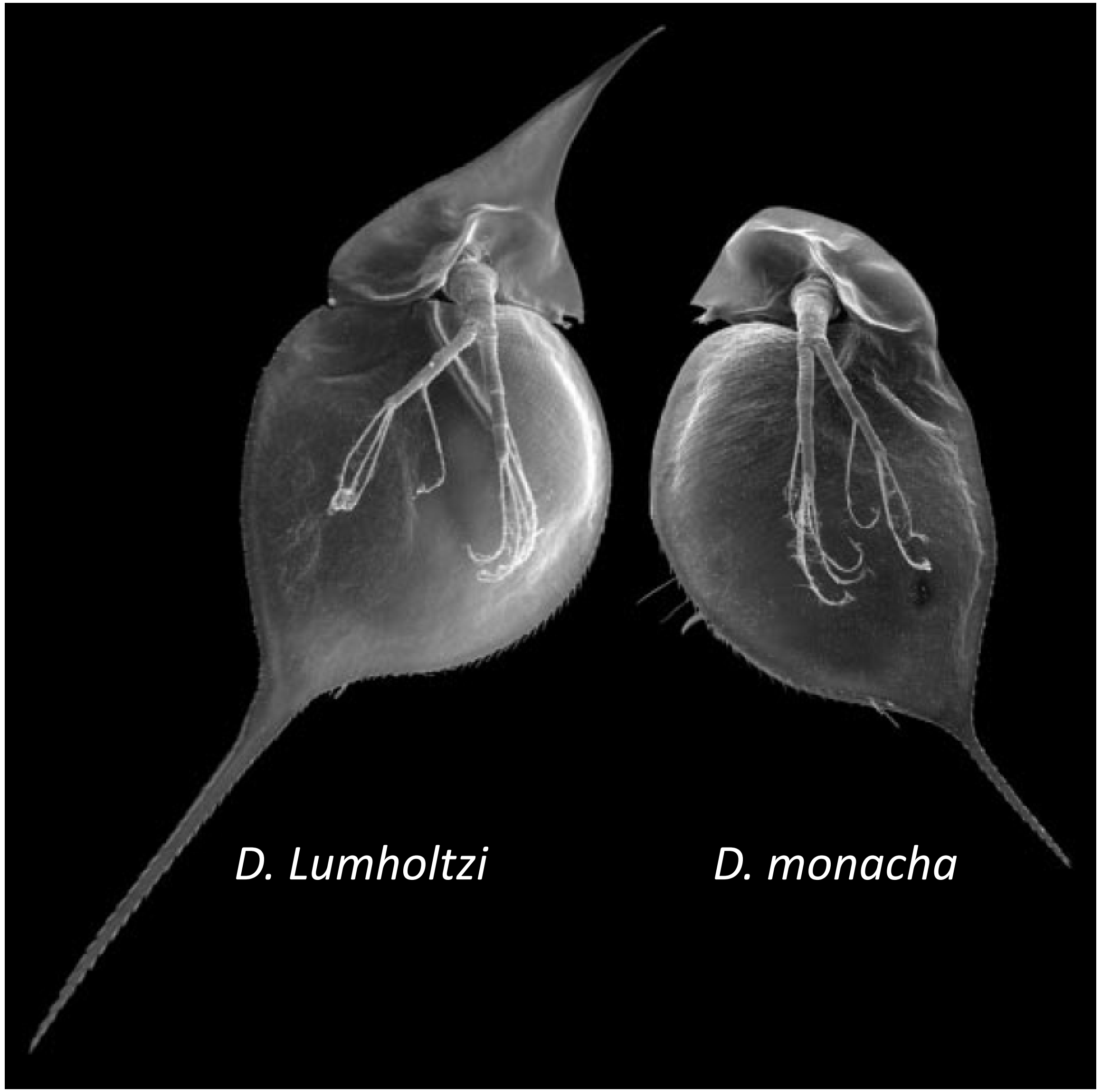
Centre d'Ecologie Fonctionnelle & Evolutive

Phenotypic plasticity and adaptation to variable or novel environments

Theoretical and empirical insights

Luis-Miguel Chevin, CEFE CNRS, Montpellier, France.

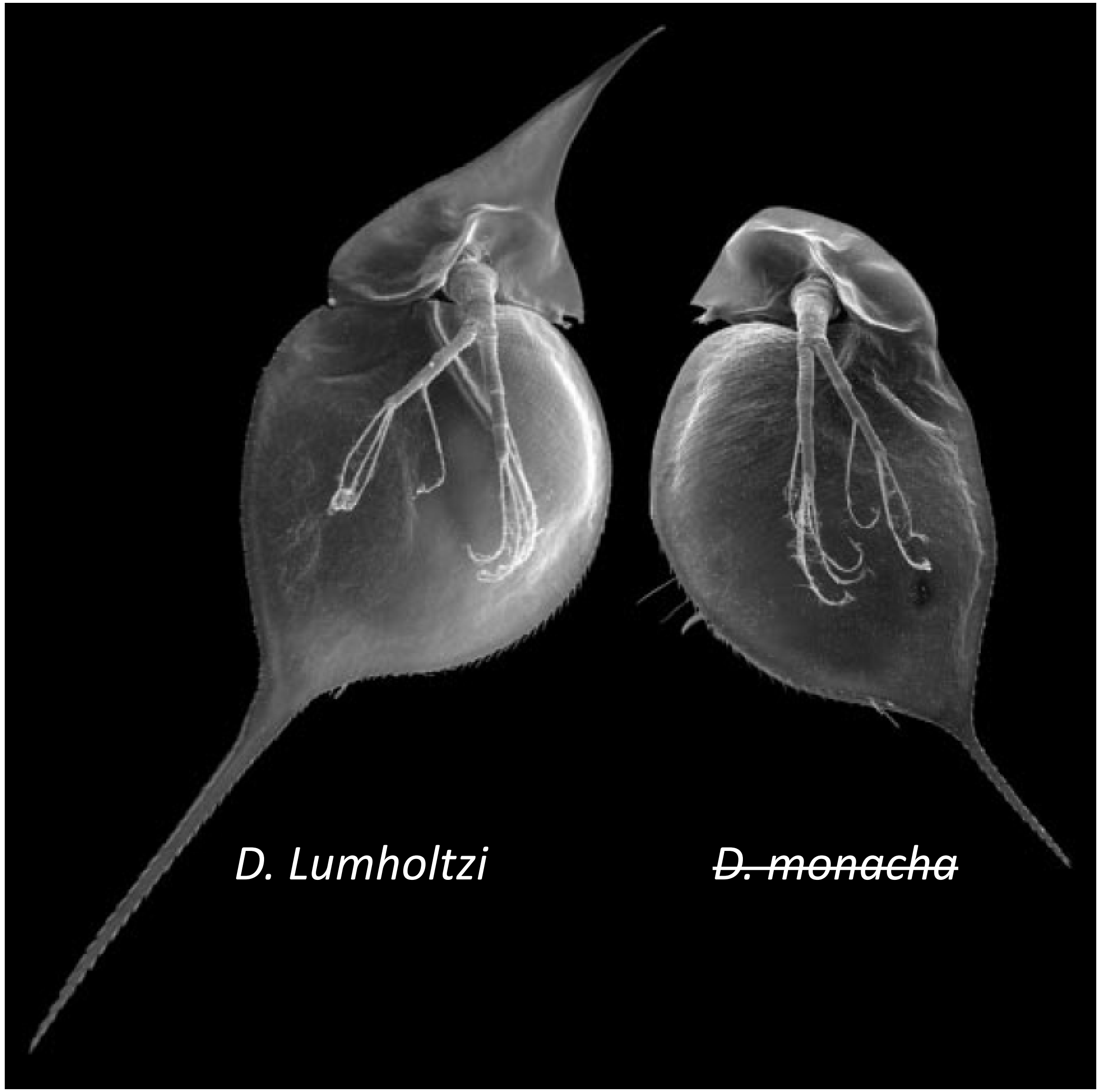
2 *Daphnia* species



Agrawal (2001, Science)

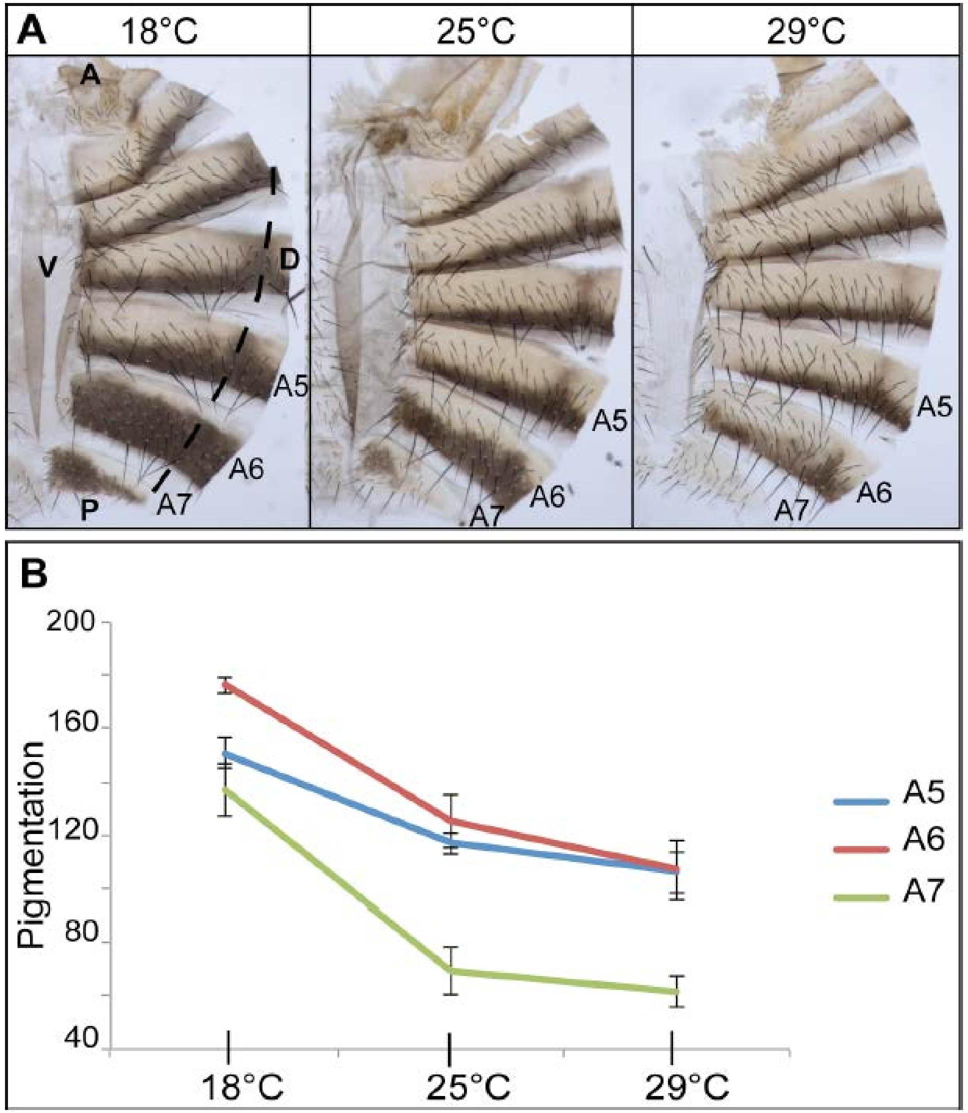
~~2 *Daphnia* species~~

A **single clone**,
with vs without **predator cues**



Agrawal (2001, Science)

Abdominal pigmentation of an **inbred line** of *Drosophila melanogaster* as a function of the **temperature of development**



Gibert et al (2016, PLoS Genetics)

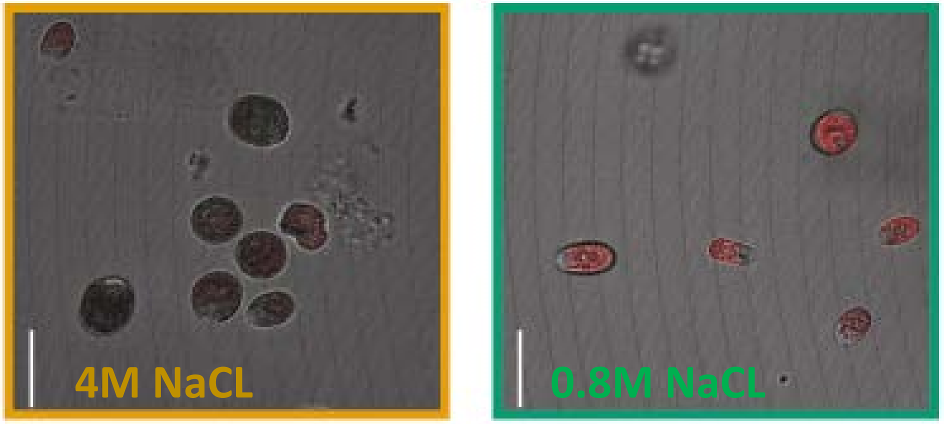
Gaudy commodore butterflies

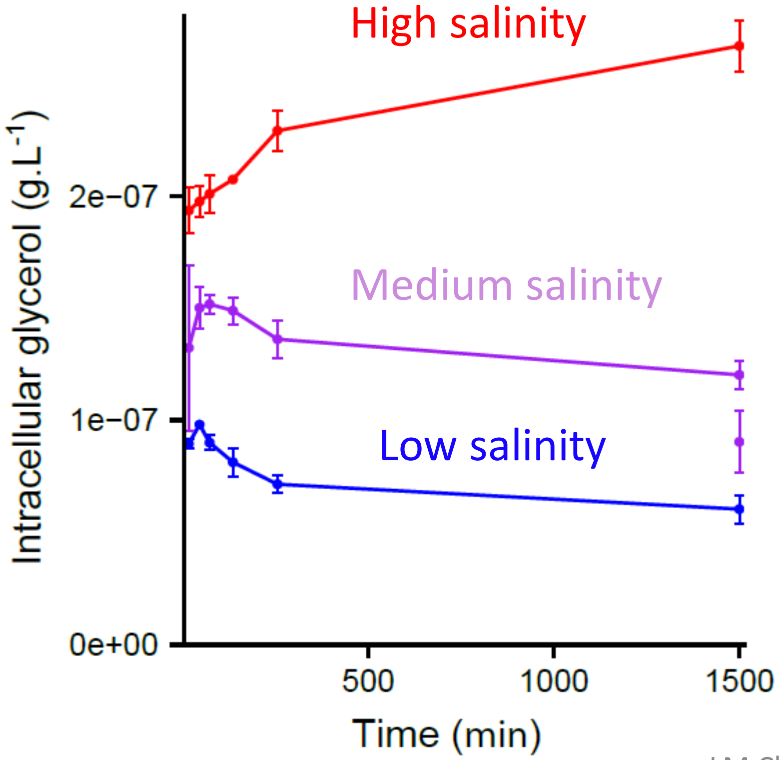
Wet-season morph

Dry-season morph

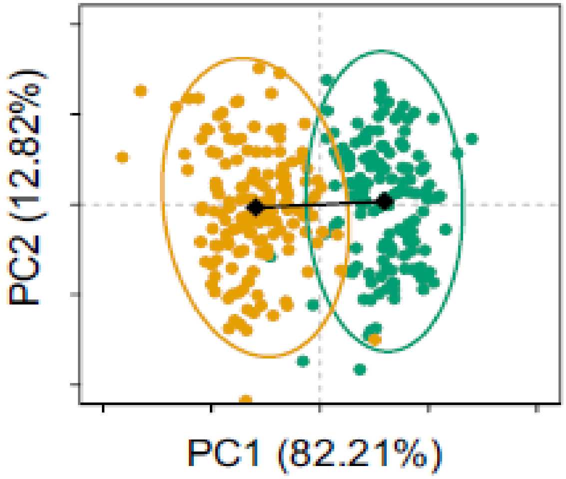
(Photo F. Nijhout, in Pfennig et al 2010 TREE)

Cell shape and chlorophyll + glycerol content of a **strain** of the microalgae *Dunaliella salina* at high vs low **salinity**





Rescan et al (2020, Nat Ecol Evol)



Leung et al (2020, Ecology Letters)

Phenotypic plasticity

- Ability of a **given genotype** to produce **different phenotypes** according to the **environment** in which it develops or is expressed
- ≠ residual phenotypic variation of a genotype in a given environment (V_e), though it could be related (microenv. variation, noise-plasticity correlation)
- Defined by contrast to a non-plastic trait with constant phenotype across environment.
  → Covers a **diversity of situations**, depending on:
  - trait: discrete/continuous, reversible vs fixed, organic vs organismic
  - environmental trigger or cue: biotic vs abiotic, simple vs composite…
  - organism: continuous vs limited growth, metamorphosis vs not, …
- Phenomenological definition, **does not necessarily imply adaptiveness**.

Adaptive plasticity ?

- Demonstrating adaptive plasticity is challenging: need non-plastic genotype for comparison
- Rare empirical demonstration using transgenic plants with plasticity turned off

A TEST OF THE ADAPTIVE PLASTICITY HYPOTHESIS USING TRANSGENIC AND MUTANT PLANTS DISABLED IN PHYTOCHROME-MEDIATED ELONGATION RESPONSES TO NEIGHBORS

JOHANNA SCHMITT,[1,*] ALEX C. MCCORMAC,[2,†] AND HARRY SMITH[2,‡]

Vol. 146, No. 6 — The American Naturalist — December 1995

"The observation that **phytochrome-mediated elongation is advantageous in dense stands**, but **disadvantageous for uncrowded plants**, indicates that a response to foliage shade allows plants to **develop an appropriate morphology for the level of competition they experience**. This observation **supports the adaptive plasticity hypothesis** for this ecologically important trait. »

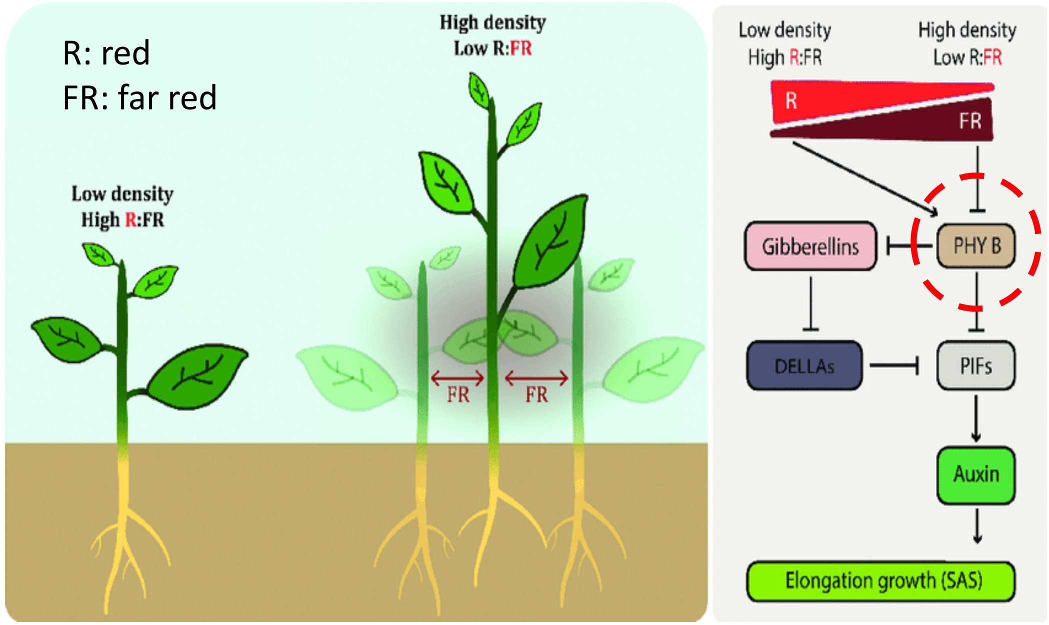


Figure: S. Courbier (2020)

Plasticity and climate change

- Climate change is an **important cause of contemporary phenotypic change** in the wild

Contemporary evolution meets conservation biology

Craig A. Stockwell[1], Andrew P. Hendry[2] and Michael T. Kinnison[3]

Climate change and evolutionary adaptation

Ary A. Hoffmann[1] & Carla M. Sgrò[2]

Ecological and Evolutionary Responses to Recent Climate Change

Camille Parmesan

Evolutionary Response to Rapid Climate Change

William E. Bradshaw and Christina M. Holzapfel

EVOLUTIONARY RESPONSES TO CHANGING CLIMATE

Margaret B. Davis,[1,3] Ruth G. Shaw,[1] and Julie R. Etterson[2]

Keeping up with a warming world; assessing the rate of adaptation to climate change

Marcel E. Visser*

The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda

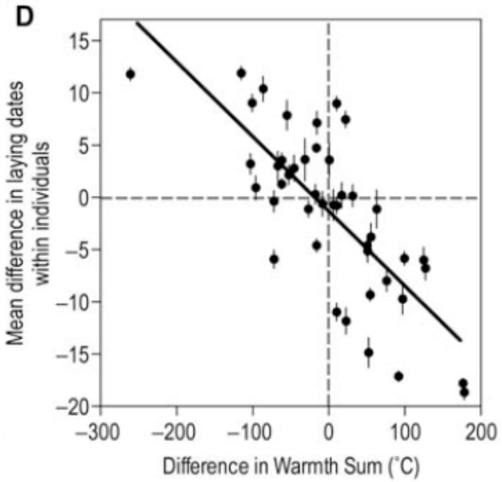
Arpat Ozgul,[1] Shripad Tuljapurkar,[2] Tim G. Benton,[3] Josephine M. Pemberton,[4] Tim H. Clutton-Brock,[5] Tim Coulson[1*]

