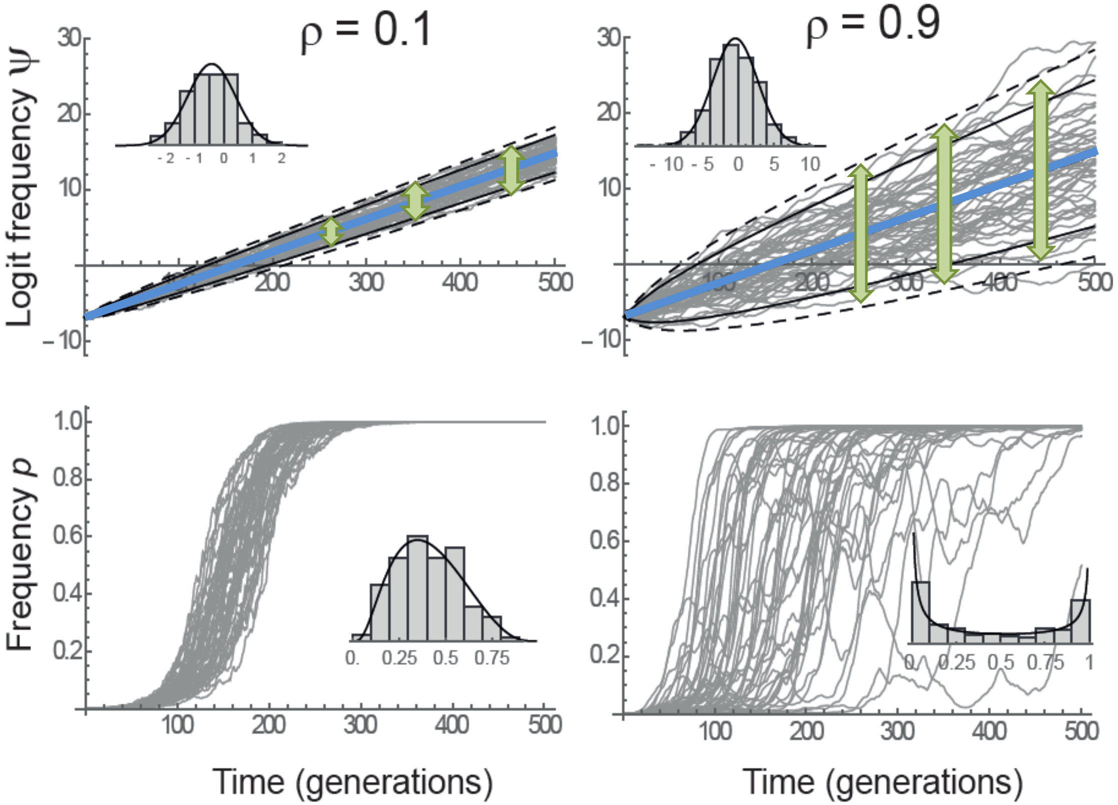
Evolutionary responses to fluctuating optimum

- Assume the optimum follows a stationary autocorrelated Gaussian process (AR1)

- Fluctuation pattern has **no influence on expected change** in (logit) frequency
- Stochastic **variance of ψ** is
  $$\sigma^2_{\psi,t} \approx \sigma^2_s \frac{1+\rho}{1-\rho} t, \text{ with } \sigma^2_s = (S\alpha\sigma_\theta)^2$$

→ Increases linearly, faster under higher autocorrelation

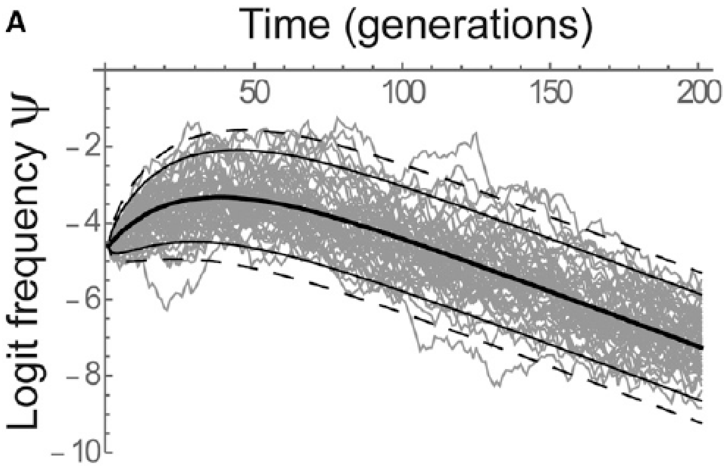
- On p scale, variance of ψ translates into variance in the timing of selective sweeps



Chevin (2019 Genetics)

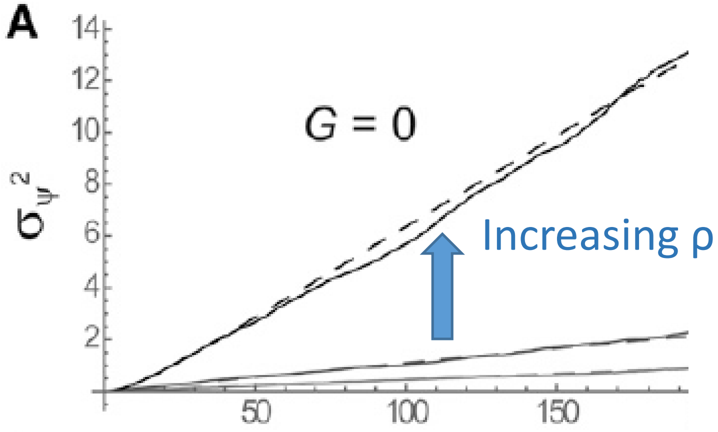
Evolutionary responses to fluctuating optimum

- If background genetic variance for the trait is normally distributed, then mean background also evolves in response to fluctuating optimum.
- The process for $\psi = \mathrm{logit}(p)$ becomes **stationary, with variance that plateaus**
  → Other polymorphic loci buffer the stochasticity perceived by major gene



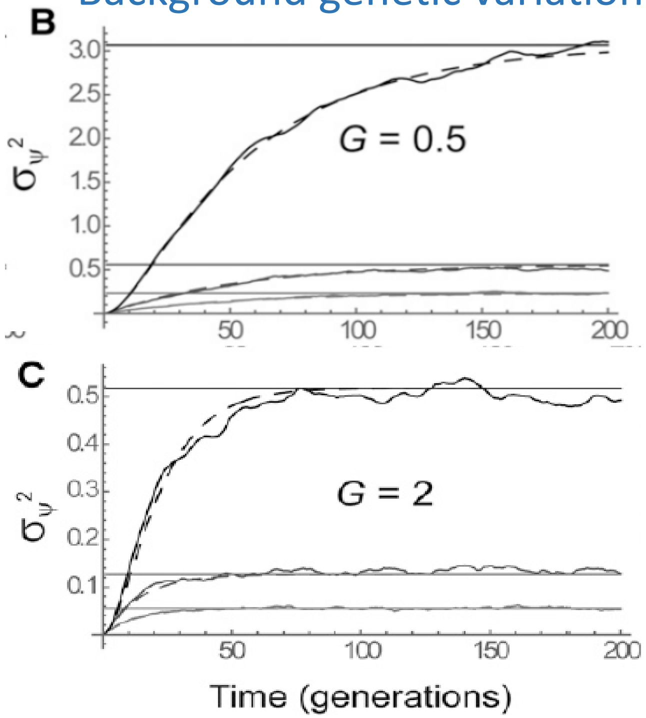
Chevin (2019 Genetics)

No background genetic variation



Increasing ρ

Background genetic variation



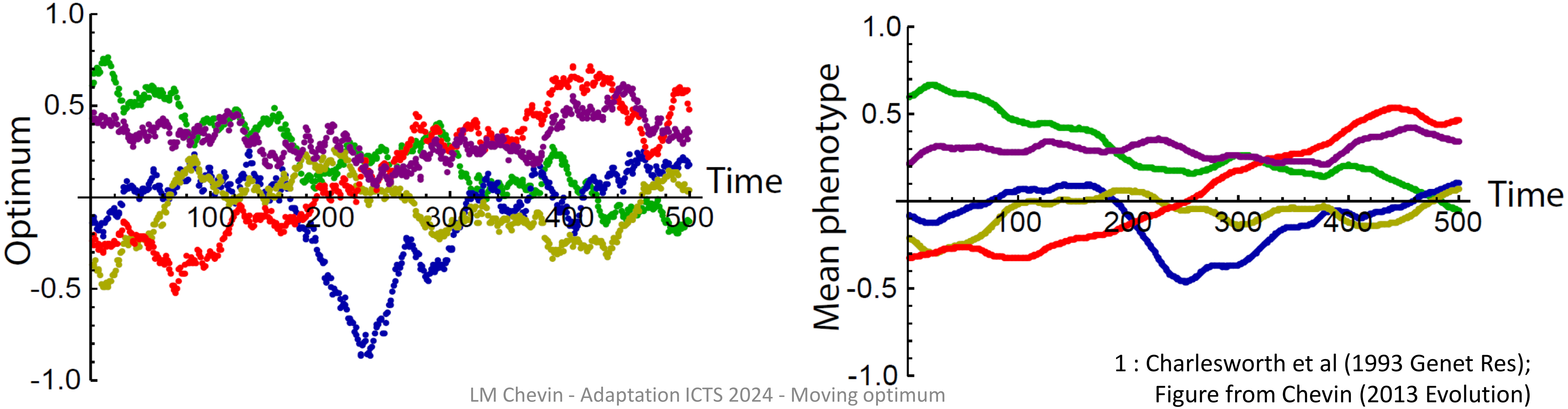
Evolutionary responses to fluctuating optimum

- For polygenic trait with constant variance, the mean phenotype[1] is

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

→ Weighted average of past optima, with more weight on more recent ones.