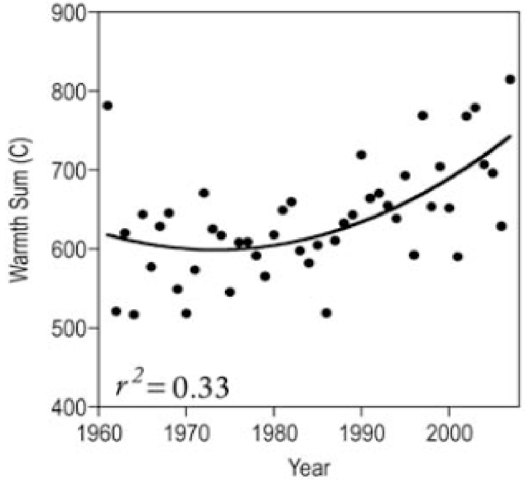
Plasticity and climate change

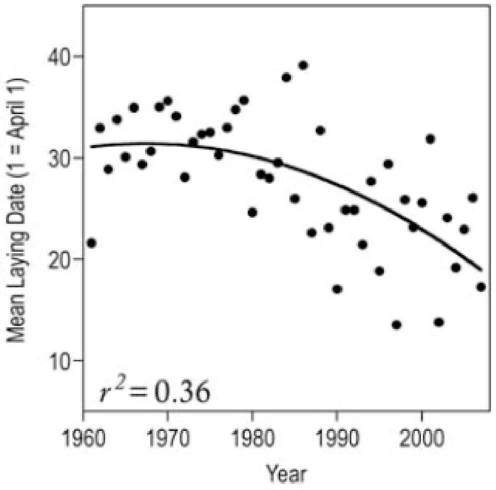
- Climate change is an **important cause of contemporary phenotypic change** in the wild
- However, often modest contribution from genetic responses to selection[1]
- On the other hand, the contribution from plasticity can be large[2]

Great tits in Oxford
© Nature

plasticity x environmental change ≈ phenotypic change





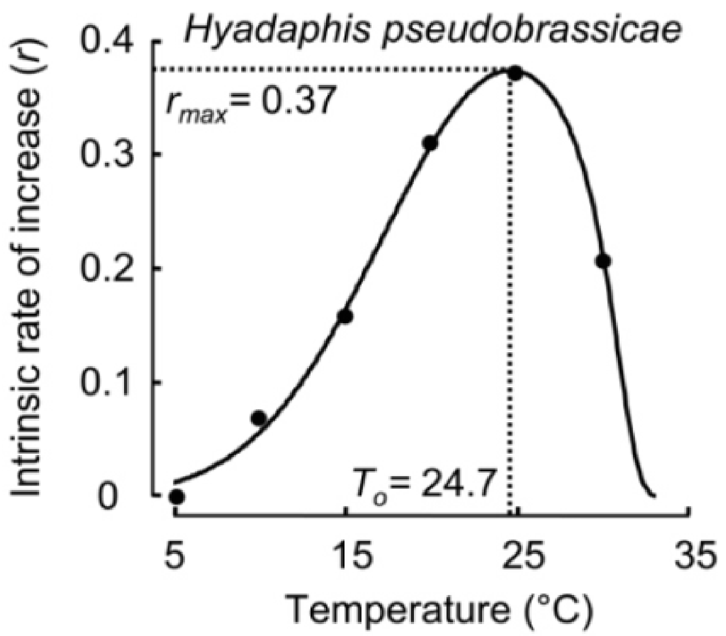


1: Gienapp et al. (2008, Mol Ecol); Hendry et al. (2008, Mol Ecol)
2: Charmantier et al (2008 Science);
Evol Appl (Special issue 2014)

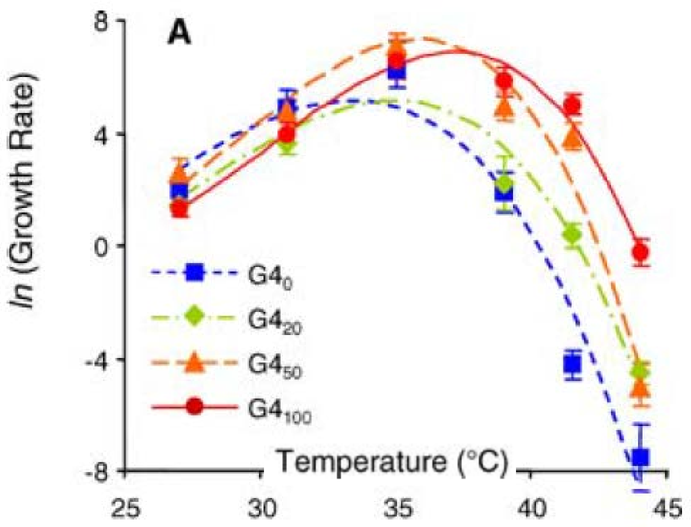
Plasticity and environmental tolerance

- Fitness (or survival, performance, etc) against environment:
  Environmental tolerance curve[1] = one axis of fundamental niche.

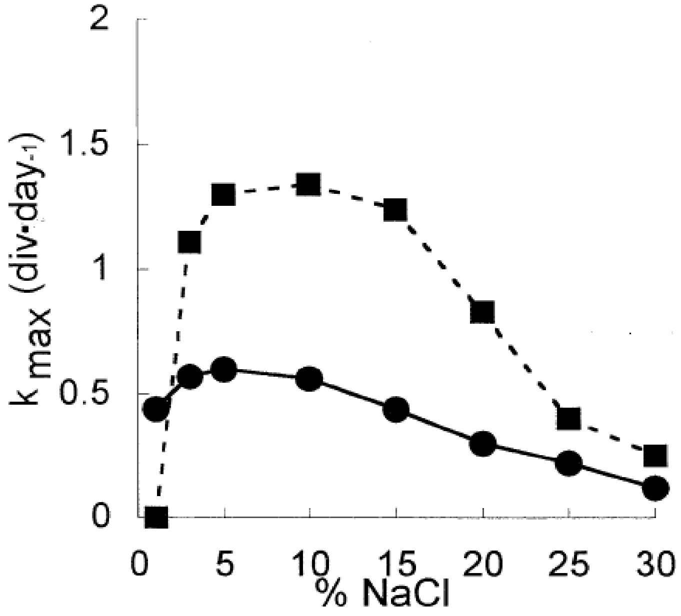
Aphid
(Frazier et al 2006)



Bacteriophage virus
(Knies et al 2006 Am Nat)



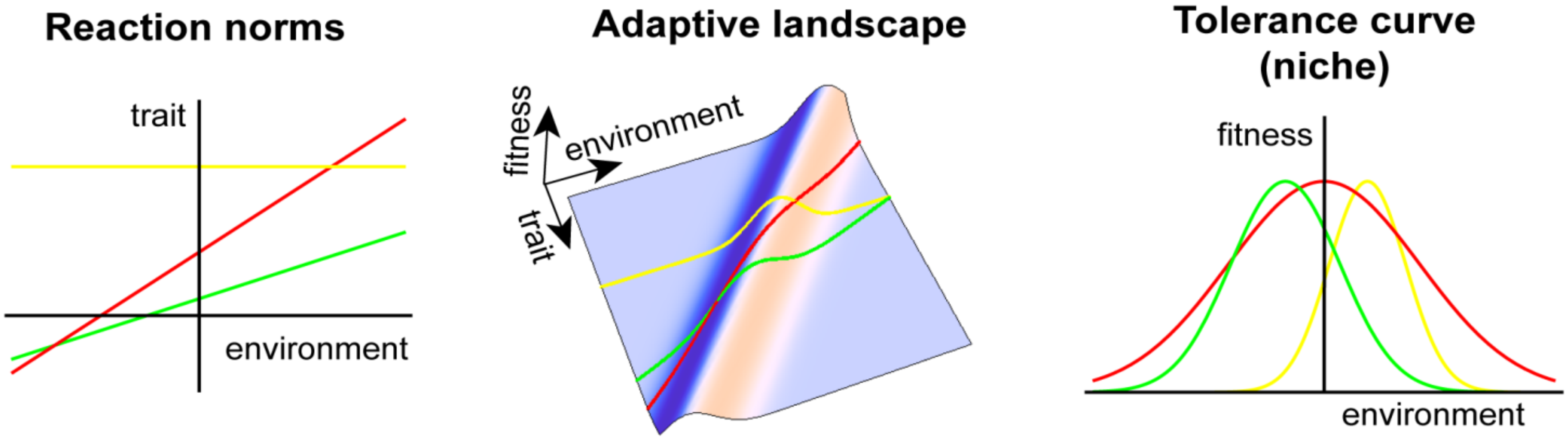
Dunaliella salina microalgae
(Cifuentes et al 2001, J. Phycol)



1: Lynch & Gabriel (1987 Am Nat); Buckley & Kingsolver (2021 ARESE)

Plasticity and environmental tolerance

- Fitness (or survival, performance, etc) against environment: **Environmental tolerance curve**[1] = one axis of fundamental niche.
- Emerges from phenotypic plasticity x fitness-trait map.



→ 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)

Outline of the talk

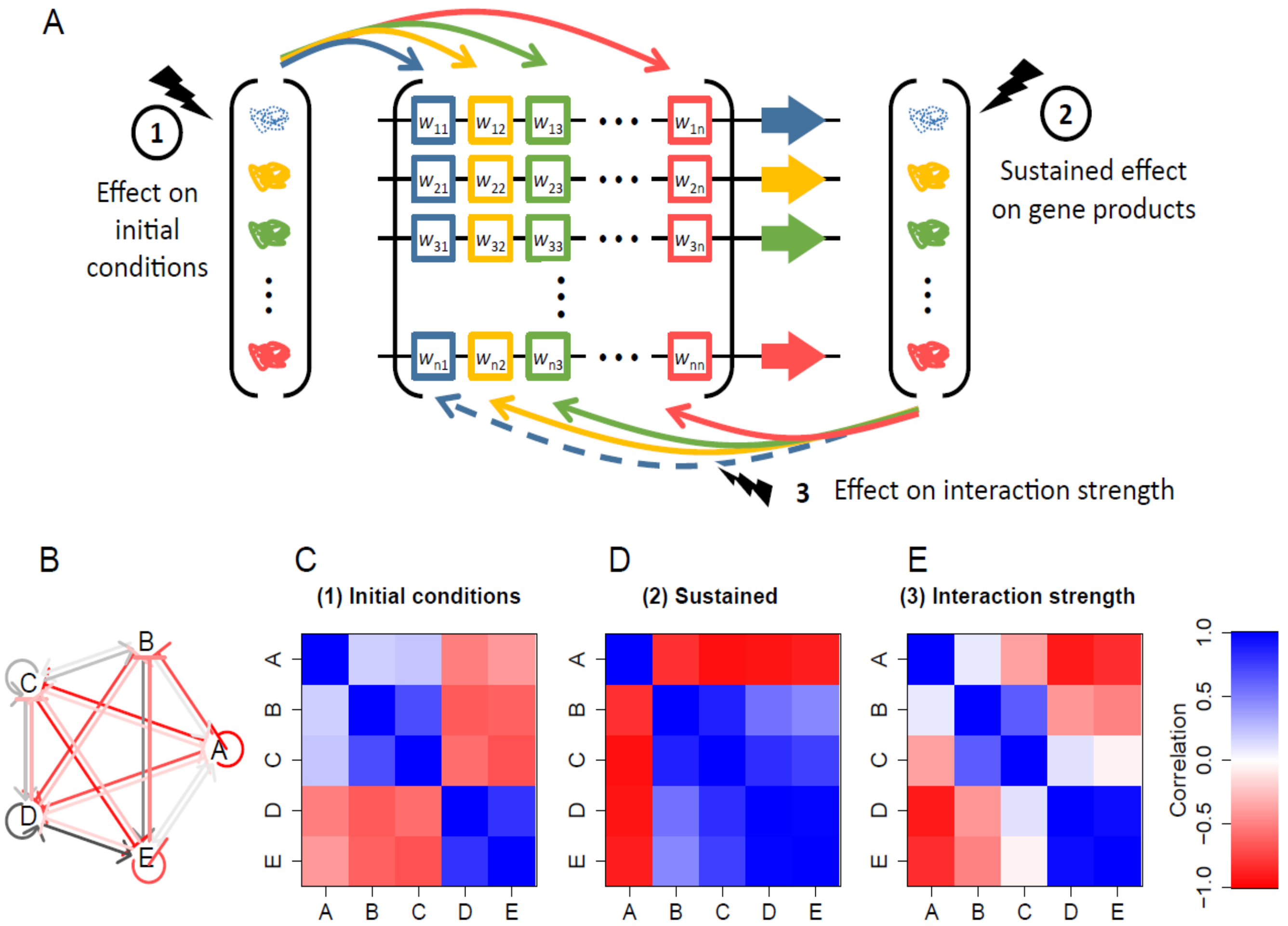
1. Genetic variation and selection on plasticity
2. Evolution of plasticity in fluctuating environments
3. Evolution of plasticity in novel and extreme environments

Outline of the talk

1. **Genetic variation and selection on plasticity**
2. Evolution of plasticity in fluctuating environments
3. Evolution of plasticity in novel and extreme environments

What is causing genetic variance in plasticity?

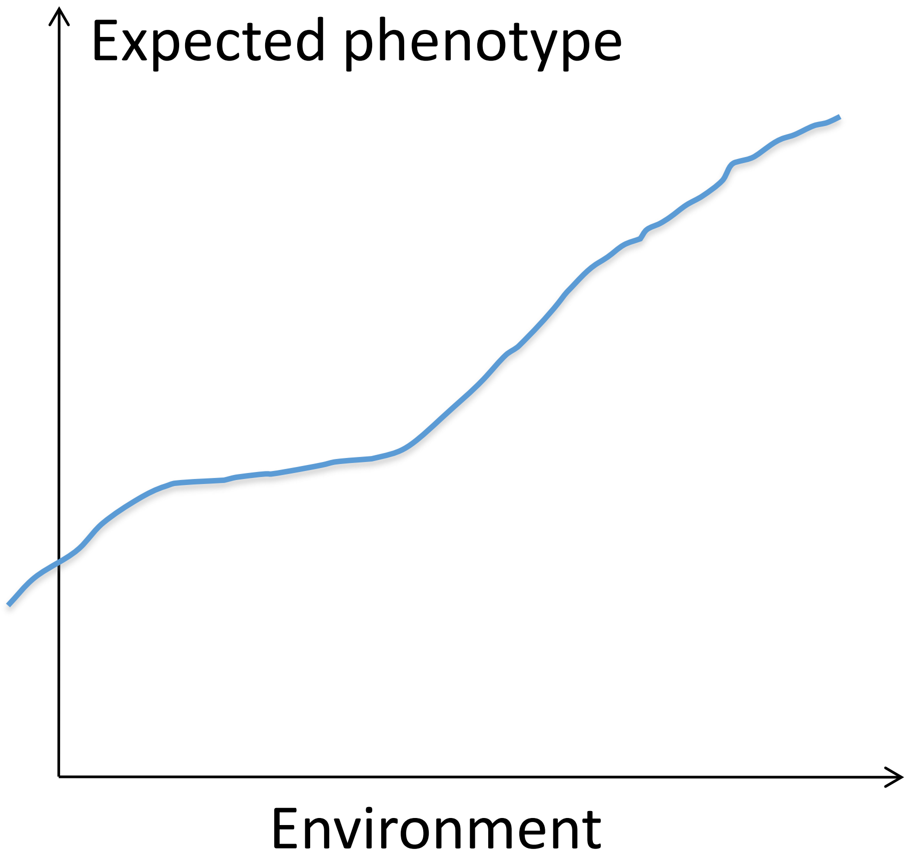
- Gene expression plasticity thought to underly phenotypic plasticity of most higher traits[1].
- But number of plastic genes >> measured traits, low resolution of mapping
- Dimensionality can be reduced by relying on co-expression clusters (eg WGCNA). But what do they mean biologically?
- **Co-expression patterns** partly reflect how the environment acts on gene regulatory network[2] → User former to infer latter?



1: Beldade et al (2011 Mol Ecol)
2: Chevin, Leung, le Rouzic & Uller (2022 Genetica)
(original model: Wagner 1994 PNAS)

Reaction norms as quantitative traits

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



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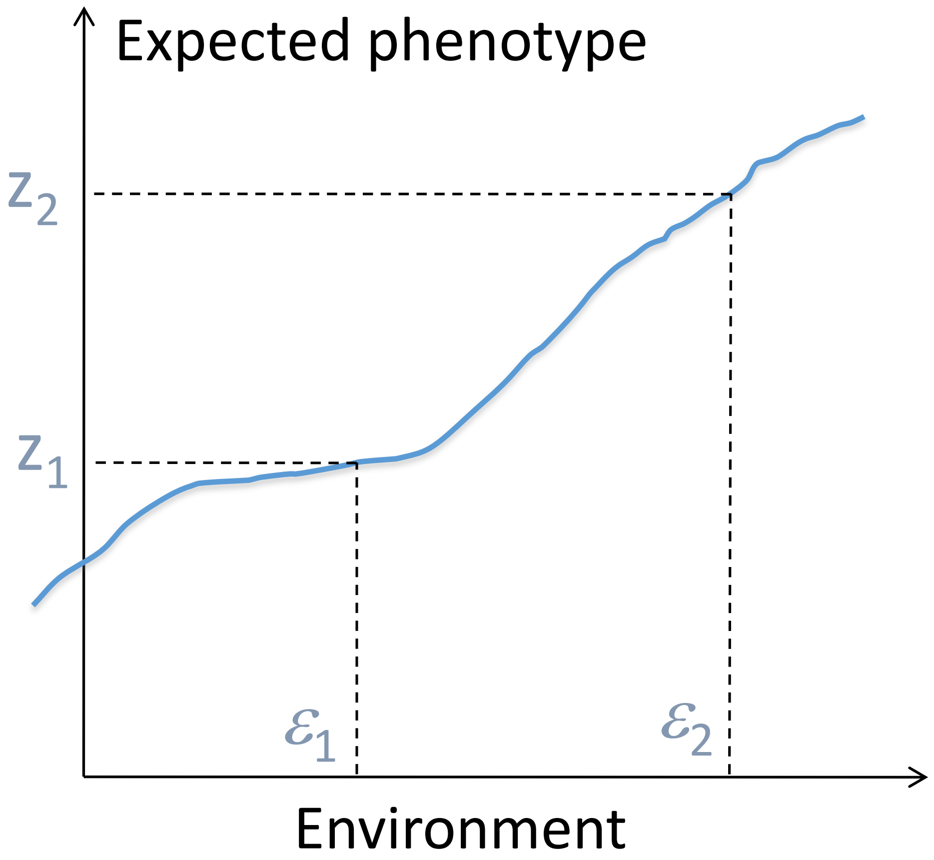

- **Character state approach**[1]
  z_1 and z_2 = 2 traits,
  possibly genetically correlated.

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

Reaction norms as quantitative traits

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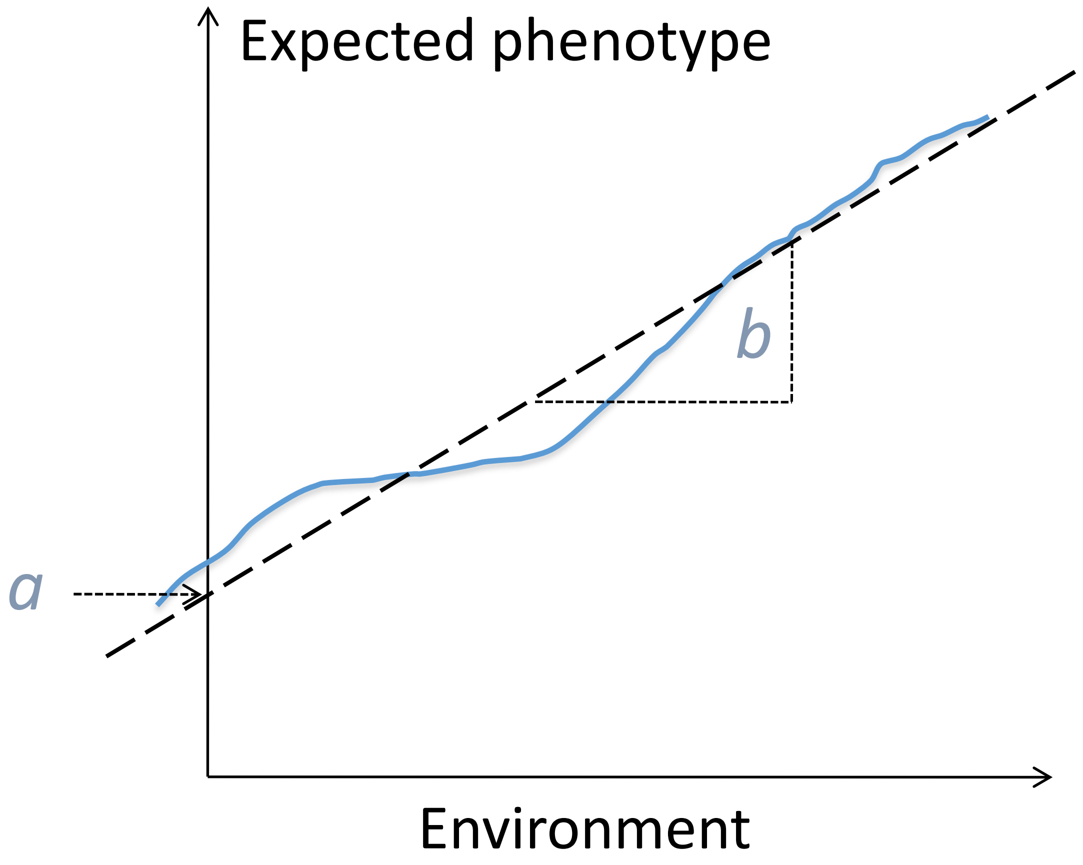


- **Character state approach**[1]
  z_1 and z_2 = 2 traits,
  possibly genetically correlated.
- **Curve parameter approach**[2]
  Reaction norm shape parameters
  (intercept *a*, slope *b*, …)
  are quantitative traits.
  If linear, slope *b* quantifies plasticity