Smoothes environmental “signal”, all the more as adaptive potential SG is small



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

Evolutionary responses to fluctuating optimum

- For polygenic trait with constant variance, the mean phenotype[1] is

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

- 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.

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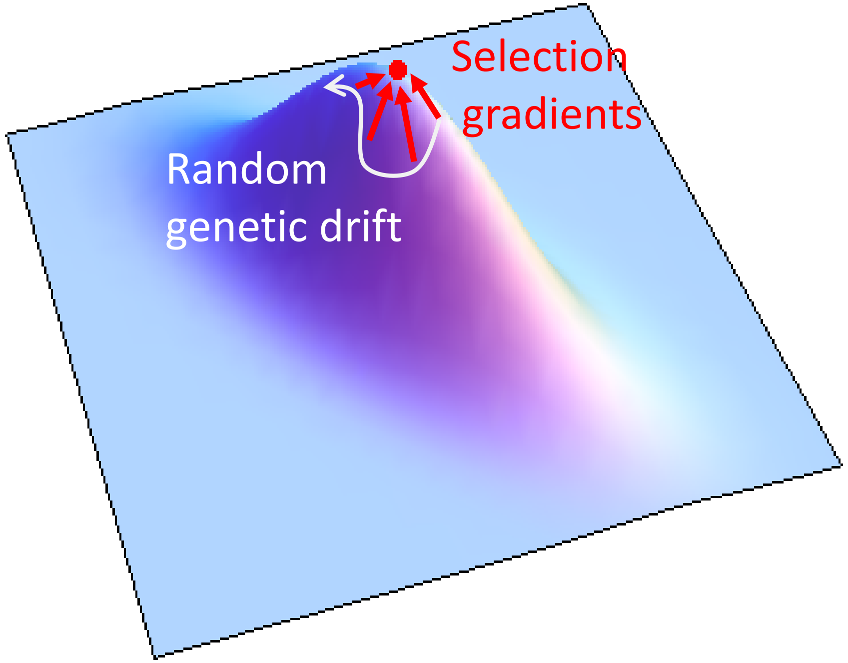
[1] : Charlesworth et al (1993 Genet Res);

Fluctuations of 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 b drift aroung the constant optimum is $\mathrm{V}(\beta) = \frac{S}{(2-SG)N_e}$

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

- The autocorrelation function of selection gradients is

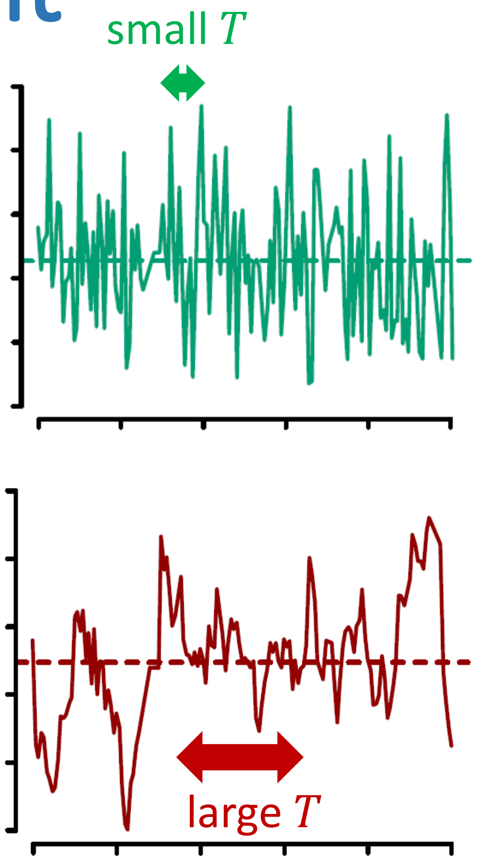
$$\mathrm{ACF}(\beta, \tau) = (1 - SG)^{\tau}$$

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

Chevin & Haller (2014 Evolution)

Fluctuations of selection gradient

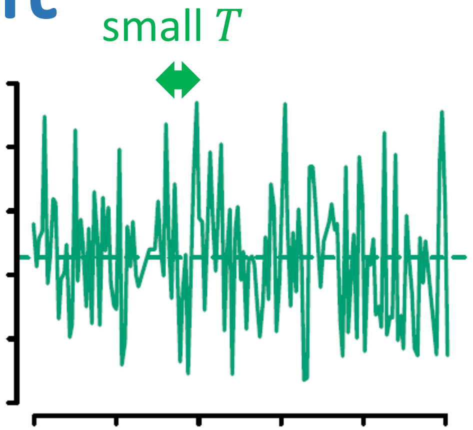
- Autocorrelated fluctuating optimum (AR1), with T the characteristic time over which optimum is autocorrelated

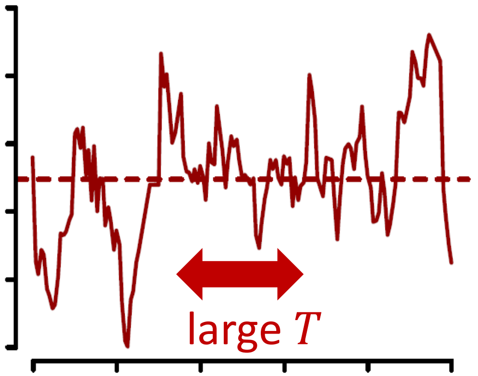


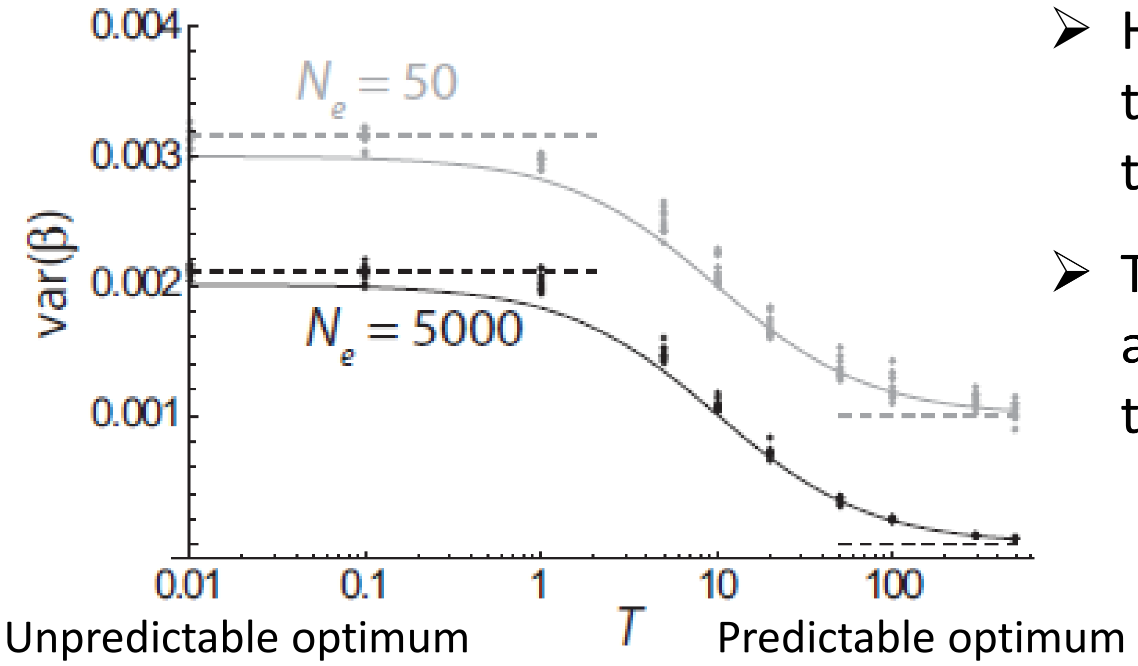
Chevin & Haller (2014 Evolution)

Fluctuations of selection gradient

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







- ➢ 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 selection gradient

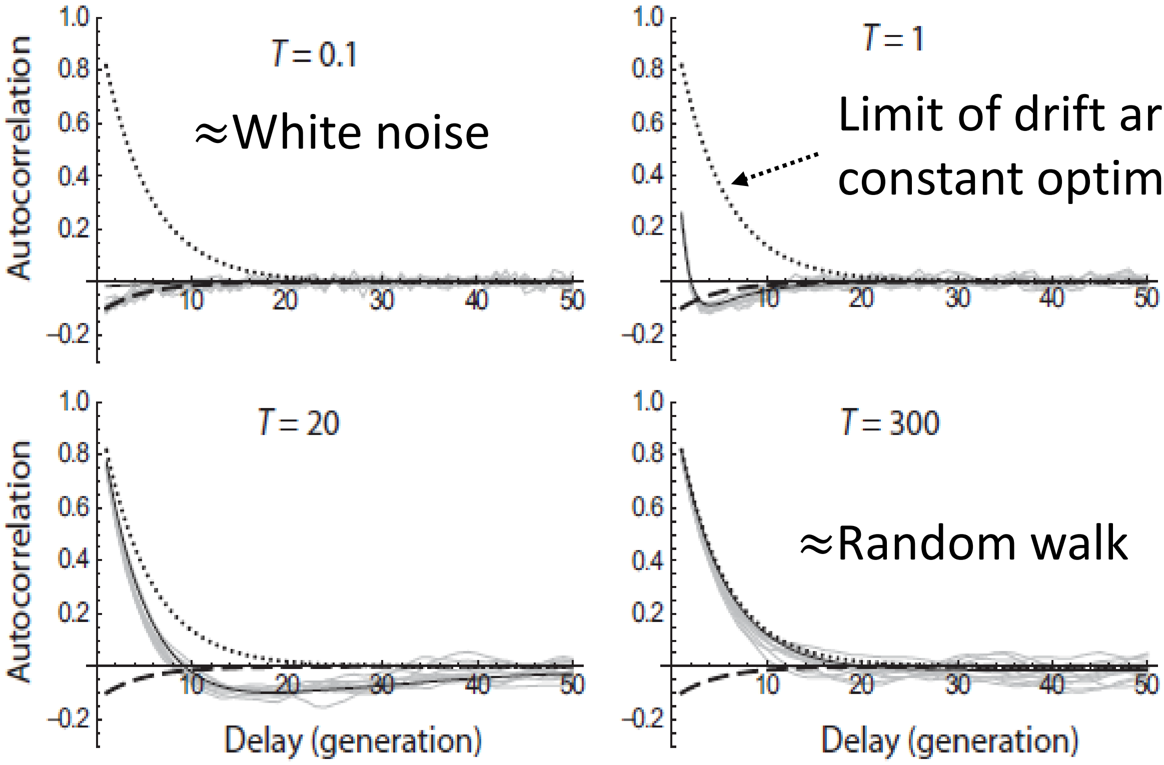
- Autocorrelated fluctuating optimum (AR1),
  with T the characteristic time over which optimum is autocorrelated