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

Genetic variance in plasticity

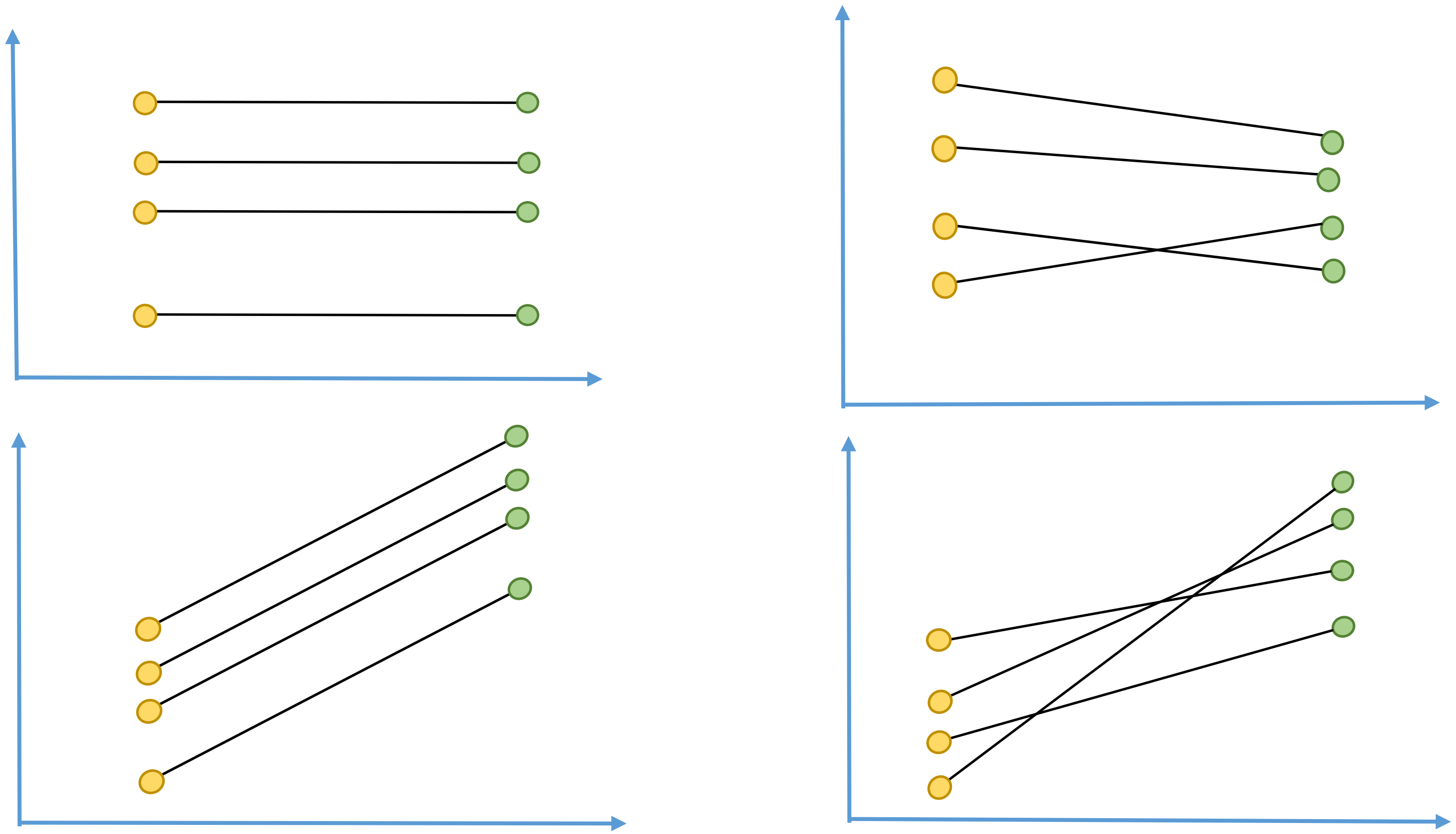
Clones or families across environments (split-brood design)

Additive genetic variance

G x E interaction:
= additive genetic variance of plasticity

No mean plasticity

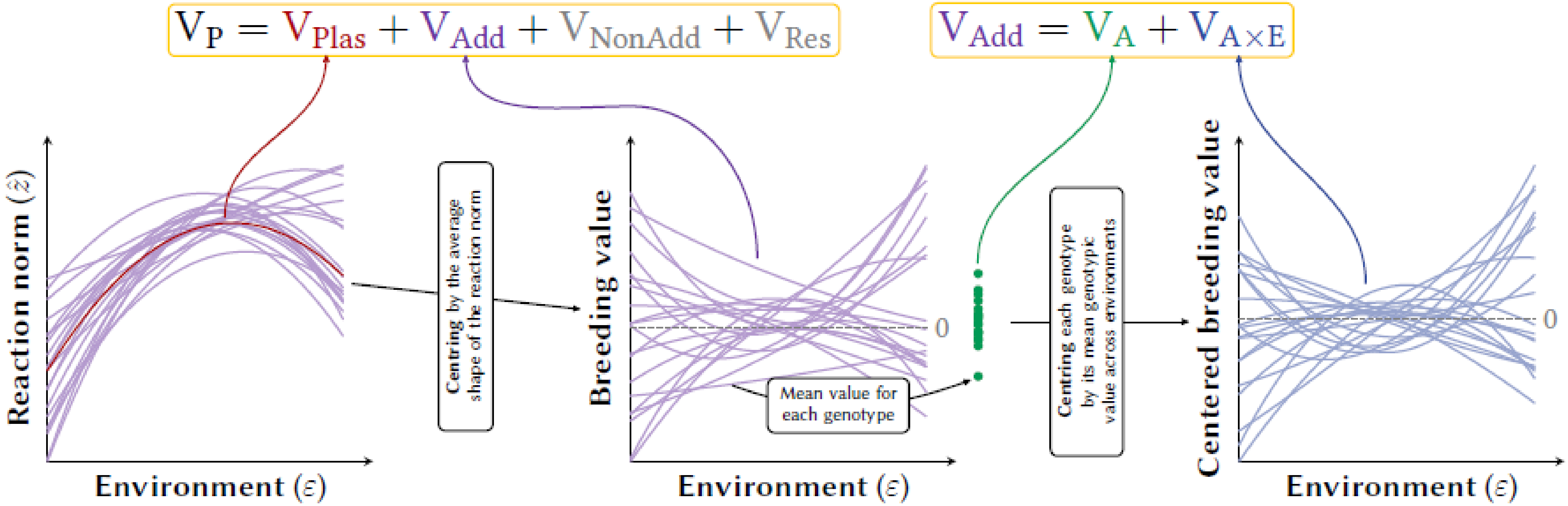
Positive mean plasticity



Genetic variance of reaction norms

Pierre de Villemereuil

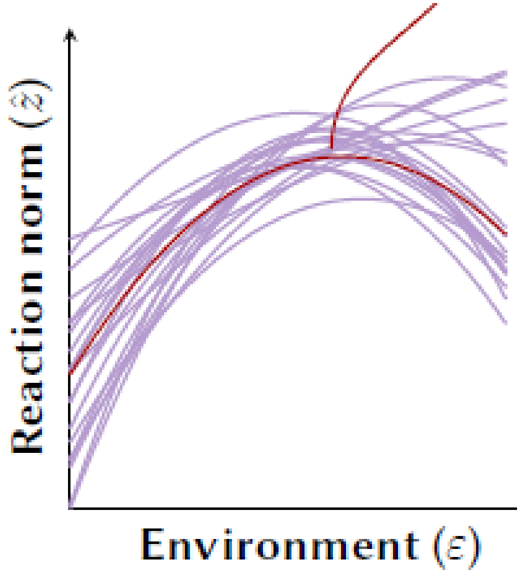
- General approach to partition the phenotypic variance of reaction norms, encompassing character state and curve parameter approach



De Villemereuil & Chevin (EcoEvorXiv)

Genetic variance of reaction norms

- General approach to partition the phenotypic variance of reaction norms, encompassing character state and curve parameter approach
- Allows quantifying the contributions of different components of reaction norm shape to (i) overall mean plasticity and (ii) additive genetic variance across environments



$P^2_{RN} = 0.56$	$\pi_{Sl} = 0.33$	Contribution of mean slope to average variation across env
	$\pi_{Cv} = 0.67$	Contribution of mean curvature to average variation across env
$h^2_{RN} = 0.26$	$\gamma_a = 0.26$	
	$\gamma_b = 0.46$	Contribution of variance in slope to genetic variance of trait
	$\gamma_c = 0.35$	
$h^2 = 0.08$	$\gamma_{ac} = -0.07$	
	$\iota_b = 0.67$	Contribution of variance in slope to genetic variance in plasticity
$h^2_I = 0.18$	$\iota_c = 0.33$	

De Villemereuil & Chevin (EcoEvorXiv)

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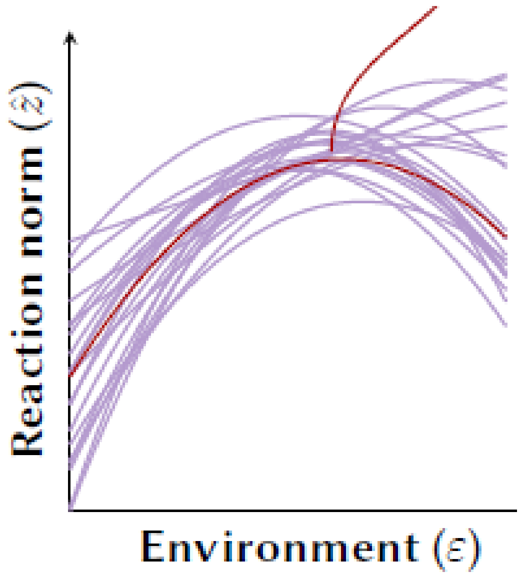
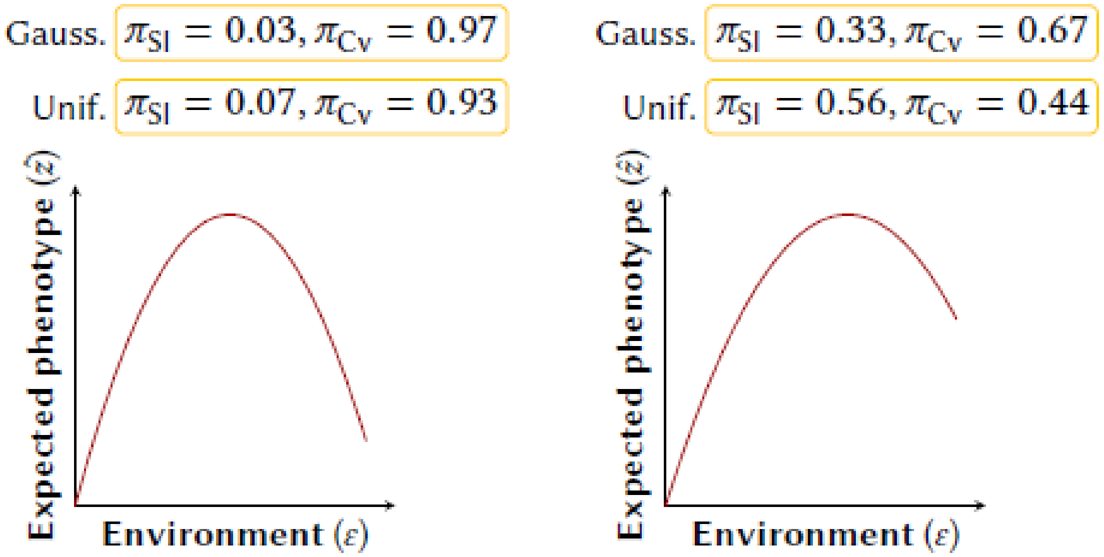


Contributions depend on environmental range and distribution

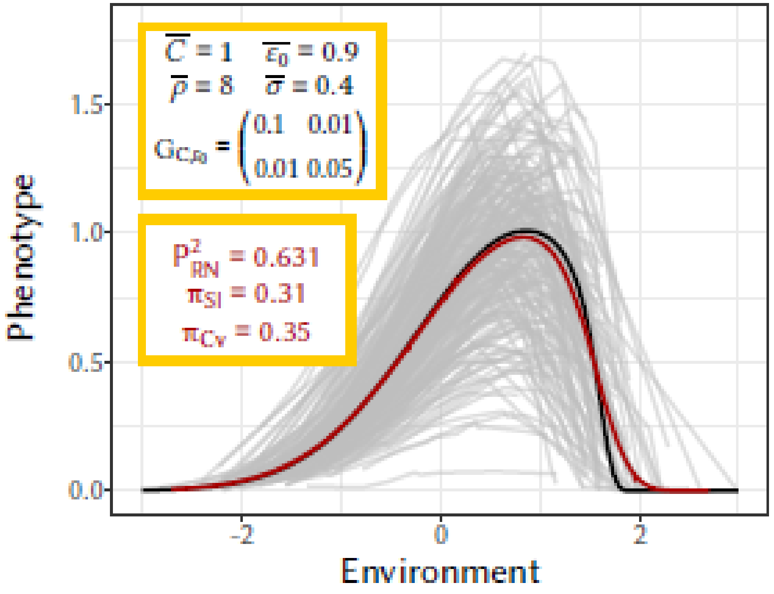


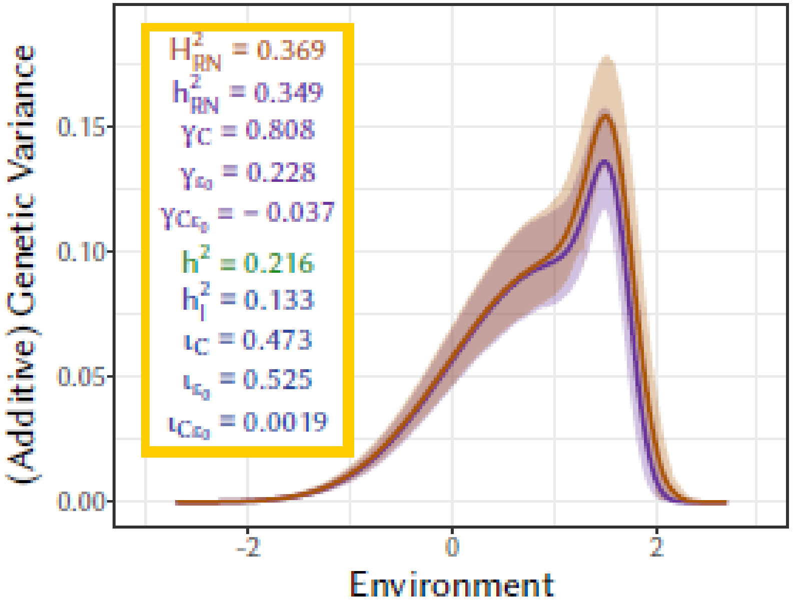
De Villemereuil & Chevin (EcoEvorXiv)

Genetic variance of reaction norms

- General approach to partition the phenotypic variance of reaction norms, encompassing character state and curve parameter approach
- Allows quantifying the contributions of different components of reaction norm shape to (i) overall mean plasticity and (ii) additive genetic variance across environments
- Applicable to reaction norms that are non-linear in their parameters

$$f(\varepsilon) = Ce^{-e^{\rho(\varepsilon-\varepsilon_0)-6}-\sigma(\varepsilon-\varepsilon_0)^2}$$





De Villemereuil & Chevin (EcoEvorXiv)

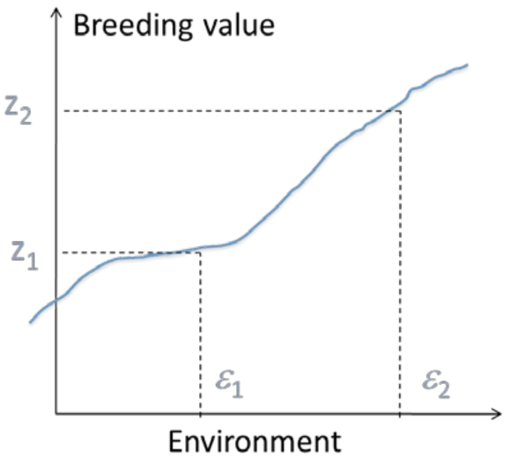
Genetic variance of reaction norms

- General approach to partition the phenotypic variance of reaction norms, encompassing character state and curve parameter approach[1]
- Allows quantifying the contributions of different components of reaction norm shape to (i) overall mean plasticity and (ii) additive genetic variance across environments
- Applicable to reaction norms that are non-linear in their parameters
- These metrics can be estimated using (non-linear) random regression (R Package on the way!)

De Villemereuil & Chevin (EcoEvorXiv)

Response to selection

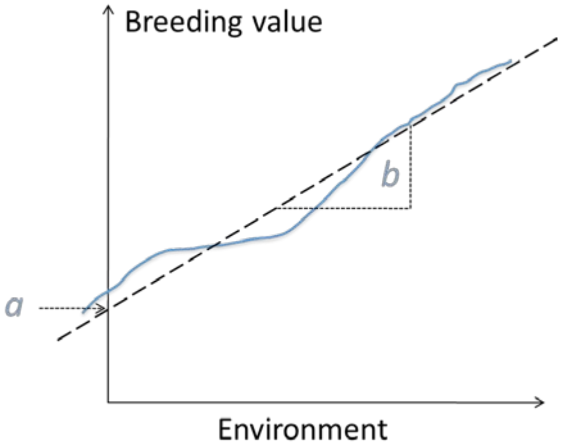
- For Gaussian polygenic traits, the multivariate breeder's equation[1] applies to parameters of the reaction norm[2]



$$\mathbf{z} = \begin{pmatrix} z_1 \\ z_2 \\ \ldots \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} a \\ b \\ \ldots \end{pmatrix}$$

Character state approach

Curve parameter approach



$$\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}$$

Change in the mean reaction norm ← $\Delta\bar{\mathbf{z}}$

$\mathbf{G}$ → Additive genetic covariance matrix of reaction norm parameters

$\boldsymbol{\beta}$ → **Directional gradient**: Strength of selection on each reaction norm parameter.

1: Lande (1979 Evolution); 2: Falconer (1952 Am Nat); Via & Lande (1985 Evolution); de Jong (1990 Am Nat); Gavrilets & Scheiner (1993 JEB)

Response to selection

- In curve parameter approach, parameters of reaction shape are selected indirectly via their effects on the trait across environments. For parameter ϑ

$$\beta_{\vartheta} = \frac{\partial ln\overline{W}}{\partial \vartheta} = \frac{\partial ln\overline{W}}{\partial \bar{z}} \frac{\partial \bar{z}}{\partial \vartheta}$$

- $\frac{\partial \bar{z}}{\partial \vartheta}$ is the reaction norm gradient, which depends on environment
- For instance with linear reaction norms $z = a + b\varepsilon + e$,

where slope b quantifies plasticity, we have $\psi_a = \frac{\partial \bar{z}}{\partial \bar{a}} = 1\,, \psi_b = \frac{\partial \bar{z}}{\partial \bar{b}} = \varepsilon$

$$\boldsymbol{\beta}_{\mathbf{RN}} = \begin{pmatrix} \beta_a \\ \beta_b \end{pmatrix} = \beta_z \begin{pmatrix} \psi_a \\ \psi_b \end{pmatrix} = \beta_z \begin{pmatrix} 1 \\ \varepsilon \end{pmatrix}$$

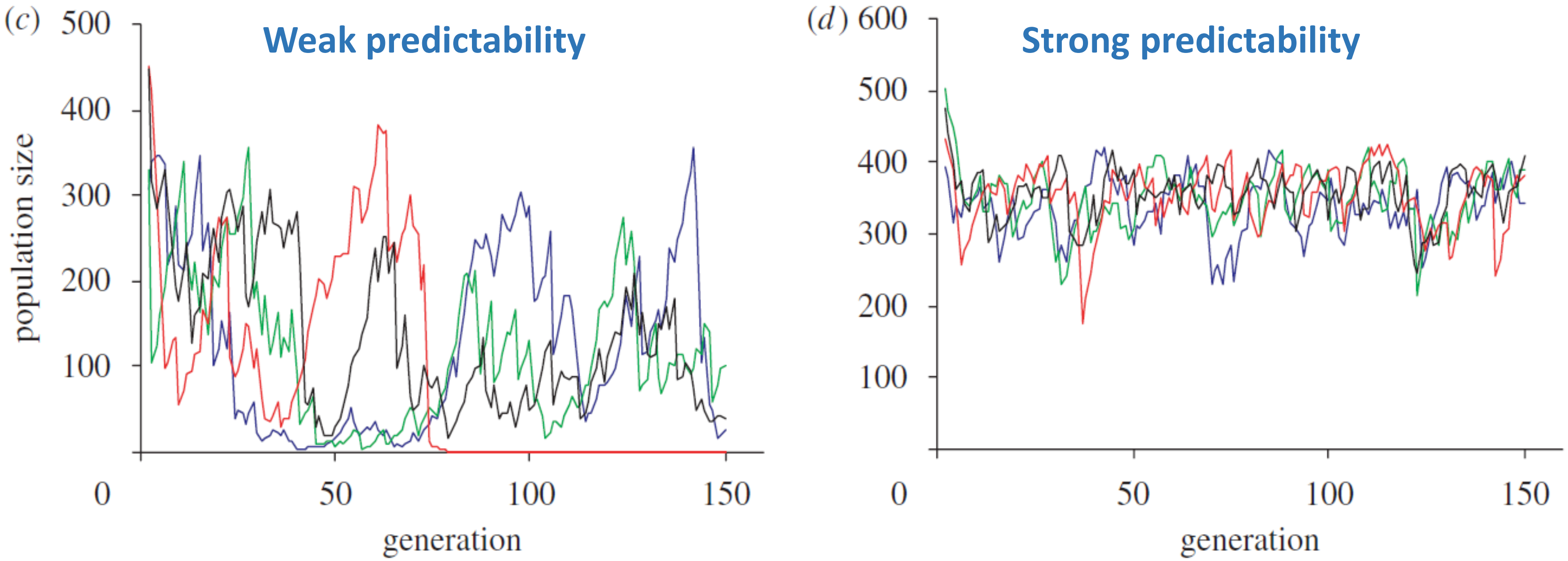
Gavrilets & Scheiner 1993 JEB, de Jong 1999 JEB

Outline of the talk

1. Genetic variation and selection on plasticity
2. **Evolution of plasticity in fluctuating environments**
3. Evolution of plasticity in novel and extreme environments