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

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

(Weighted) difference between autocorrelation of optimum and evolutionary inertia

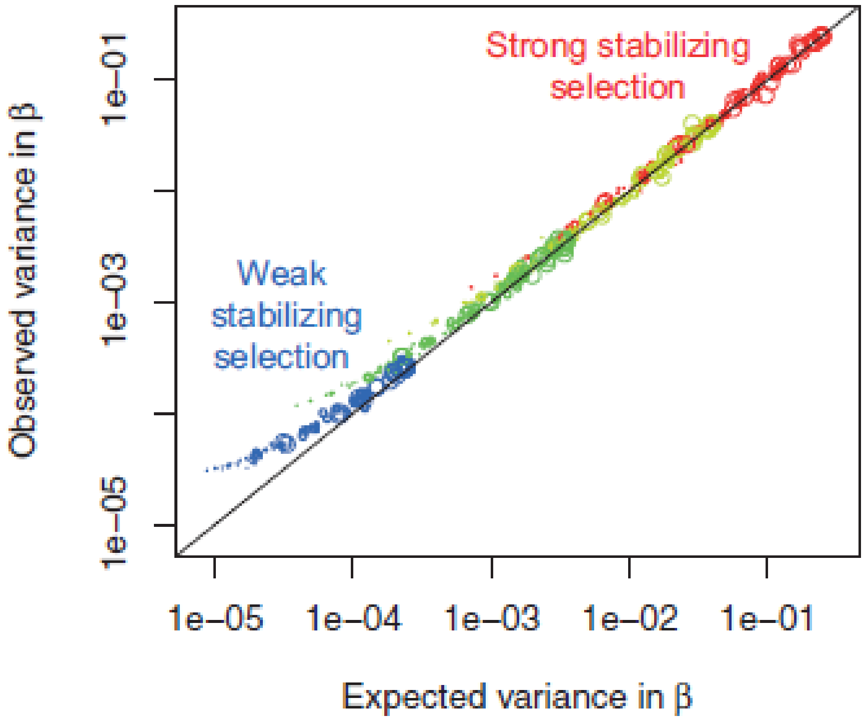
→ Fluctuations in β do not tell the whole story about fluctuating selection!

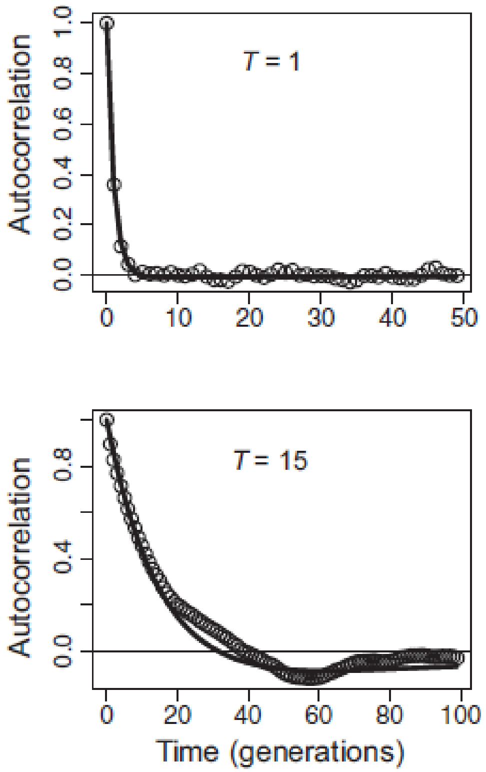


Chevin & Haller (2014 Evolution)

Fluctuations of selection gradient

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





Chevin & Haller (2014 Evolution)

Population dynamics under moving optimum

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

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

Evolution: $\Delta\bar{z} = G\,\dfrac{\partial ln\overline{W}}{\partial\bar{z}}$

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

Demography: $\ln N_{t+1} = \ln N_t + r_{\max} - g(N_t) - \frac{S}{2}(\bar{z}_t - \theta_t)^2$