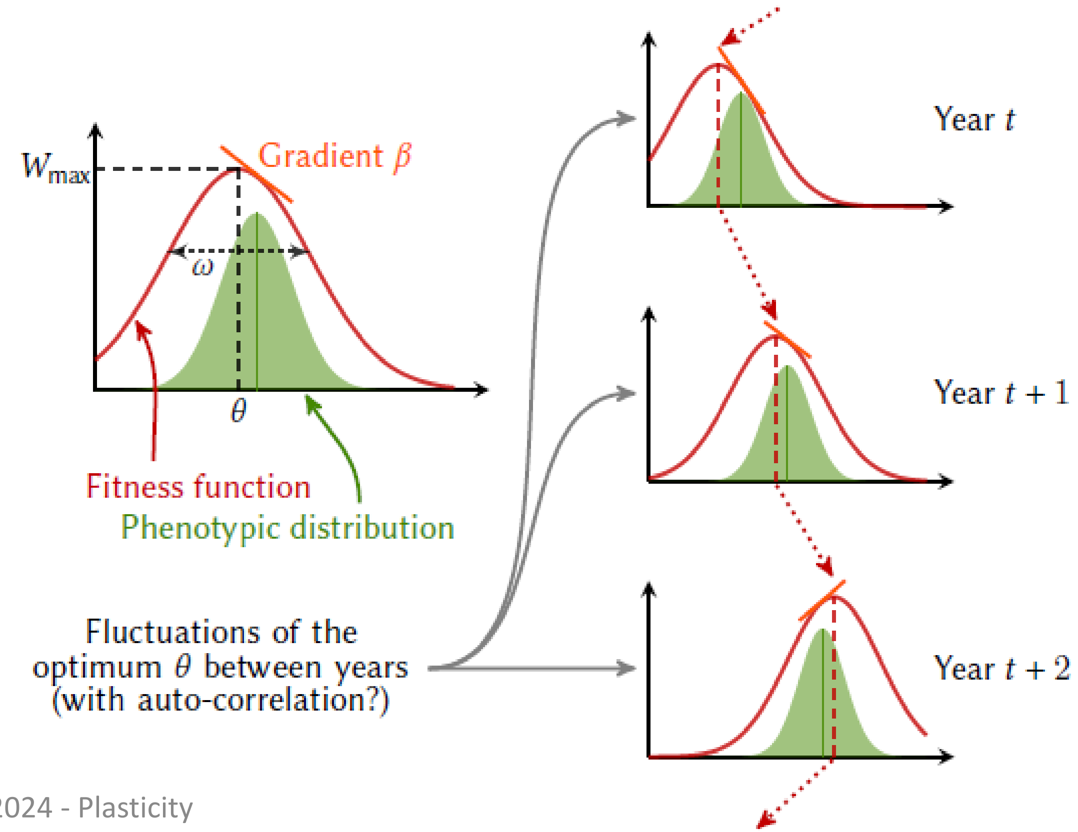
Plasticity and fluctuating environments

- Under stationary fluctuations, reaction norm slope affects the **variance of phenotypic mismatch $\bar{z} - \theta$**
- Plasticity buffers impacts of fluctuating environment **only if the inducing environment accurately predicts future selective pressure**
- Otherwise plasticity increases phenotypic mismatches (eg overshoots optimum), amplifies fluctuations in fitness, and may cause extinction[1]



Plastic tracking of fluctuating optimum in the wild

- Estimating fluctuating optimum on breeding date in birds and mammals
- Variance of mismatch is $\mathrm{V}(\bar{z}-\theta) = \mathrm{V}(\theta) + V(\bar{z}) - 2\mathrm{Cov}(\bar{z},\theta)$
- Fluctuating selection can be buffered if $\mathrm{Cov}(\bar{z},\theta) > 0$ (adaptive tracking)



De Villemereuil et al (2020 PNAS)

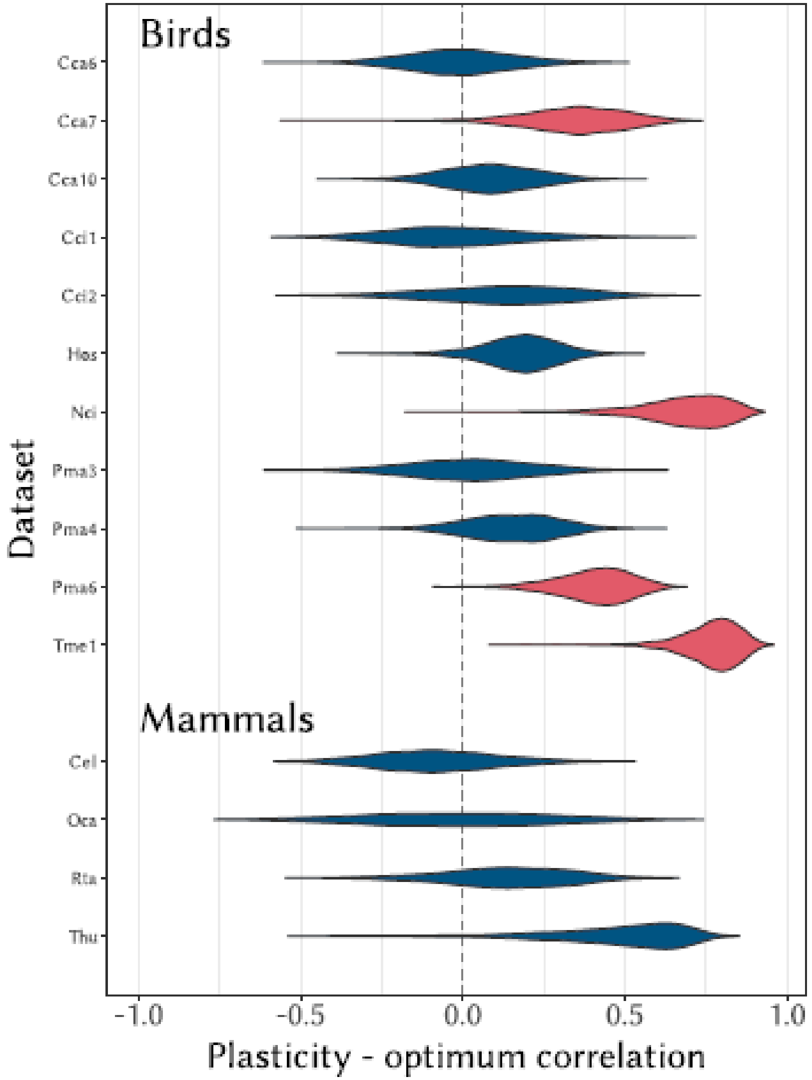
Plastic tracking of fluctuating optimum in the wild

- **Plastic changes in $\bar{z}$** 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)



De Villemereuil et al (2020 PNAS)

Evolution in fluctuating environment

- Focus on linear reaction norms: $z = a + b\varepsilon_d + e$
  Phenotype depends on environment of development ε_d
- Optimum phenotype assumed to also change linearly with environment of selection:
  $\theta = A + b\varepsilon_s$
- Response to selection in one generation: $\Delta\begin{pmatrix}\bar{a}\\ \bar{b}\end{pmatrix} = \mathbf{G\beta} = \beta_z \begin{pmatrix} G_a & G_{ab} \\ G_{ab} & G_b \end{pmatrix}\begin{pmatrix}1\\ \varepsilon_d\end{pmatrix}$
  with $\beta_z = -S(\bar{z} - \theta) = -S\left(\bar{a} - A + \bar{b}\varepsilon_d - B\varepsilon_s\right)$
- In a stationary fluctuating environment with mean 0 and variance σ_ε^2

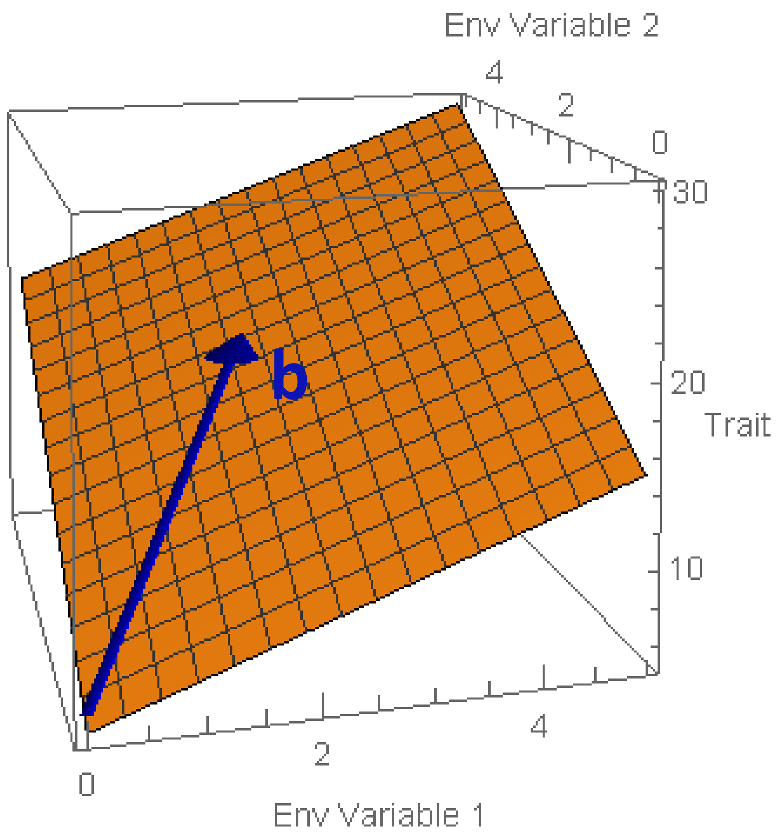
$$\mathrm{E}(\boldsymbol{\beta}) = -S\begin{pmatrix} \bar{a} - A \\ (\bar{b} - B\rho_{ds})\sigma_\varepsilon^2 \end{pmatrix}$$

→ Plasticity evolves to slope of optimum B discounted by correlation ρ_{ds} between environment of development of selection.
Faster evolution under larger magnitude σ_ε^2 of environmental fluctuations

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

Complex cues

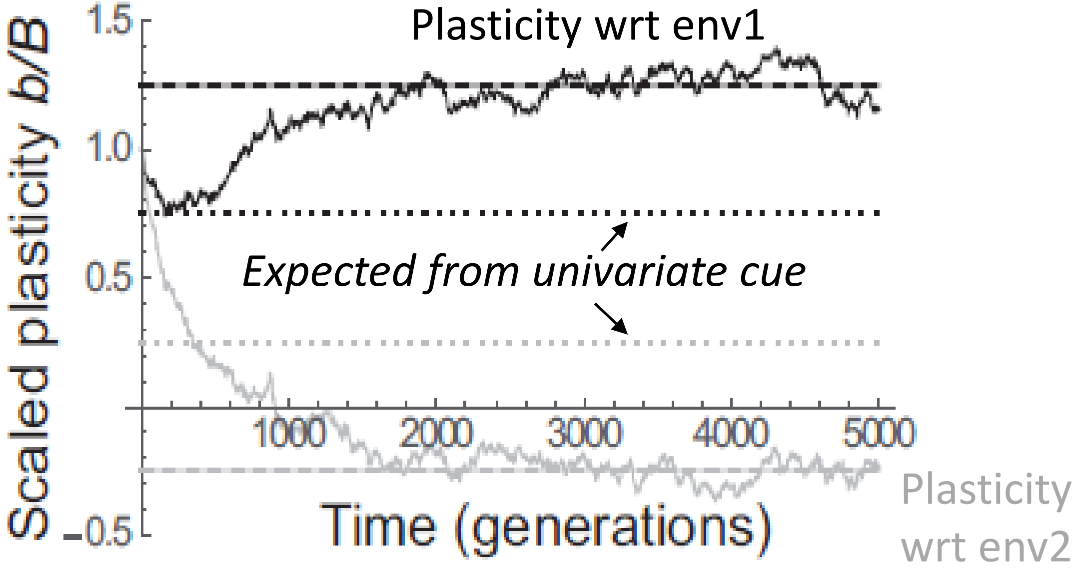
- In complex multidimensional environments, reaction norm becomes a (hyper)plane
- Plasticity vector **b** gives direction of steepest slope on this plane → linear combination of environments eliciting larger plastic response = **multivariate cue**



1: Chevin & Lande (2015 Evolution)

Complex cues

- In complex multidimensional environments, reaction norm becomes a (hyper)plane
- In fluctuating environment, equilibrium cue is linear combination of environmental variables that best predicts movements of optimum
- Plasticity wrt specific environmental variables can be in excess/opposite to changes of optimum[1], but plastic response to full multivariate cue is still adaptive.



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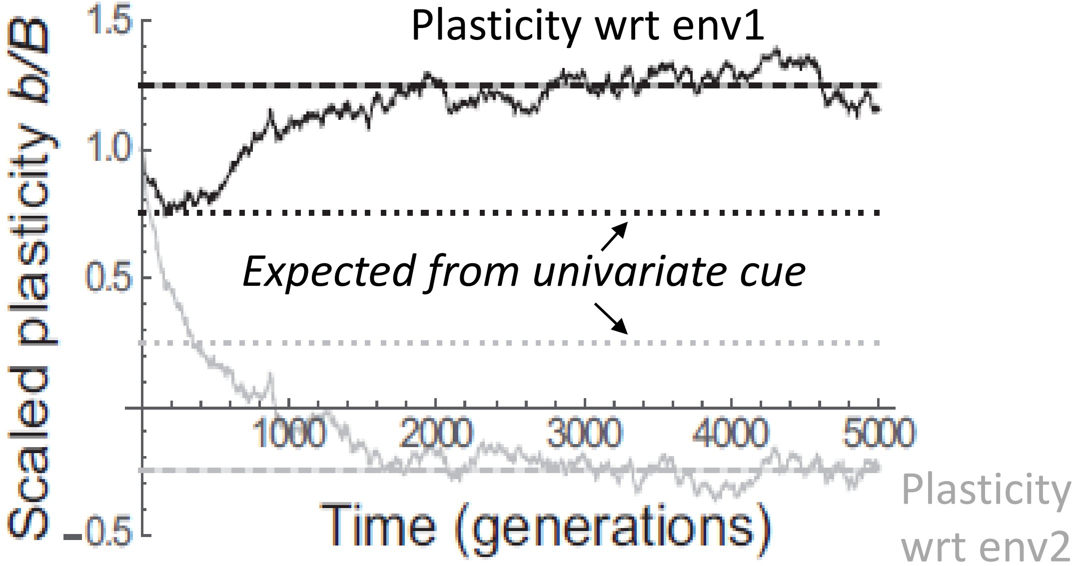
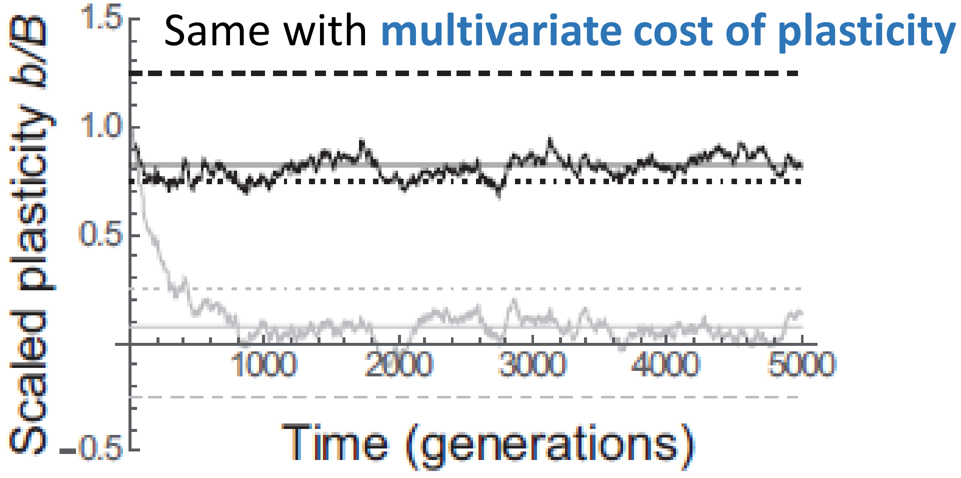
- In fluctuating environment, equilibrium cue is linear combination of environmental variables that best predicts movements of optimum
- Plasticity wrt specific environmental variables can be in excess/opposite to changes of optimum[1], but plastic response to full multivariate cue is still adaptive.
- Multivariate costs of plasticity can make plasticity closer to slope of optimum wrt single cues

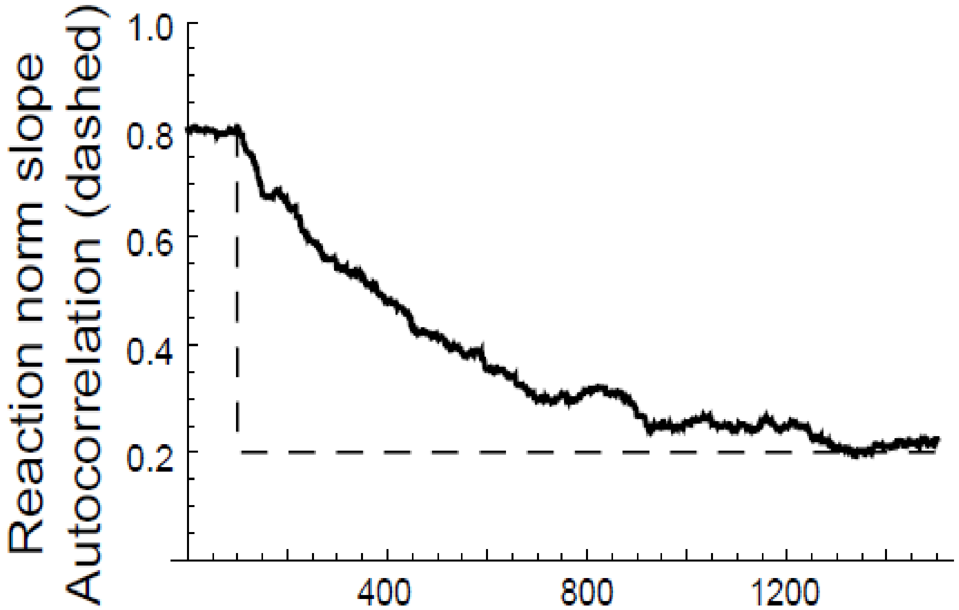


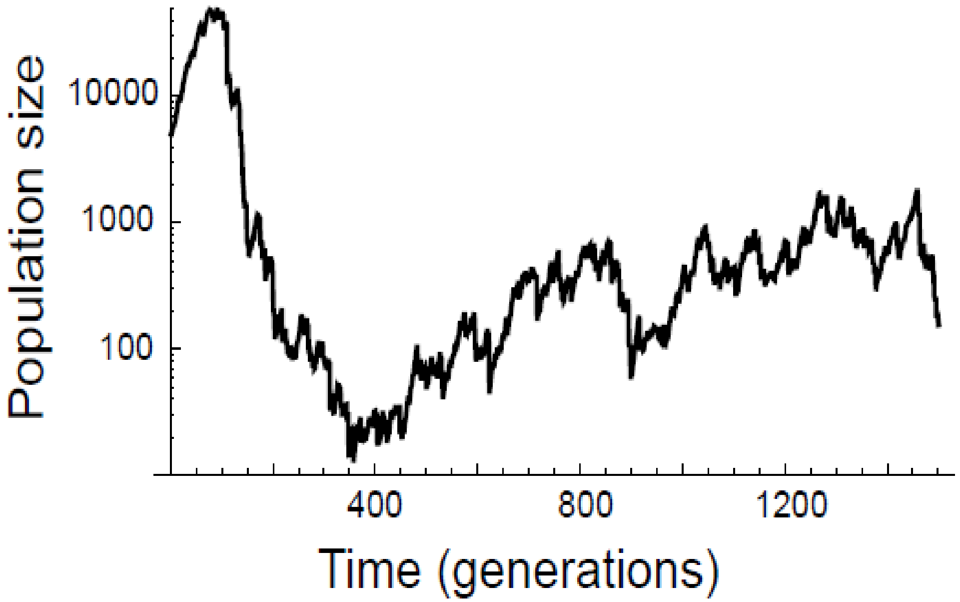


1: Chevin & Lande (2015 Evolution)

Plasticity and environmental 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)

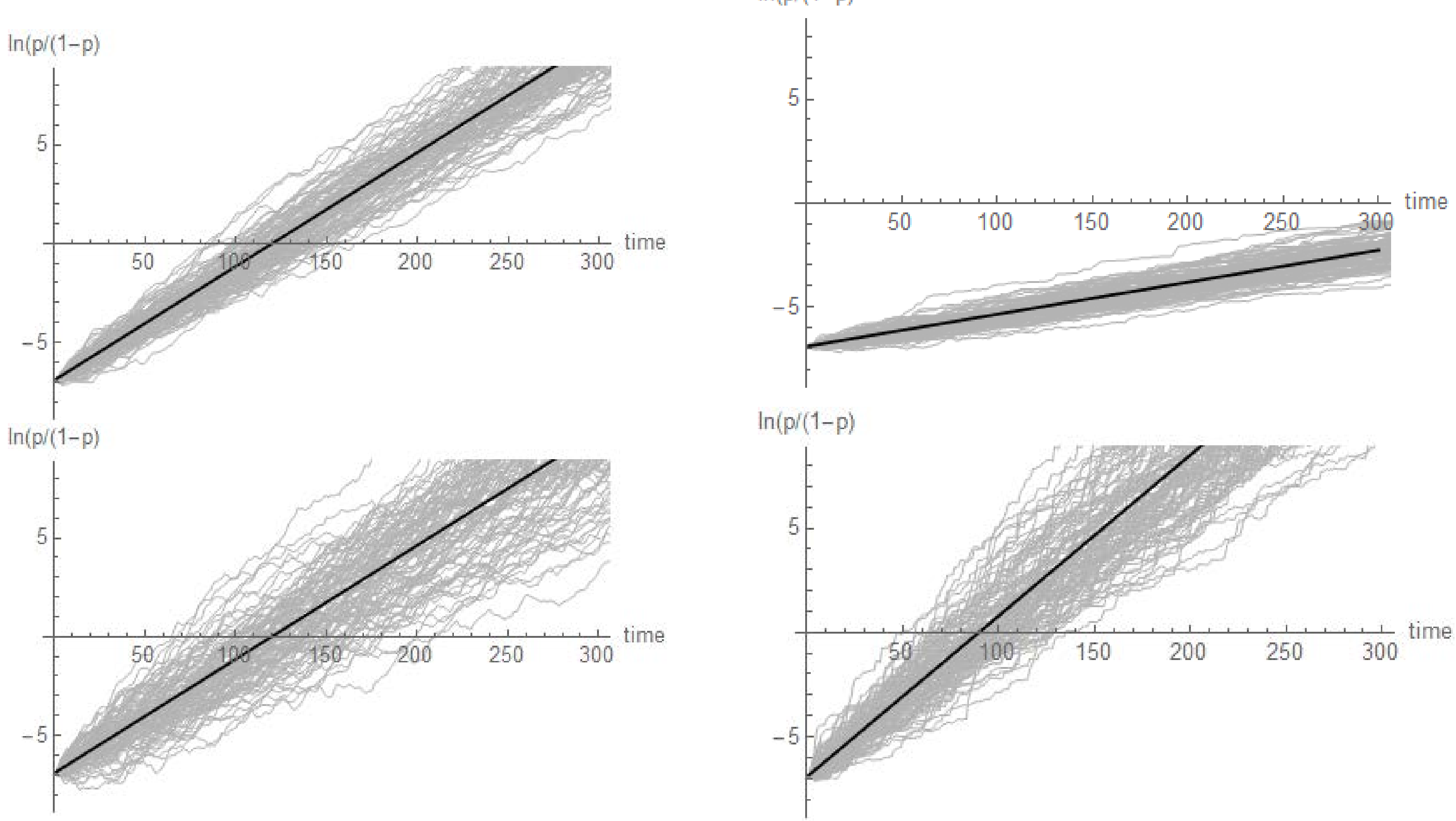
Selection at QTL for plasticity

- For a plasticity QTL (environment-dependent effect), **environmental fluctuations of optimum phenotype influence expected frequency change**, unlike for classic QTL

Classic QTL **Plasticity QTL**

Small environmental fluctuations

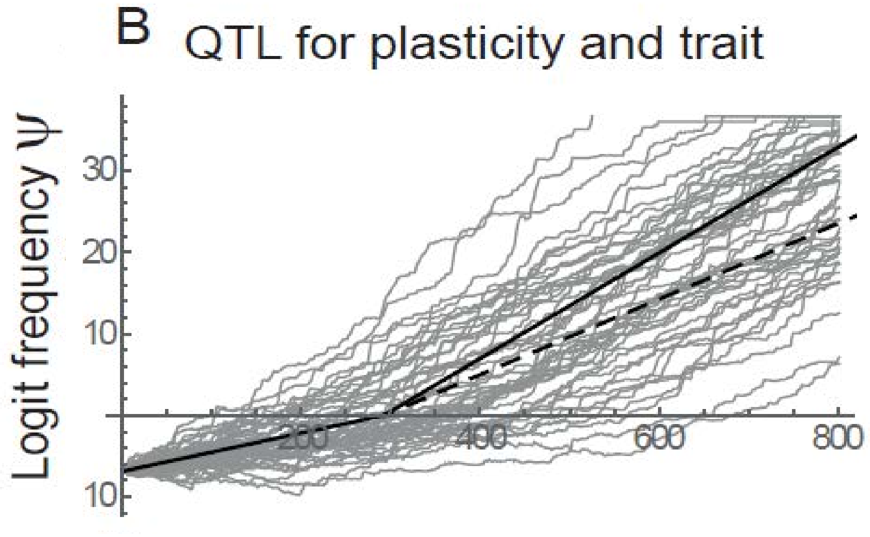
Large environmental fluctuations

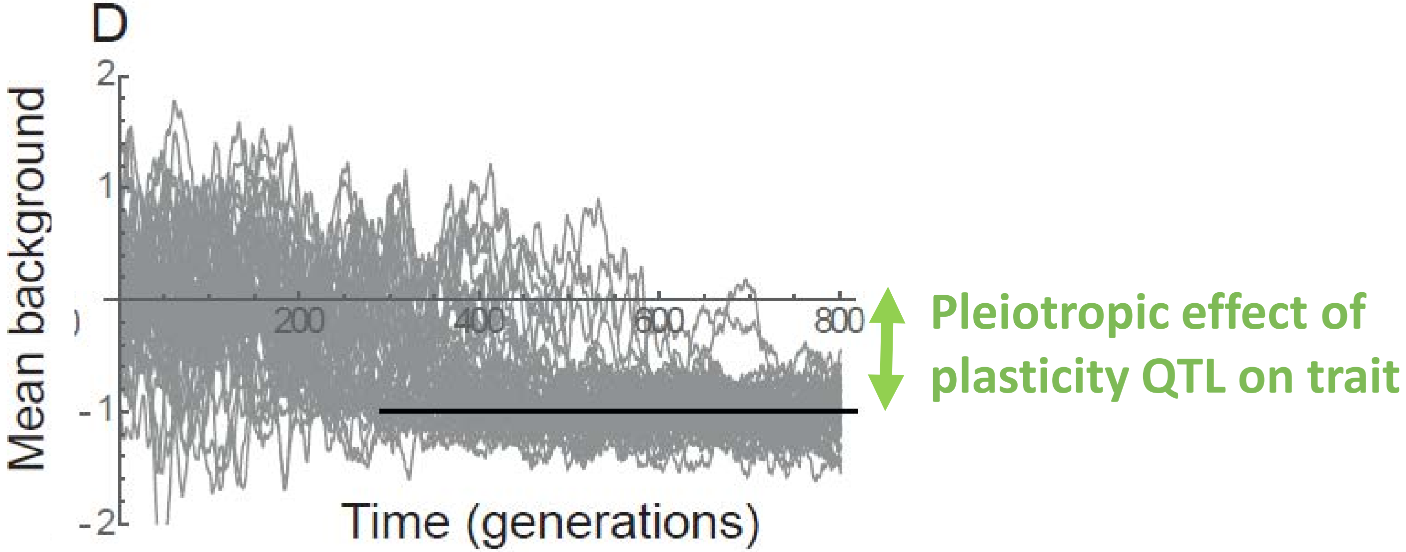


Chevin (2019 Genetics)

Selection at QTL for plasticity

- For a plasticity QTL (environment-dependent effect), **environmental fluctuations of optimum phenotype influence expected frequency change**, unlike for classic QTL
- An allele with a beneficial effect on plasticity (adaptation to fluctuations) can **spread despite detrimental side effect on the mean trait** (deviation from expected optimum)
- The mean background phenotype then evolves to **compensate for the pleiotropic effect**

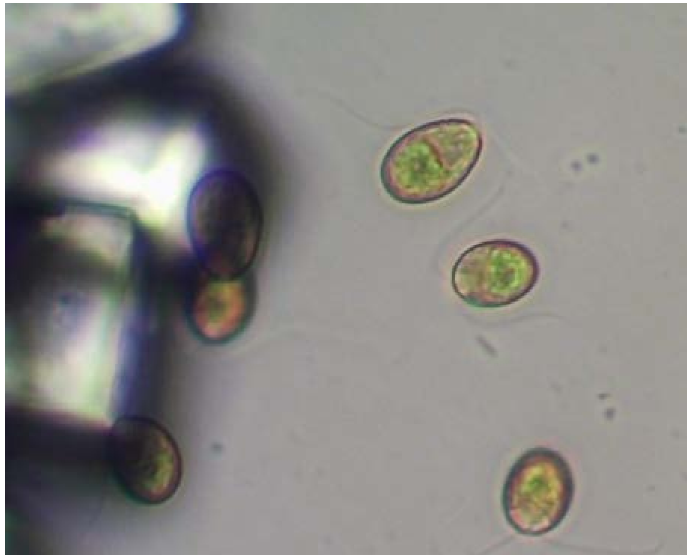




Chevin (2019 Genetics)

Experiments under randomly fluctuating salinity

- Microalga ***Dunaliella salina*****:**
  model organism for salinity tolerance
  Most halotolerant eukaryote (freshwater to saturated brine).
- Common in shallow coastal lagoons & salterns.
  Salinity fluctuates with precipitation, wind, sunlight…
- **Extremophile**: few ecological interactions
  → Niche easily mimicked in the lab
- **Short generation time** ~ 1 day
- Produces β-carotene: well-studied for bio-industry



Oren (2005); Ben Amotz et al (2009)
Polle (2020 Algal Research)

Experiments under randomly fluctuating salinity

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

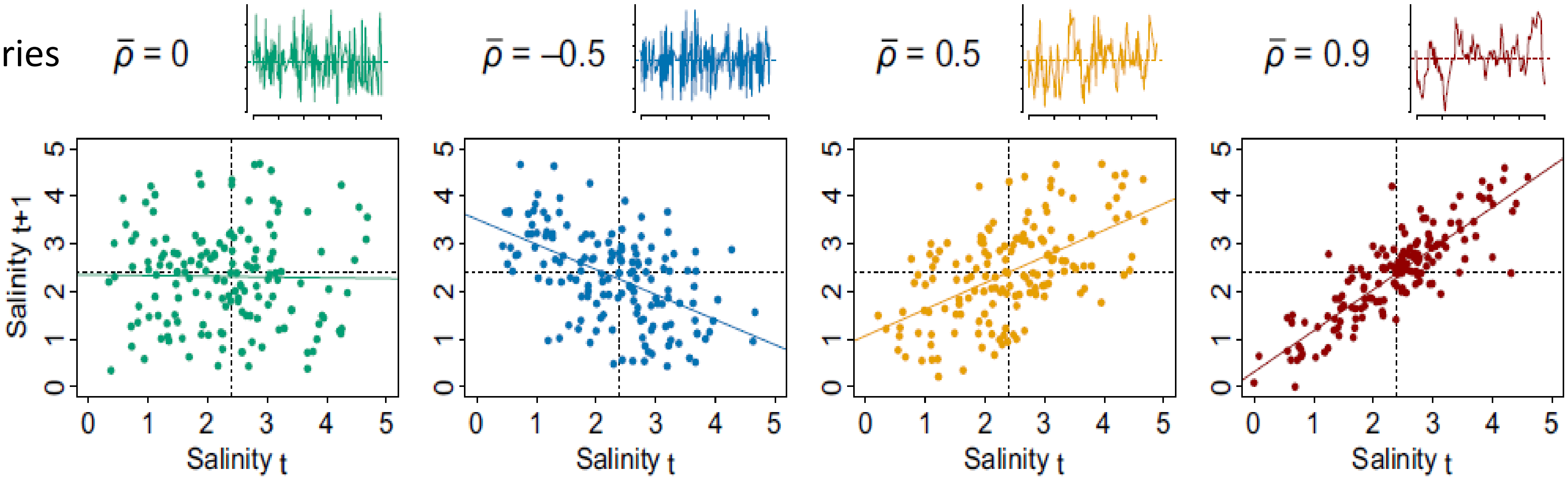
- Exposed during several months
  = hundreds of generations.

Experiments under randomly fluctuating salinity

- Random change on continuous range, with **autocorrelation as the treatment**

Salinity time series

Subsequent time points



Predictability

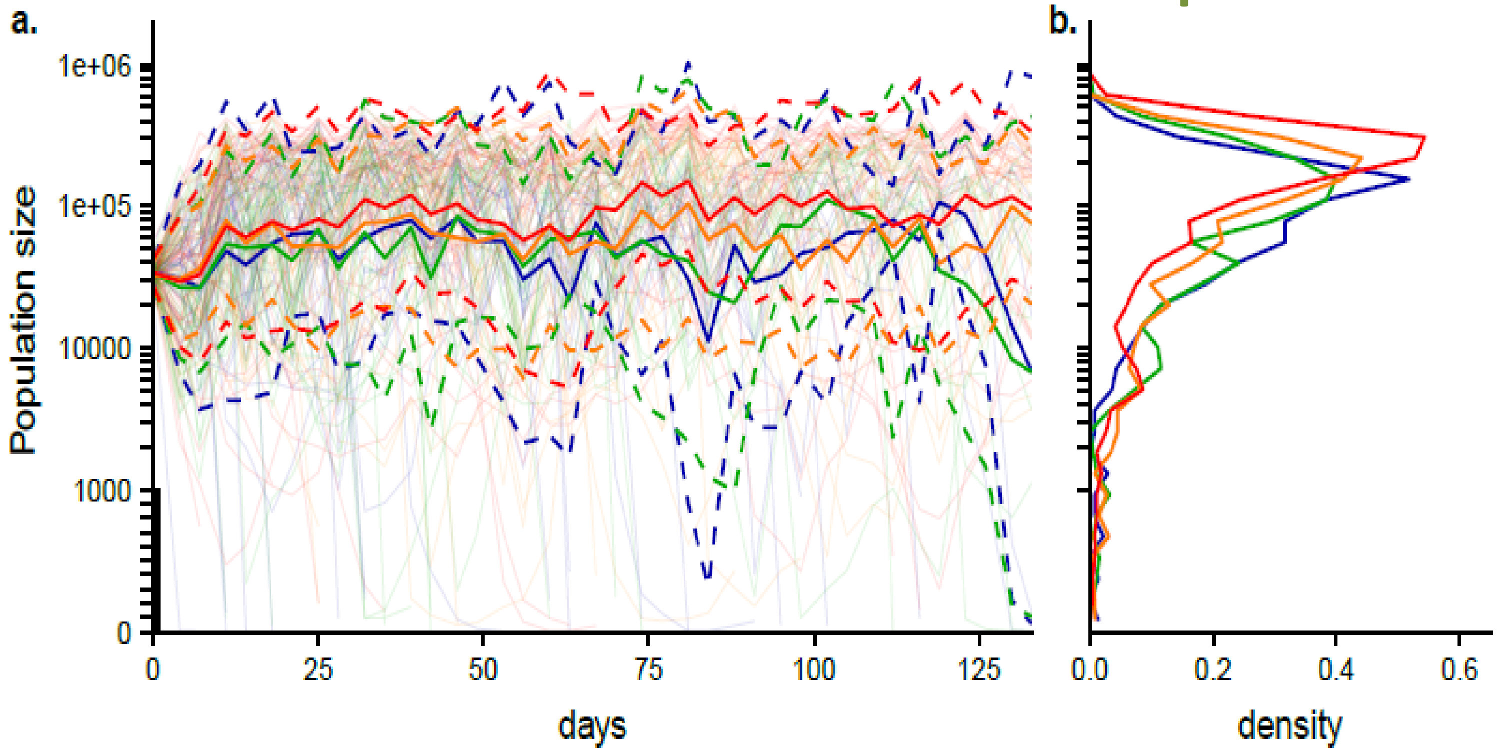
Population fluctuations

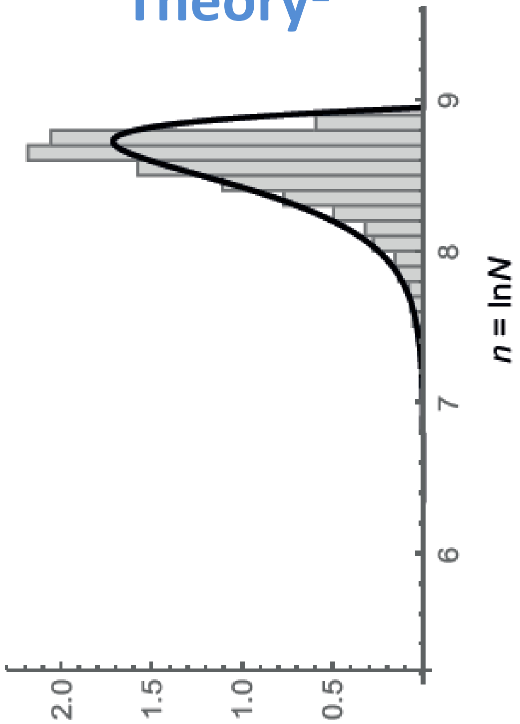
- Tracking population size through time (flow cytometry)
- Distribution of ln$N$ **similar to moving optimum theory**[1]

Marie RESCAN

Experiment[1]

Theory[2]



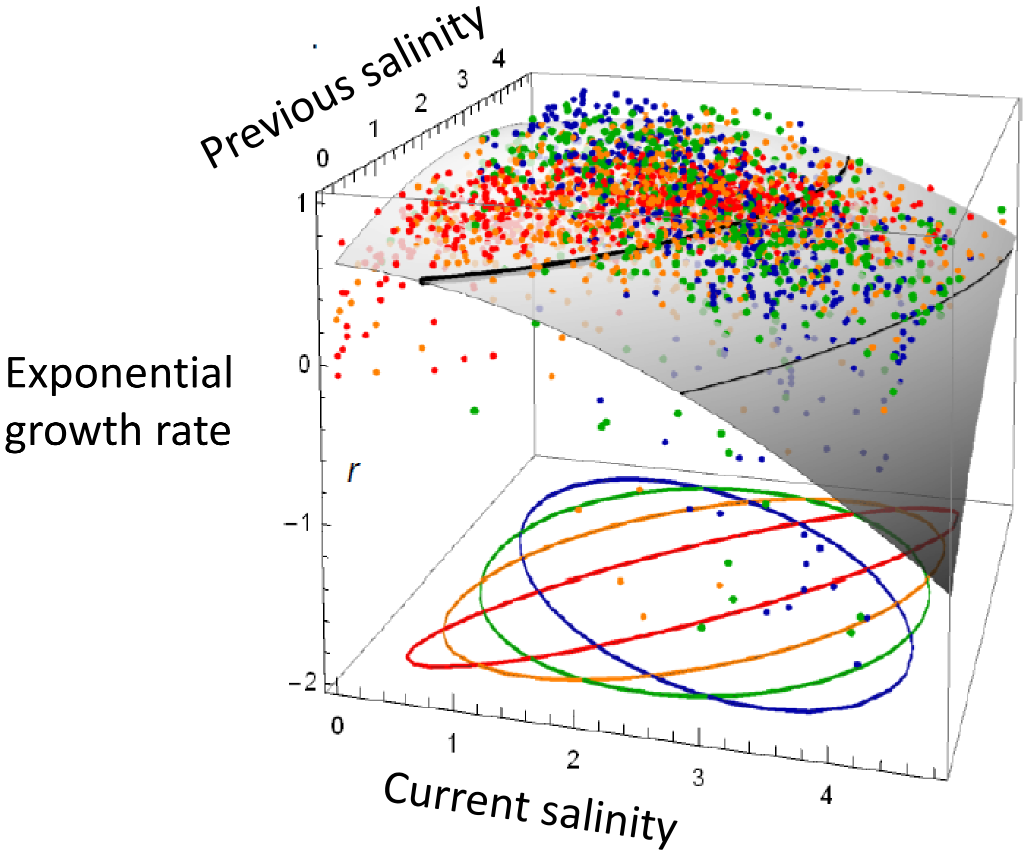


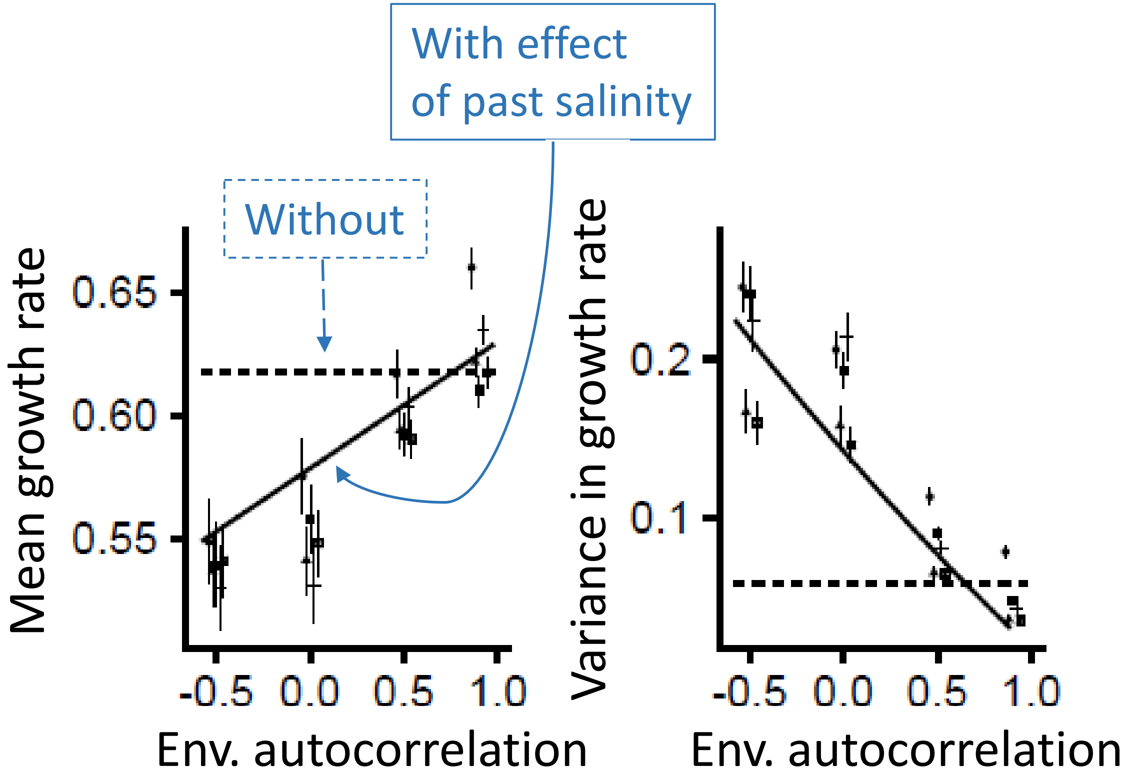
1: Rescan et al (2020 Nat Ecol Evol)
2: Chevin et al (2017 Am Nat)

Lagged plastic effects on tolerance curve

- Population growth rate depends on **current and previous salinity**
  → Phenotypic memory, persistent influence of plasticity

Marie RESCAN



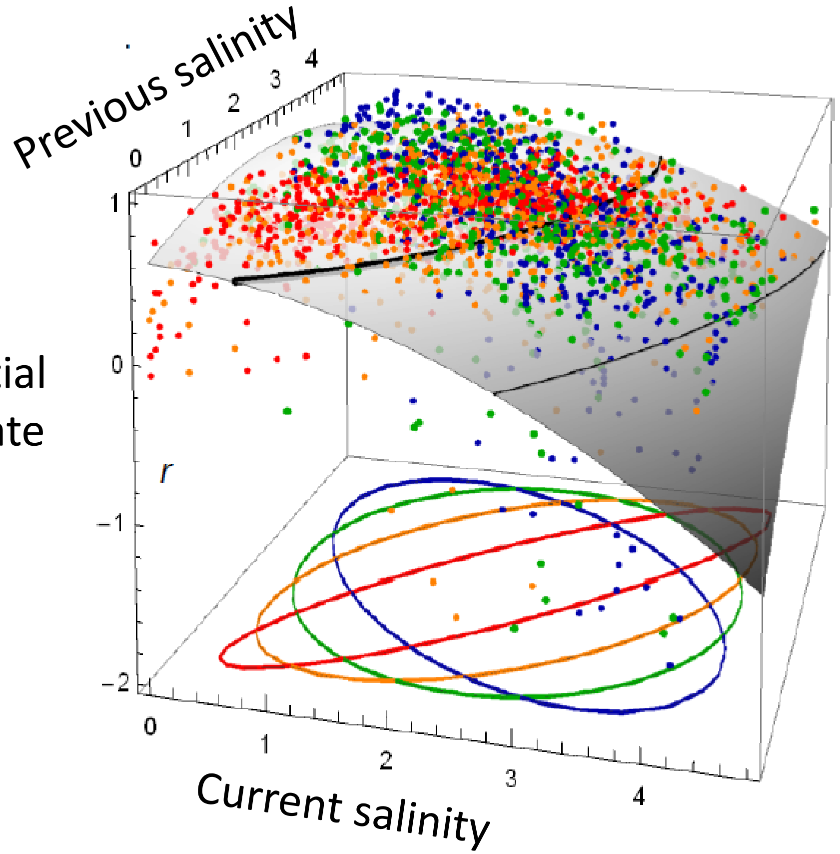


Rescan et al (2020 Nature EE)