Evolution: $\Delta\bar{z} = -GS(\bar{z}_t - \theta_t)$

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

Population dynamics under moving optimum

- **Neglecting density dependence** (eg under severe stress):
  $n_t = \ln N_t = n_0 + r_{\max} t - \frac{S}{2} \sum_{k=0}^{t-1} (\bar{z}_k - \theta_k)^2$

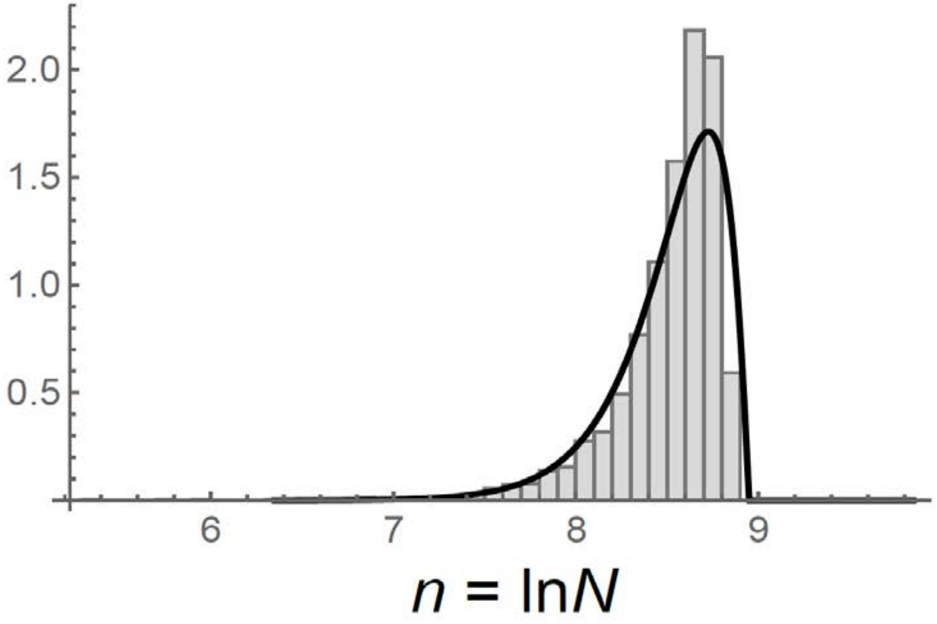
Unweighted sum of all **past maladaptation**
→ Past extreme events may have long-lasting consequences

- If θ is a Gaussian process, so are $\bar{z}$ and $(\bar{z} - \theta)$
  Then $n = \ln N$ is related to chi-square,
  or gamma distribution with shape parameter increasing with time

Chevin et al 2017 (Am Nat)

Distribution of population size

- The reverse gamma distribution is:
  - ➢**Bounded above** by growth of optimum phenotype
  - ➢**Left skewed**
    → **excess of small population sizes** at high extinction risk



Chevin et al 2017 (Am Nat)

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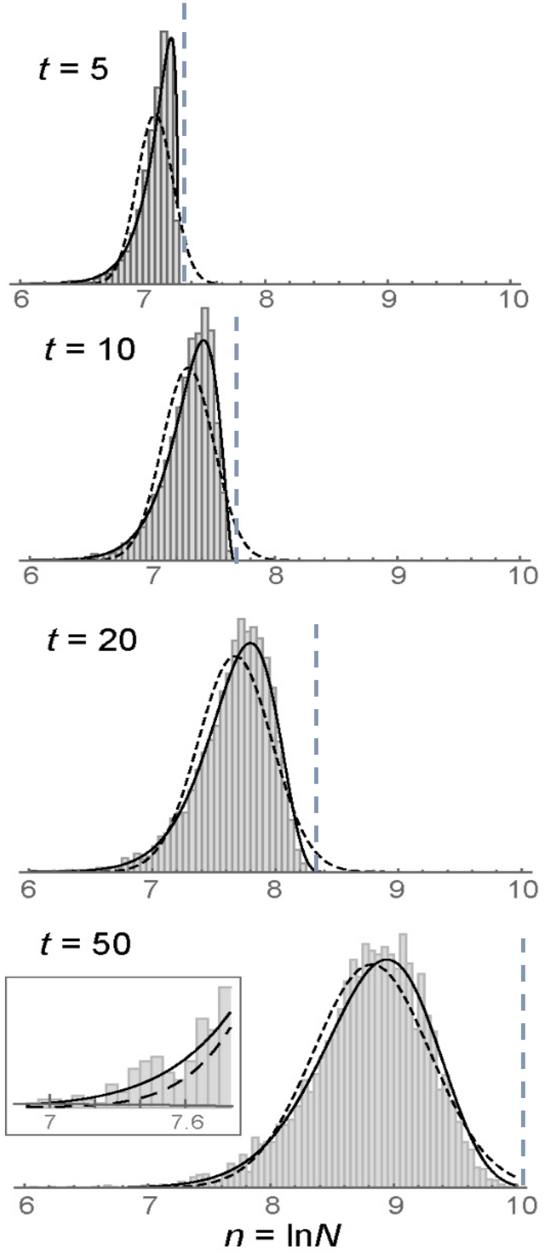