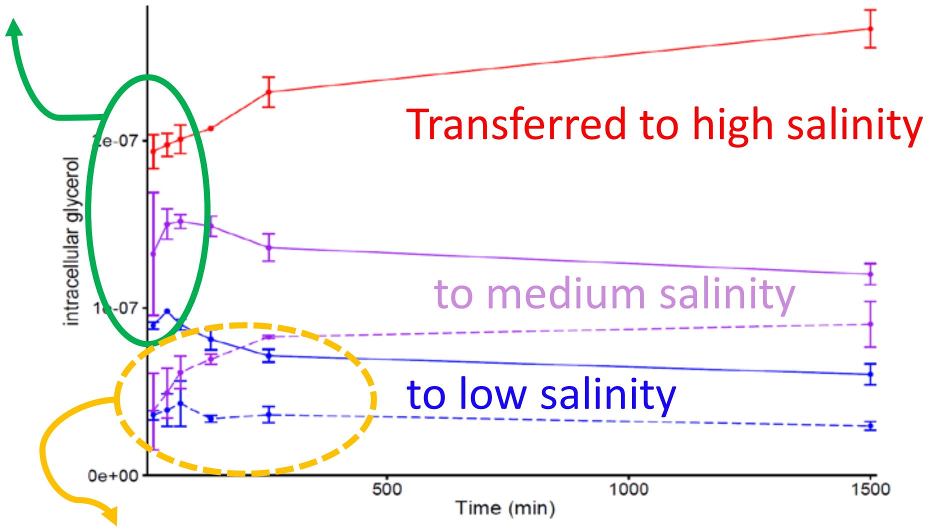
Lagged plastic effects on tolerance curve

Marie RESCAN

- Population growth rate depends on **current and previous salinity**
  → Phenotypic memory, persistent influence of plasticity
- Contribution from dynamics of glycerol = osmoregulator



Coming from high salinity:
Rapid change via **excretion**



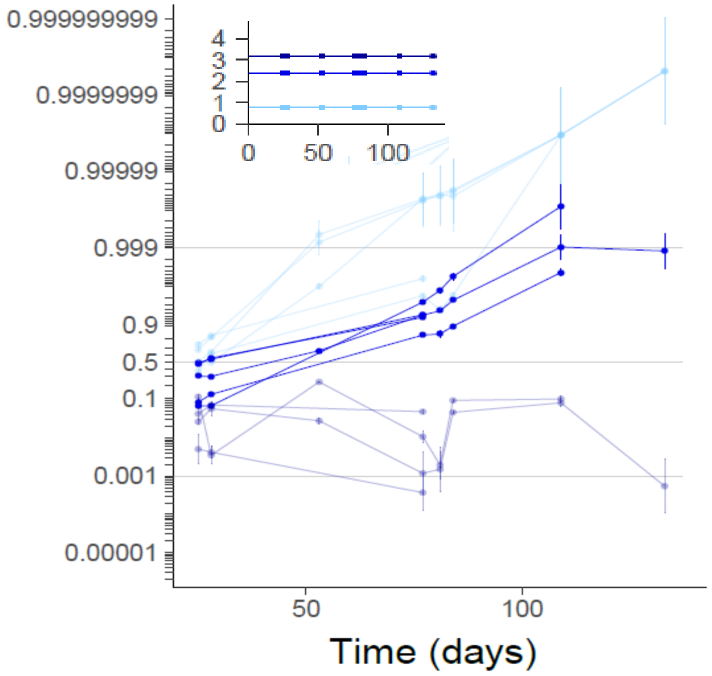
Coming from low salinity:
Slower change requiring **production**

Rescan et al (2020 Nature EE)

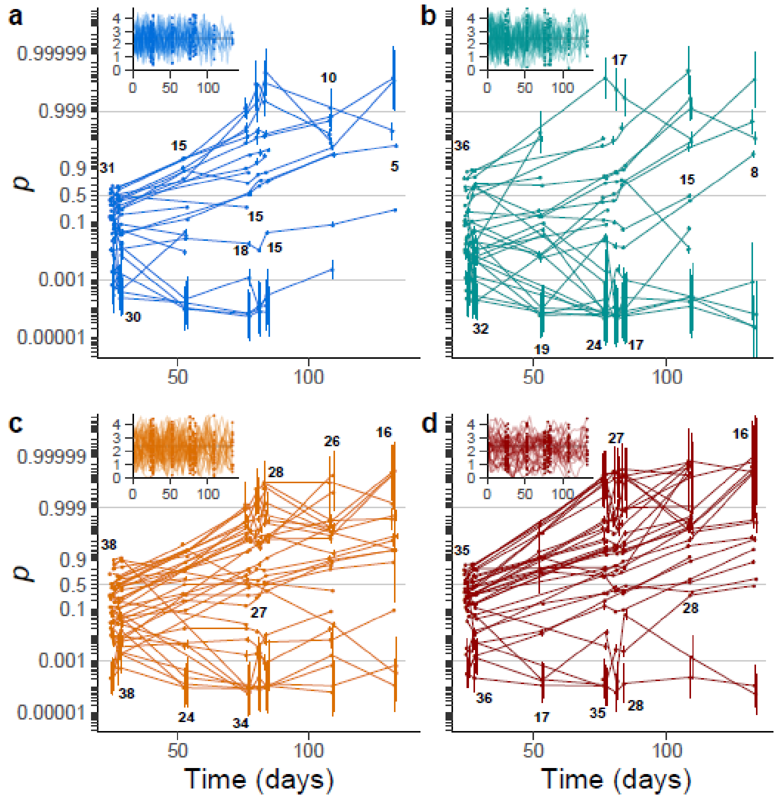
Plasticity influences competition among strains

- Tracking frequency of two strains in a mixture by amplicon sequencing of two loci (ITS and chloroplastic) at regular time points

Constant salinity



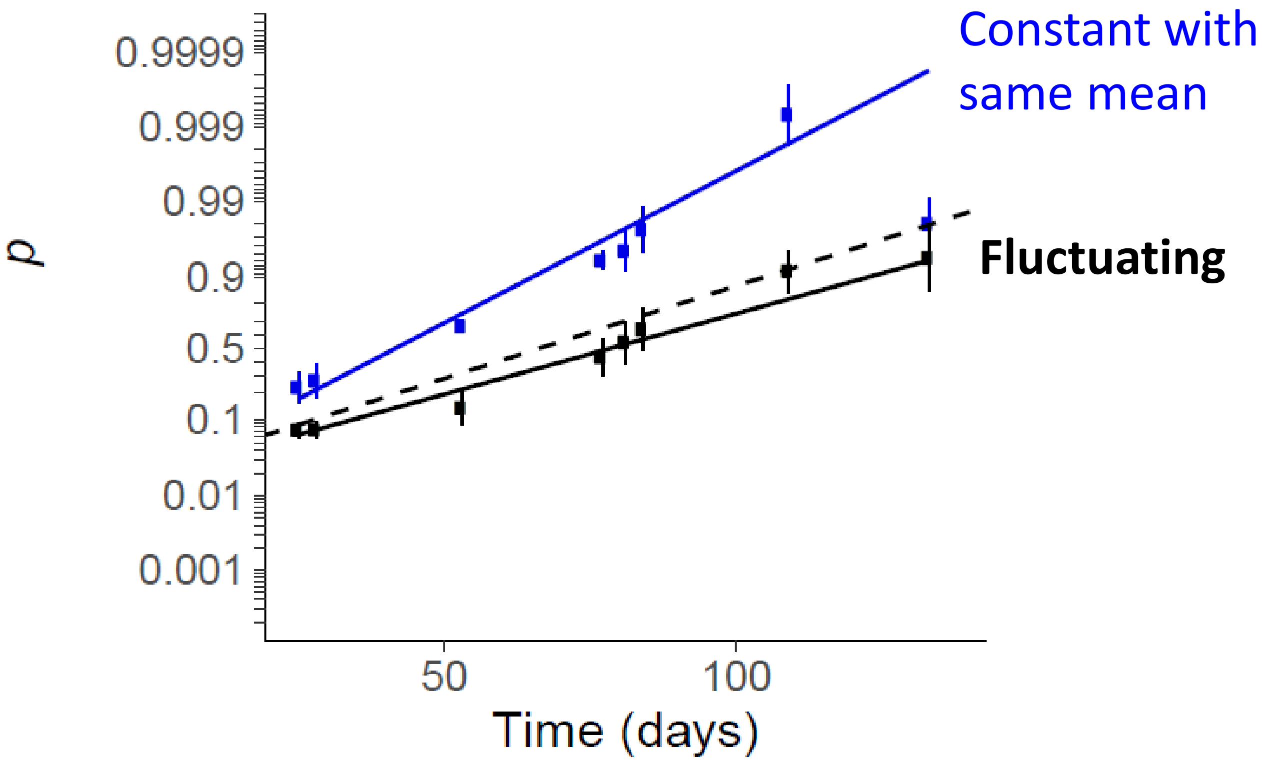
Fluctuating salinity



Rescan et al (2021 Plos Gen)

Plasticity influences competition among strains

- Analyzed by logistic regression in GLM (s = slope on logit scale)
- Environmental **fluctuations reduces the mean selection coefficient**



Rescan et al (2021 Plos Gen)

Plasticity influences competition among strains

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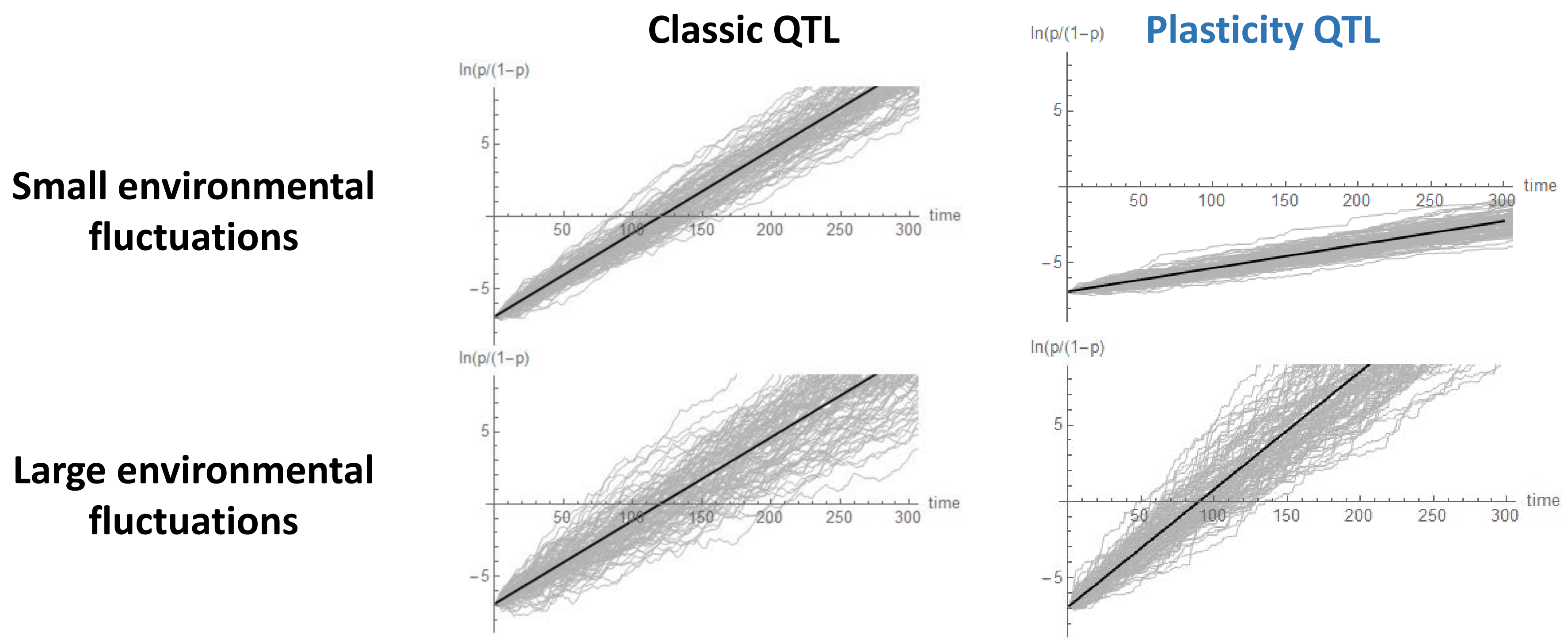
- Expected if **strains differ in plasticity/tolerance breadth**

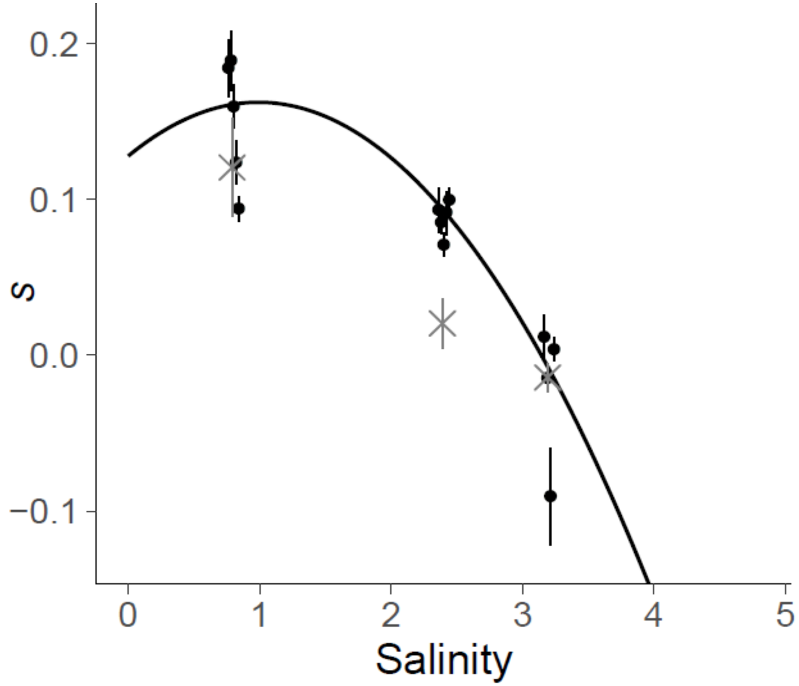


Chevin (2019 Genetics)

Rescan et al (2021 Plos Gen)

Plasticity influences competition among strains

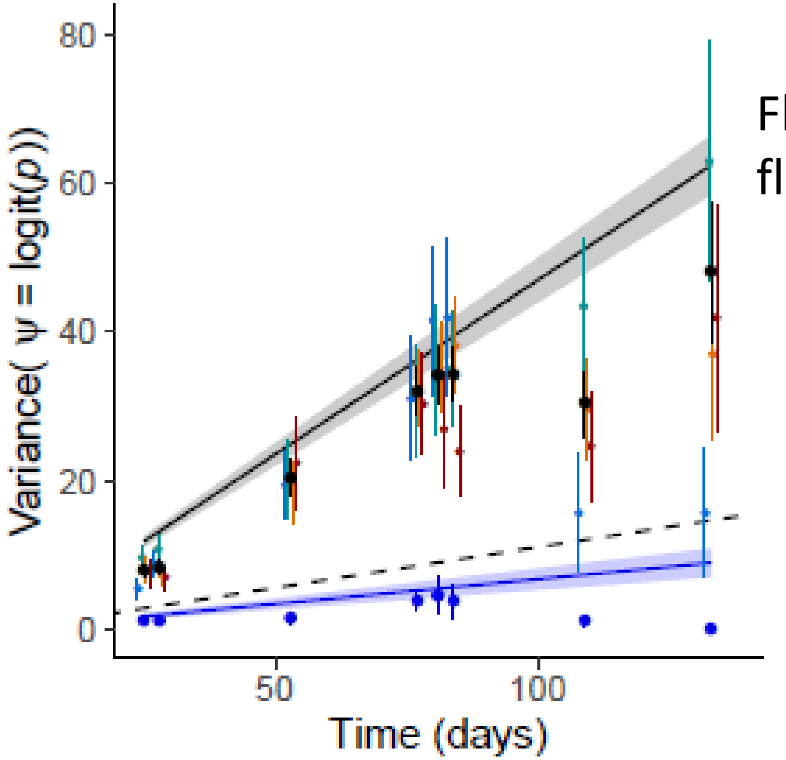
- Analyzed by logistic regression in GLM (s = slope on logit scale)
- Environmental **fluctuations reduces the mean selection coefficient**
- Expected if **strains differ in plasticity/tolerance breadth**
- Consistent with **concave relation** between selection coefficient and environment (Jensen's inequality).



Rescan et al (2021 Plos Gen)

Plasticity influences competition among strains

- Variance in frequency change estimated as random slope in logistic regression (GLMM)
- Larger in randomly fluctuating environments.
  But no detectable influence of the autocorrelation treatment on variance



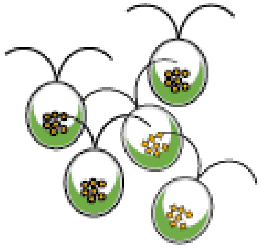
Fluctuating salinity:
fluctuating selection + drift + microenv variation

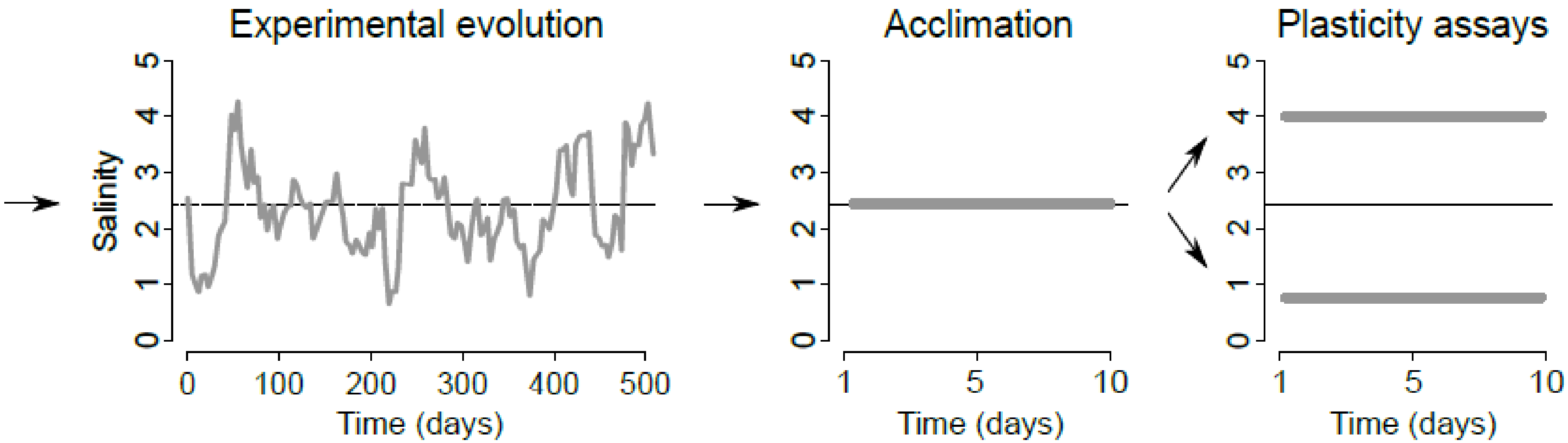
Constant salinity:
Drift + microenv variation

Rescan et al (2021 Plos Gen)

Experimental evolution of plasticity

Christelle LEUNG





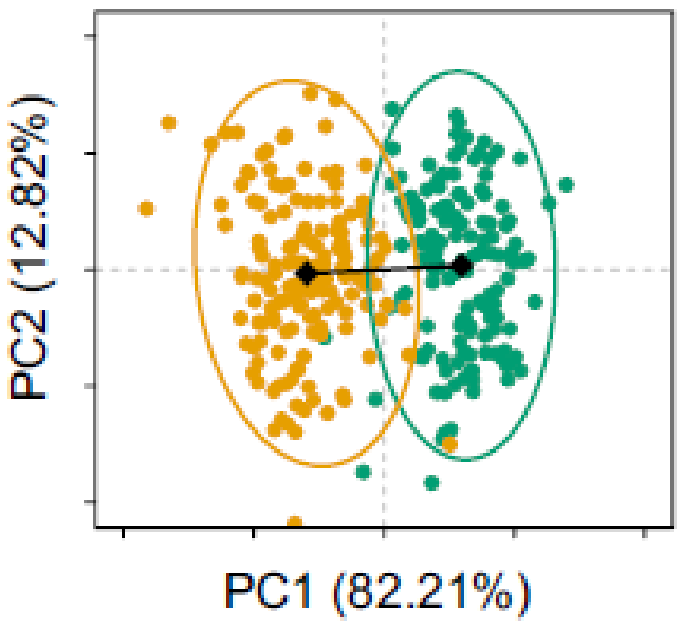
High-throughput morphological phenotyping:

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

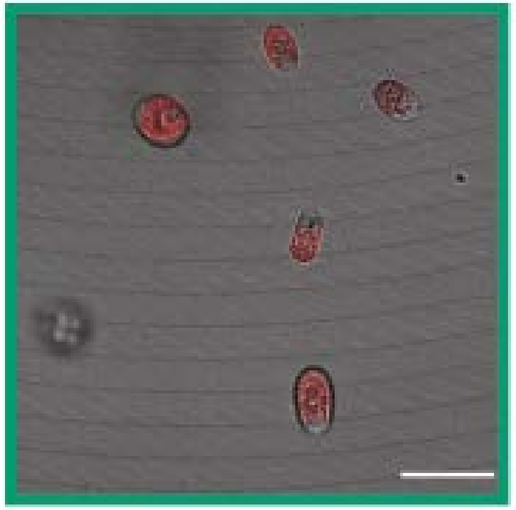
Leung et al (2020 Ecol Lett)

Experimental evolution of plasticity

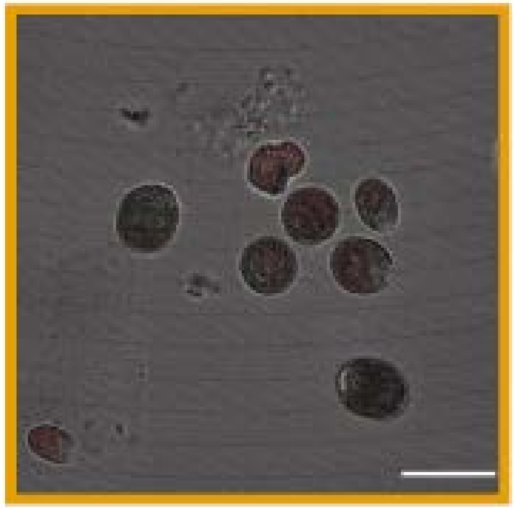
- Plastic responses of cell morphology to salinity



Low salinity



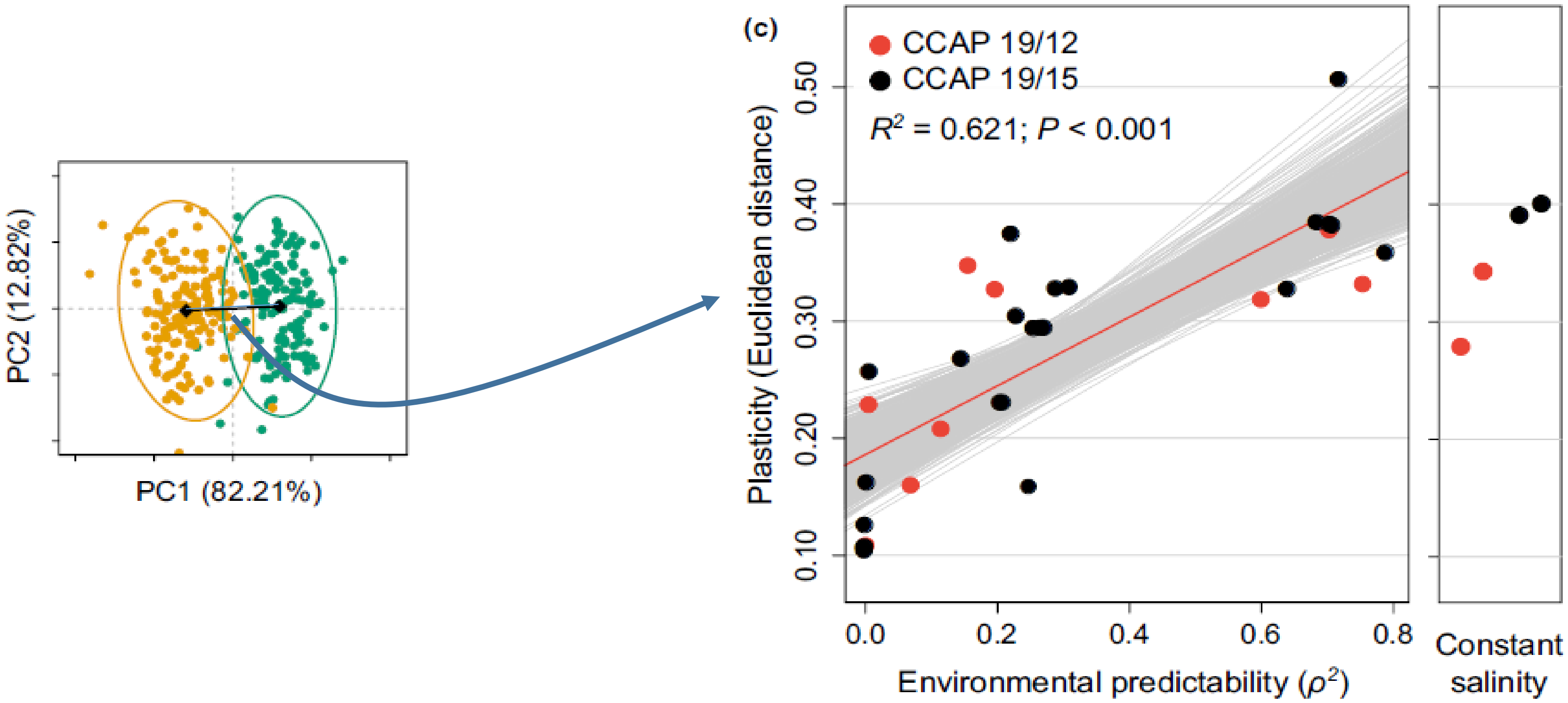
High salinity



Leung et al (2020 Ecol Lett)

Experimental evolution of plasticity

- Comparing lines from treatments with different autocorrelations:
  Reduced plasticity evolved in lines that experienced **less predictable environments**

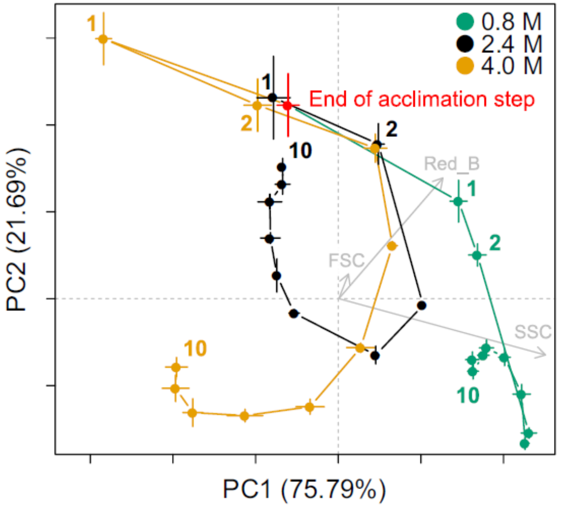


Leung et al (2020 Ecol Lett)

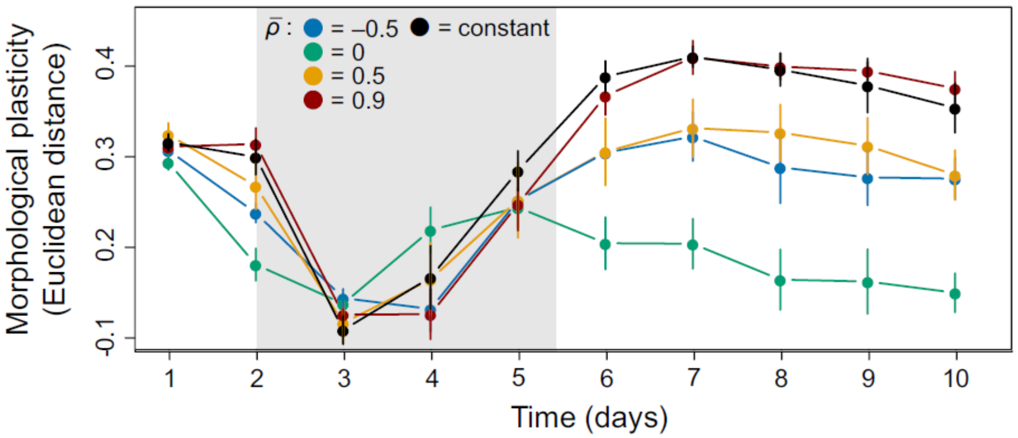
Experimental evolution of plasticity

- **Plasticity is dynamic**, and lowest during exponential growth phase

Morphological trajectories



Dynamics of plasticity

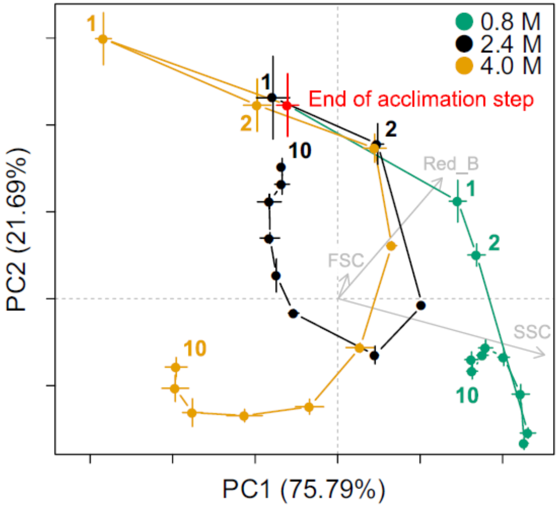


Leung et al (2020 Ecol Lett)

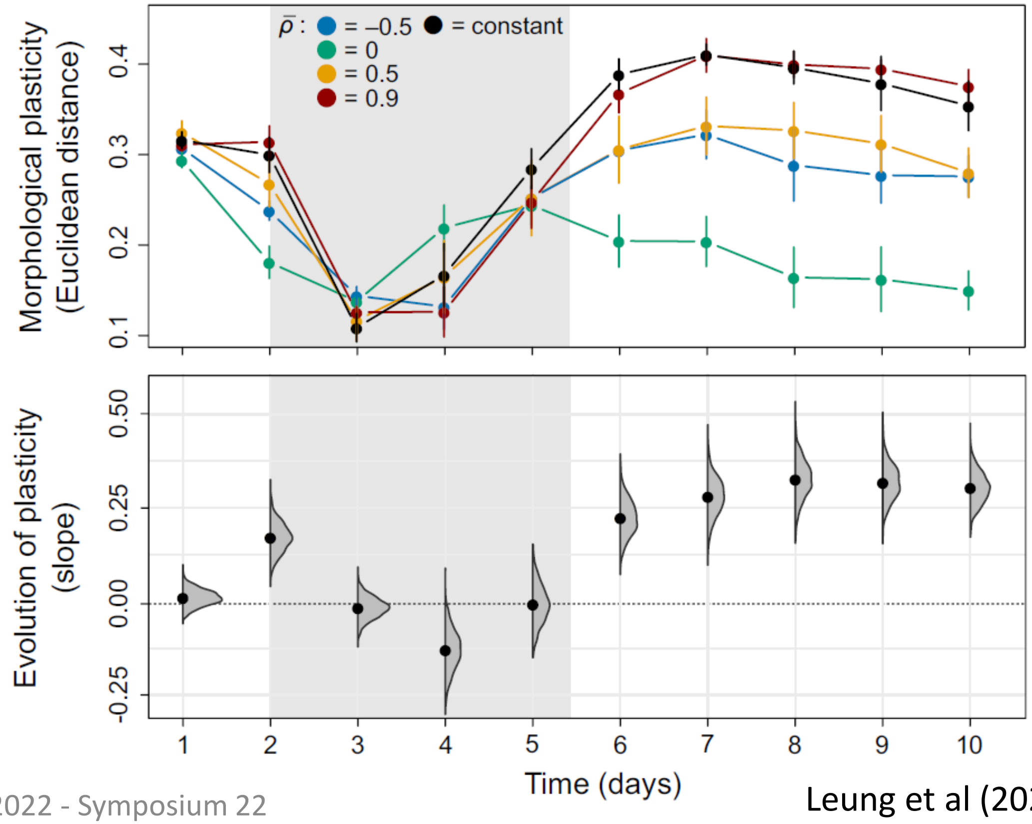
Experimental evolution of plasticity

- **Plasticity is dynamic**, and lowest during exponential growth phase
- Most evolution of plasticity concerns **late responses**

Morphological trajectories



Dynamics of plasticity

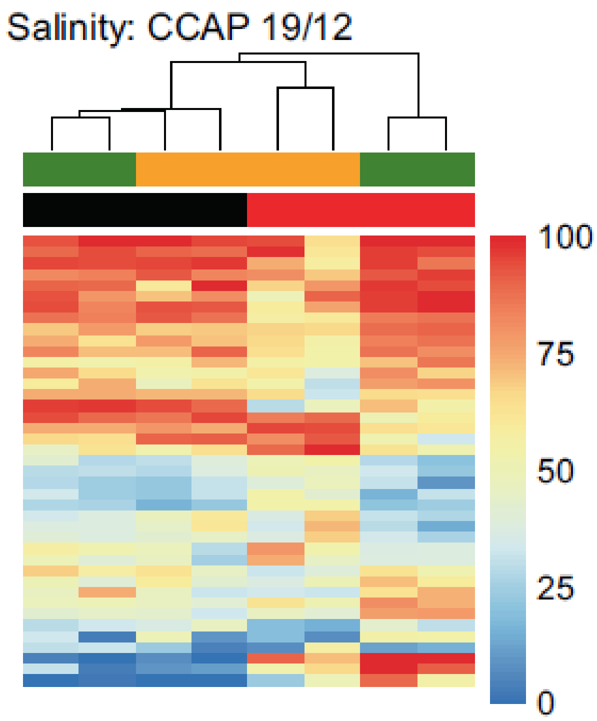


Leung et al (2020 Ecol Lett)

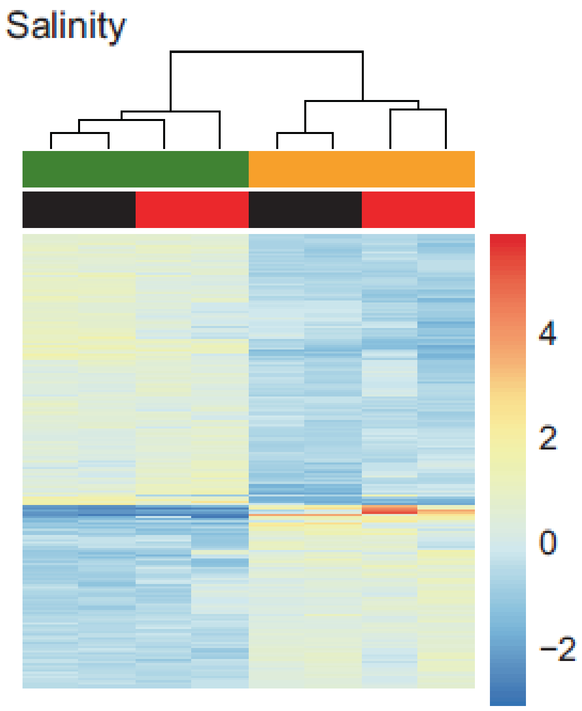
Experimental evolution of plasticity

- Plastic responses to salinity for **gene expression, much less for DNA methylation**[1]

DNA methylation (CpG context)



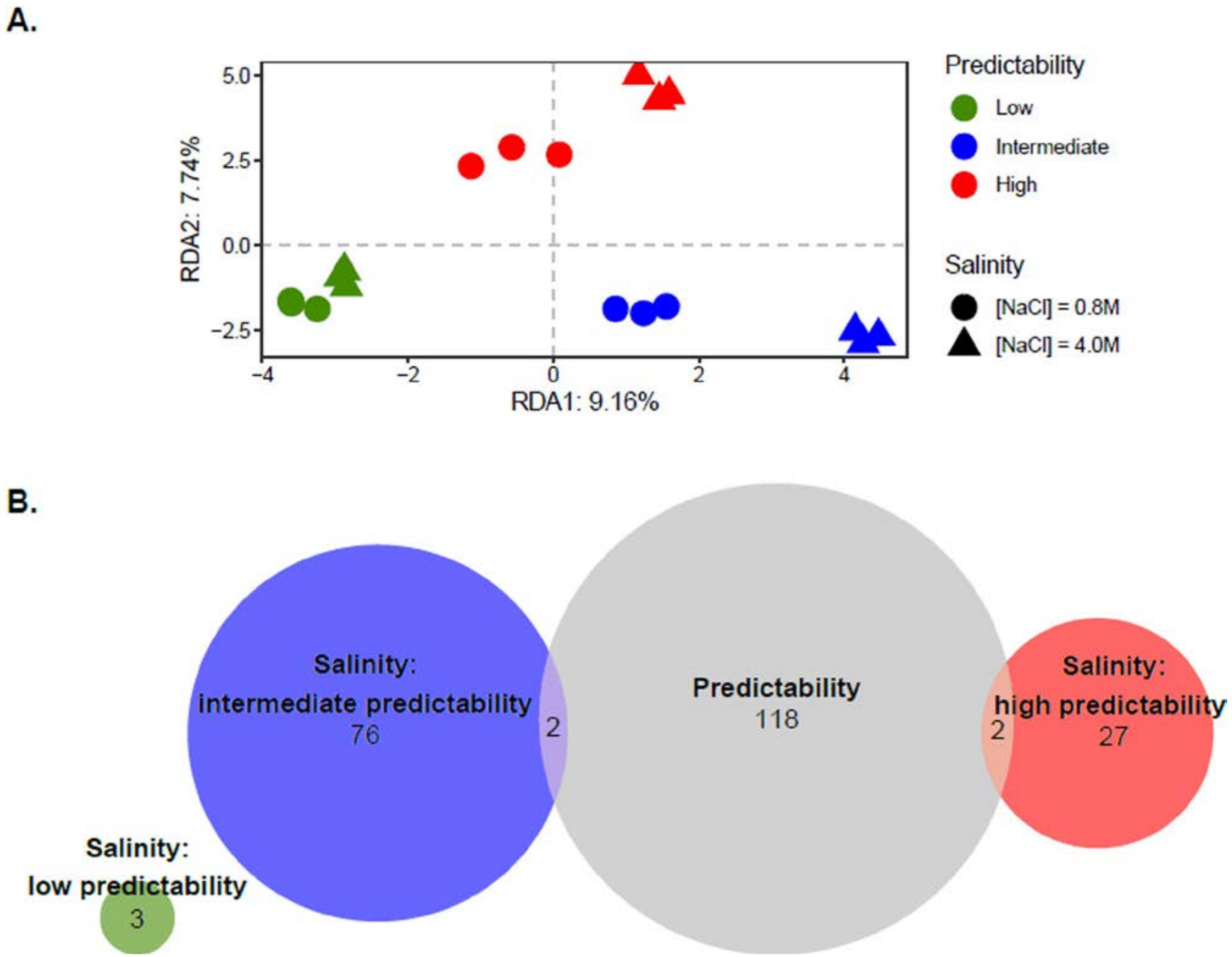
Gene expression



1: Leung et al (2022 Mol Ecol)

Experimental evolution of plasticity

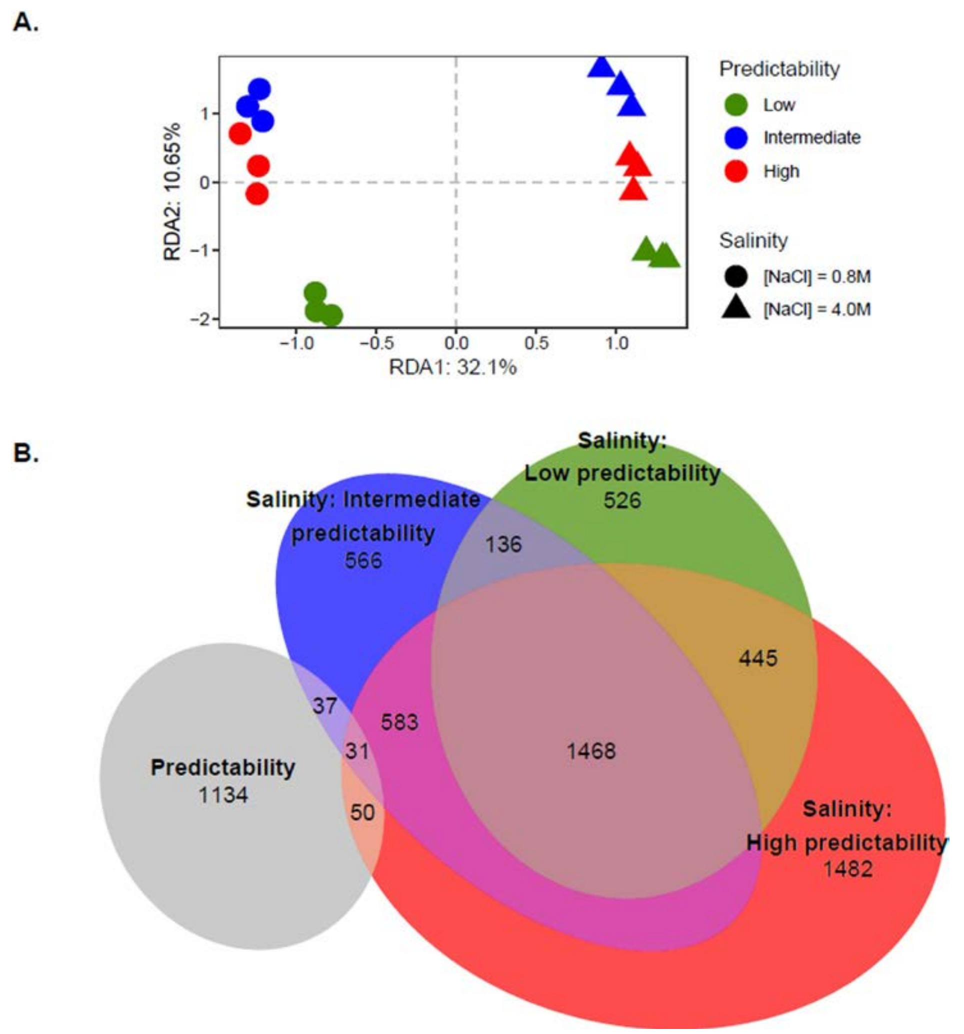
- Evolution and plasticity of DNA methylation



Leung et al (2023 PLoS Biol)