Chevin et al 2017 (Am Nat)

Distribution of population size

- The reverse gamma distribution is:
  - **Bounded above** by growth of optimum phenotype
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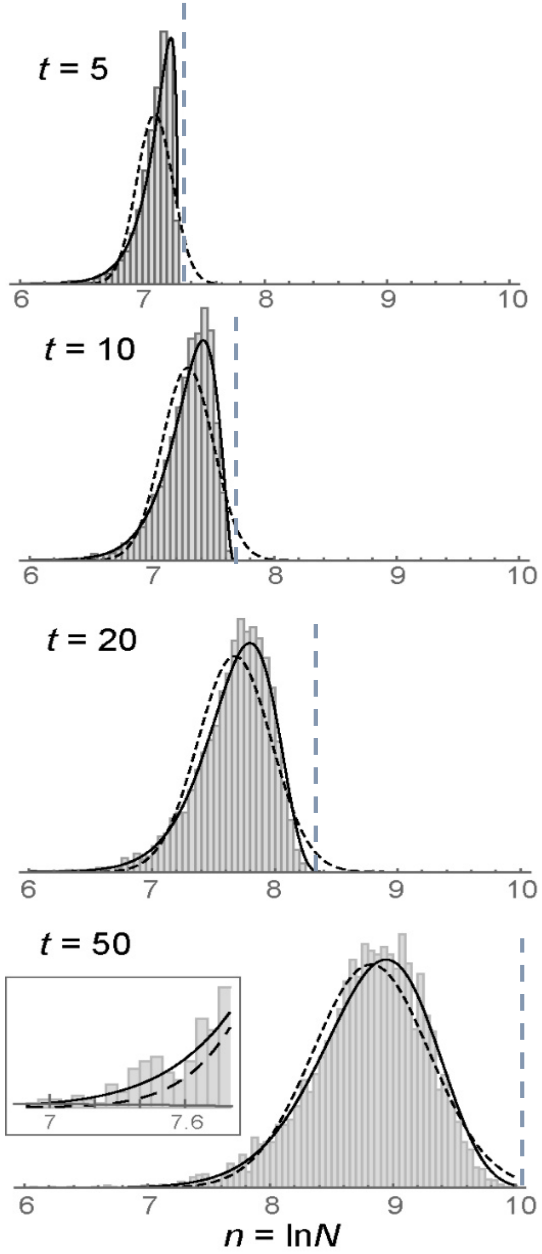
    → **excess of small population sizes** at high extinction risk
  - Starting from fixed size, **tends to normal** over time, but slowly (excess of small *N* remains)
  - **Autocorrelation** of optimum :
    - **increases the expected** ln*N* (facilitates adaptive tracking[1,2])
    - increases **variance** of population size (among independent lineages)[1].

    → possibly antagonistic for extinction risk



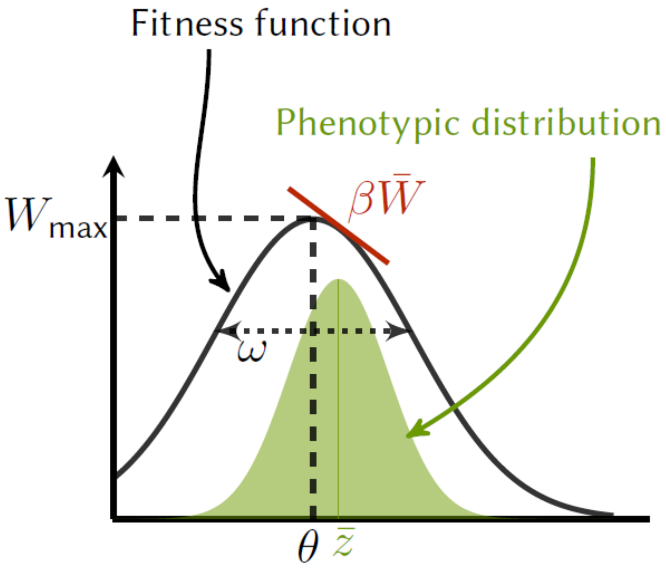
Chevin et al 2017 (Am Nat)

Conclusion

- Models of adaptation to an optimum phenotype rely on plausible biological assumptions
- They yield predictions about adaptation across a range of conditions (low/high mutation, fitness and traits).
  → Combine several lines of evidence.
- Can help understand adaptation, but only a starting point: reality is more complex! Multiple peaks, frequency dependence (flattening fitness peaks…), space, phenotypic plasticity…

Thanks!

Questions?



Gaussian fitness peak

<u>Recursion for the mismatch with optimum</u>:

$$x_t = \bar{z}_t - \theta_t = \bar{z}_{t-1} - GS(\bar{z}_{t-1} - \theta_{t-1}) - \theta_{t-1} + \theta_{t-1} - \theta_t$$

$$x_t = (1 - GS)x_{t-1} + \theta_{t-1} - \theta_t$$
$$\Delta x = -GSx_{t-1} - \Delta\theta$$

Lande (1976 Evolution)

Gaussian fitness peak

- Recursion for mean phenotype $\bar{z}$:

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

$$\bar{z}_1 = \bar{z}_0(1 - GS) + GS\theta_0, \quad \bar{z}_2 = \bar{z}_0(1 - GS)^2 + GS(1 - GS)\theta_0 + GS\theta_1,$$
$$\bar{z}_3 = \bar{z}_0(1 - GS)^2 + GS(1 - GS)^2\theta_0 + GS(1 - GS)\theta_1 + \theta_2 \ldots$$

- Full solution for $t \geq 1$ is

$$\bar{z}_t = \bar{z}_0(1 - GS)^t + GS\sum_{k=0}^{t-1}(1 - GS)^{t-1-k}\theta_k$$

Replacing $j = t - k$, such that $k = t - u$

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

Charlesworth et al (1993 Genet Res);

Directional environmental change

- Highly polymorphic regime:
- Recursion for distance to optimum $x = \bar{z} - \theta$:

$$x_t = (1 - GS)x_{t-1} - v$$

$$x_0 = 0, x_1 = -v, x_2 = -v(1 + (1 - GS)), x_3 = -v[1 + (1 - GS) + (1 - GS)^2], \ldots$$

- Full solution for $t \geq 1$ is

$\Delta\bar{z} = G\beta = -GS\boldsymbol{x}$

$$x_t = \; - v\sum_{k=0}^{t-1}(1 - GS)^k = -v\frac{1 - (1 - GS)^t}{1 - (1 - GS)} = -\frac{v}{GS}[1 - (1 - GS)^t]$$

- At equilibrium

$$x_{\text{eq}} = (1 - GS)x_{\text{eq}} - v \quad \Leftrightarrow \quad x_{\text{eq}} = -\frac{v}{GS}$$

1: Pease et al 1989; Lynch et al 1991; Lynch & Lande 1993

Cycling environment

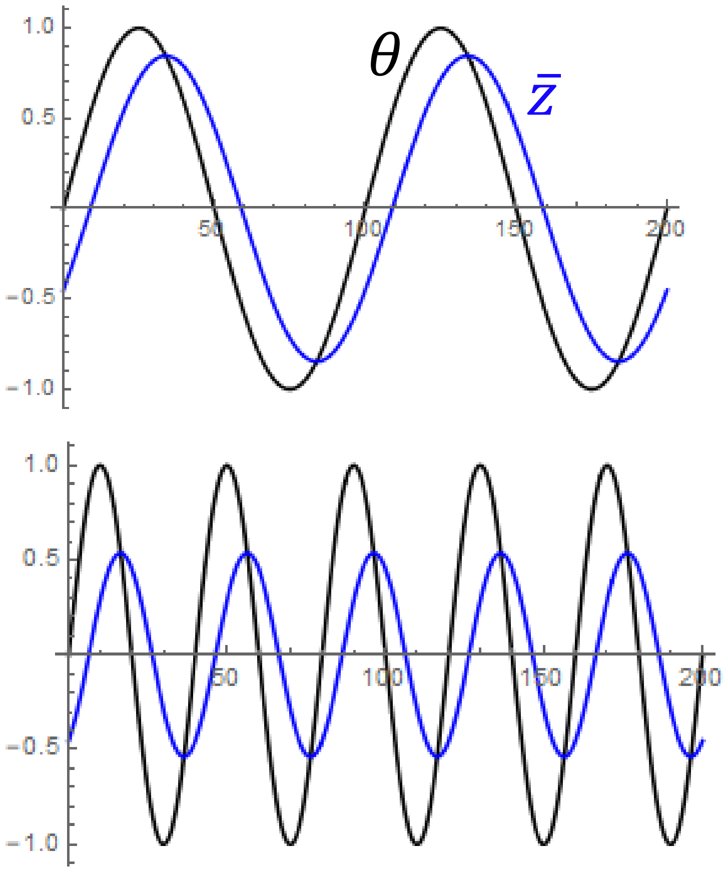
- **Model**[1]: Sine wave with amplitude A and period T

$$\theta = A \sin\left(\frac{2\pi t}{T}\right)$$

- Continuous-time evolutionary dynamics

$$\frac{d\bar{z}}{dt} = -GS\left[\bar{z} - A\sin\left(\frac{2\pi t}{T}\right)\right]$$

$$\frac{d\bar{z}}{dt} + GS\bar{z} = A\sin\left(\frac{2\pi t}{T}\right)$$



Lynch et al 1991; Lande & Shannon 1996