Experimental evolution of plasticity

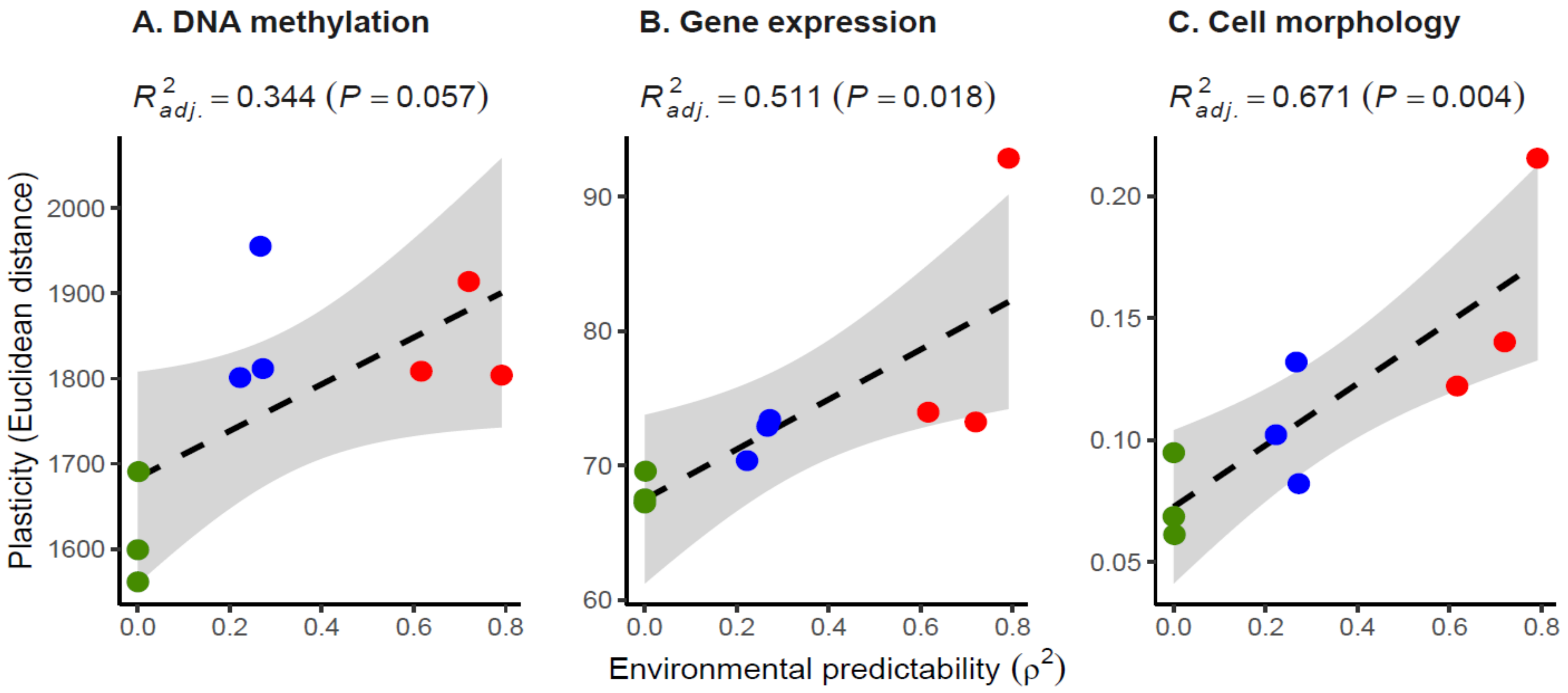
- Evolution and plasticity of transcriptome



Leung et al (2023 PLoS Biol)

Experimental evolution of plasticity

- Plastic responses at different levels evolved in same direction in response to predictability

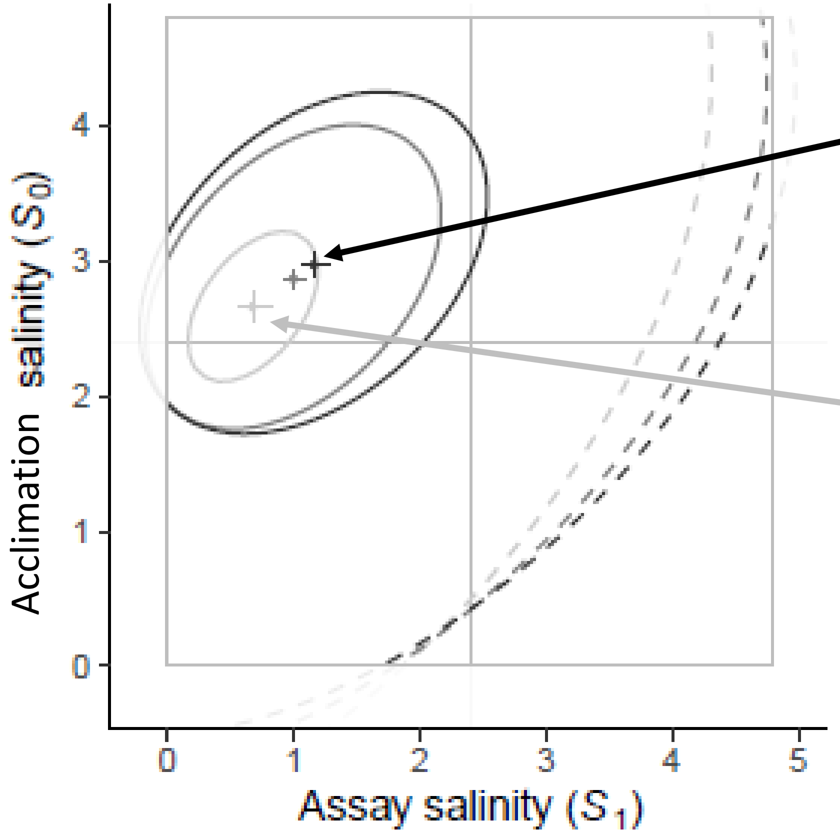


Leung et al (2023 PLoS Biol)

Experimental evolution of tolerance curves

- **Tolerance curves evolved**:

In constant salinity: evolutionary **shift in current and past salinity optimum**



Selected at highest constant salinity

Selected at lowest constant salinity

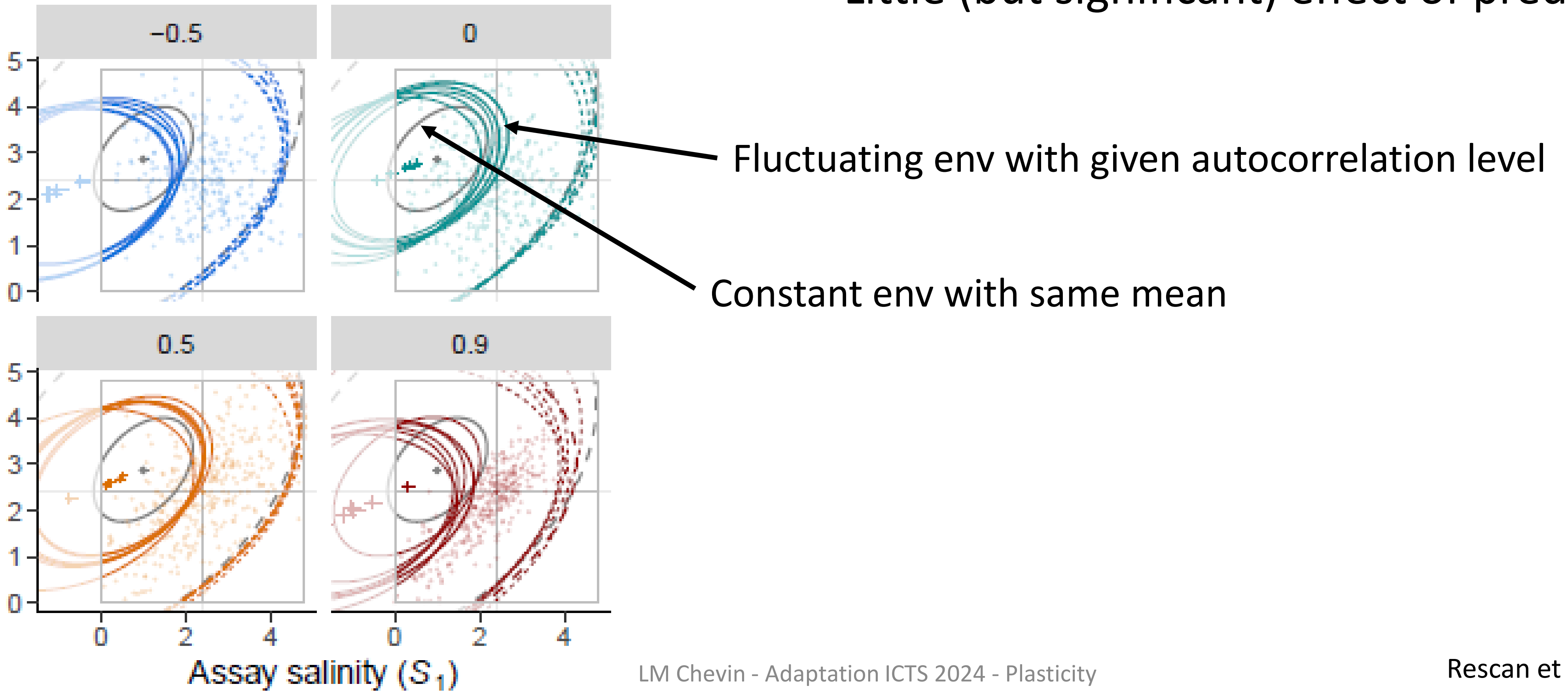
Rescan et al (2022 Evol Letters)

Experimental evolution of tolerance curves

- **Tolerance curves evolved**:

In fluctuating salinity: evolution of **broader tolerance to current and past salinity**.

Little (but significant) effect of predictability



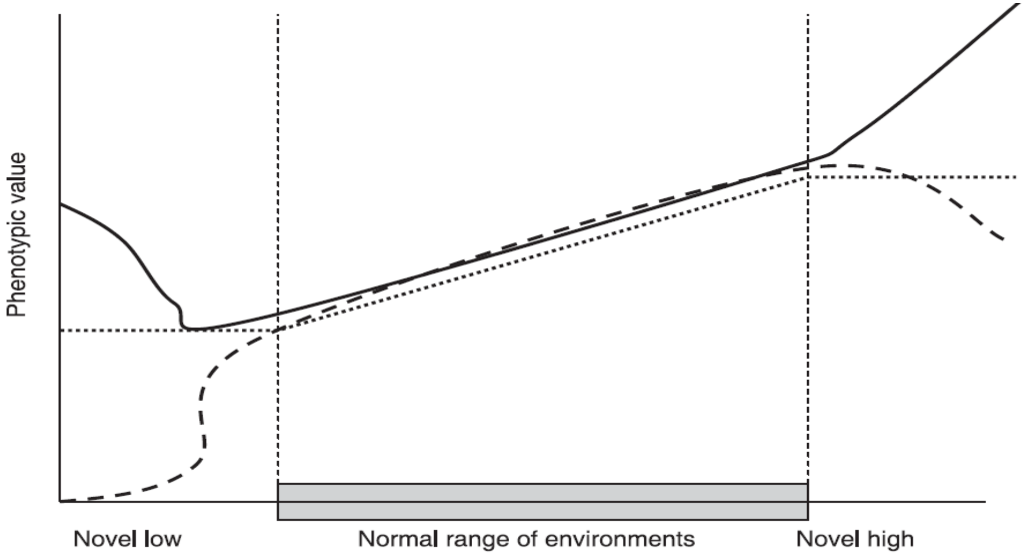
Rescan et al (2022 Evol Letters)

Outline of the talk

1. Genetic variation and selection on plasticity
2. Evolution of plasticity in fluctuating environments
3. **Evolution of plasticity in novel and extreme environments**

Adaptiveness of plasticity in novel & extreme environments

- Under intense or sustained environmental change, populations become exposed to **environments that were previously rare/extreme**
- A classic argument: **relaxed selection** in evolutionary history could lead to non-adaptive, erratic reaction norms in these environments[1]



- But verbal argument, assuming reaction norm shape evolves freely.

1: Ghalambor et al (2007 Funct Ecol)

Adaptiveness of plasticity in novel & extreme environments

- Evolution of reaction norm shape in extreme environments depends on:

- How relaxed selection has been there
  → Rareness of extreme environment
- How much genetic drift the reaction norm undergoes
  → Effective population size
- How stressful extremes environments are
  → Continuity of selection between common and extreme environments
- How constrained reaction norm shape is
  → **Genetic correlations** of trait values across environments

1: Chevin & Hoffmann (2017 Phil Trans)

Adaptiveness of plasticity in novel & extreme environments

- **Simple character-state quantitative genetic model**
  Expected response to selection in the extreme environment:

$$E(\Delta\bar{z}_e) = G_e E(\beta) \frac{r + \rho\sqrt{G_c/G_e}}{1 + r}$$

$E(\beta)$	Expected directional selection on expressed trait value (0 if not expressed)
G_e, G_c	Additive genetic variance in extreme/common environment
ρ	Genetic correlation between trait value in common and rare environment
r	Odds ratio of rare/common environments

- Total response to selection in extreme environment is at least ρ (for very rare extremes), and increases with the frequency of the extremes

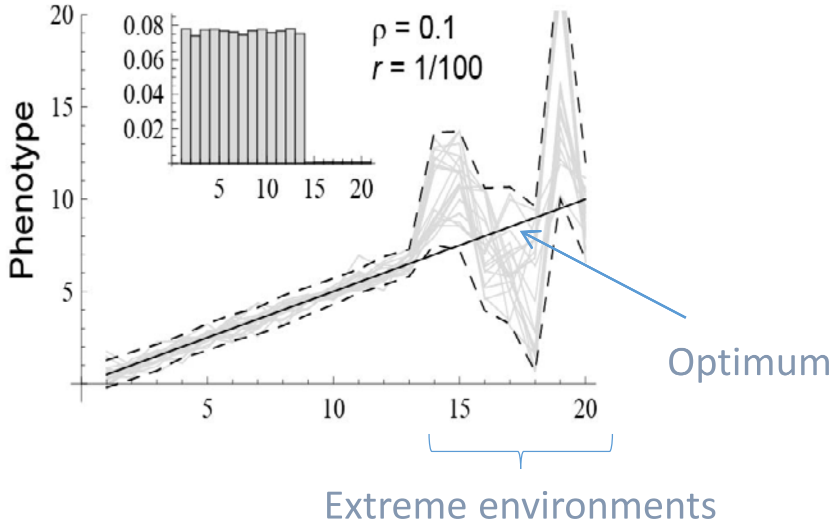
→ Reaction norm evolution in rare/extreme environments need not be dominated by drift

1: Chevin & Hoffmann (2017 Phil Trans)

Adaptiveness of plasticity in novel & extreme environments

- Simulations of character-state reaction norm, with ρ the genetic correlation among trait values 1 environmental unit apart (e.g. +/- 1°C)
- Extreme environments (right end) are *r* times less frequent (inset below)
- Smooth (linear) change in optimum across environments.
- Run for 40000 generations at N_e = 1000 → Drift - stabilizing selection equilibrium

Rare extremes, weak genetic constraints



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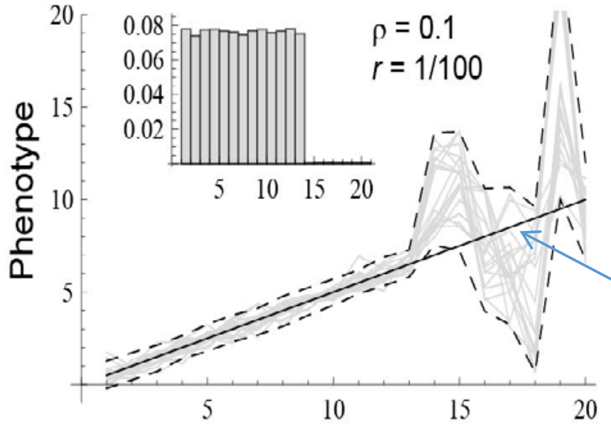
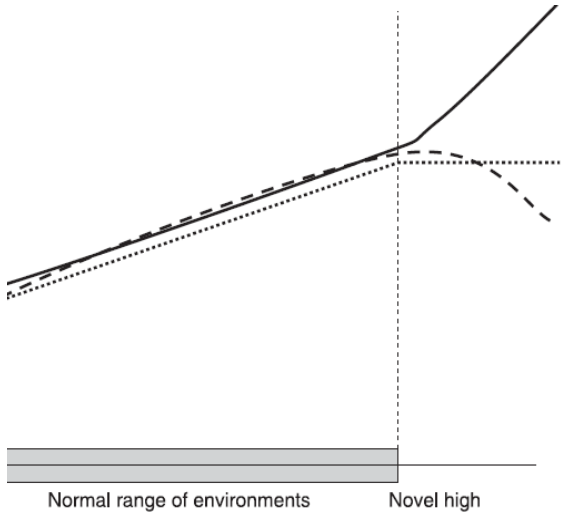


Optimum

Extreme environments

Similar to Ghalambor et (2007)



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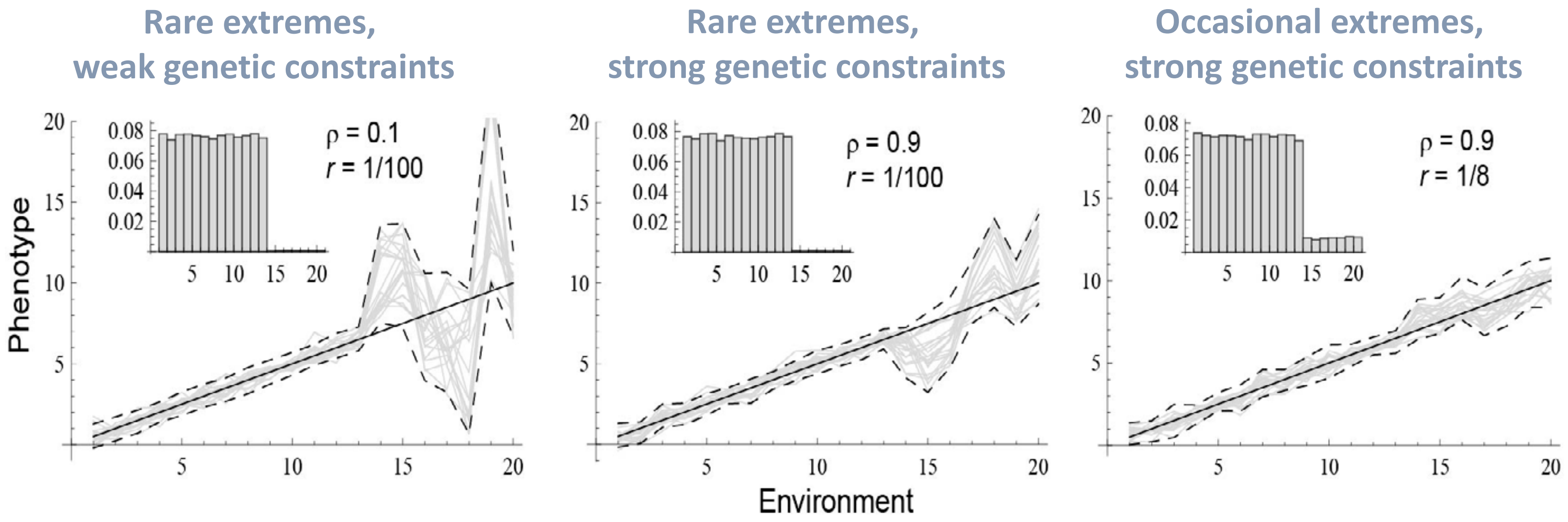


1: Chevin & Hoffmann (2017 Phil Trans)

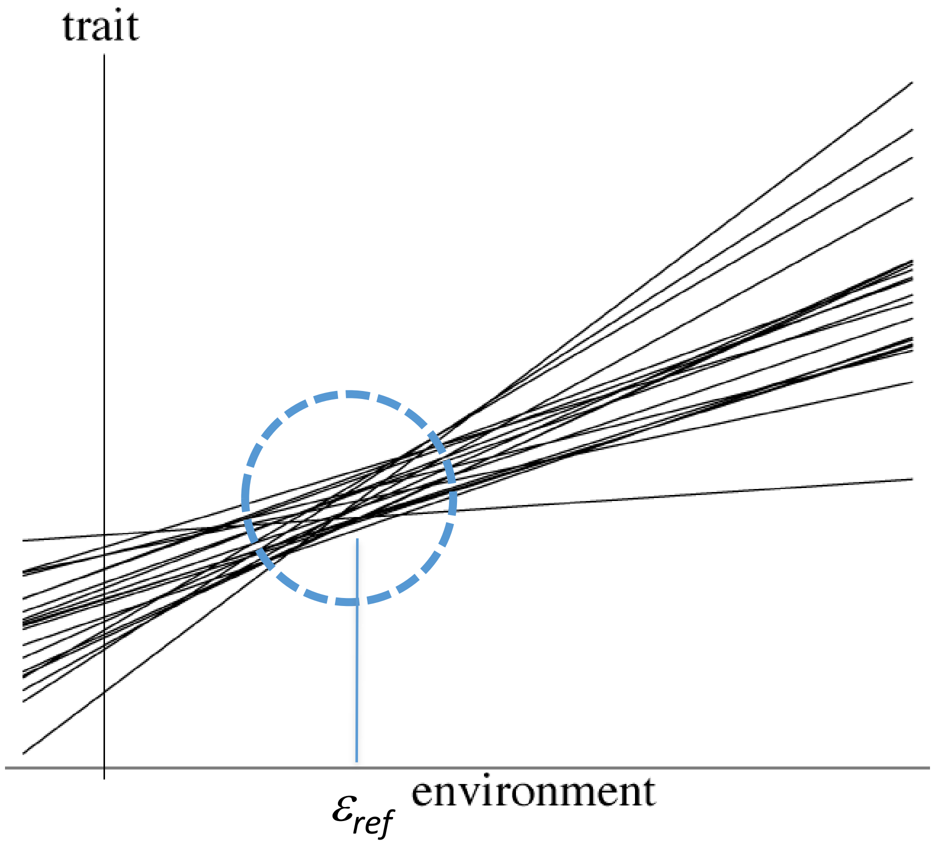
Plasticity and evolutionary rescue

- Abrupt environmental change causing large maladaptation and negative population growth rate r can put populations at risk of extinction
- Rapid adaptation can prevent extinction if $r > 0$ is restored before $N < 1$ (**evolutionary rescue, ER**[1])
- Biological contexts:
  Colonization/invasion, antibiotic resistance, disease emergence…
- Evolution[2] and plasticity[3] both shown to be important for invasion success
  How does the evolution of plasticity contribute to evolutionary rescue in a drastically new environment?

→ Quantitative genetic model of evolution of linear reaction norms

1: Gomulkiewicz & Holt 1995 Evolution, Phil Trans special issue (2013)
2: Colautti & Barrett (2013 Science)
3: Davidson et al 2011 (Ecol Lett), Sultan & Matesanz (2016 Ann. N.Y. Acad. Sci)

Genetic (co)variance of reaction norm traits

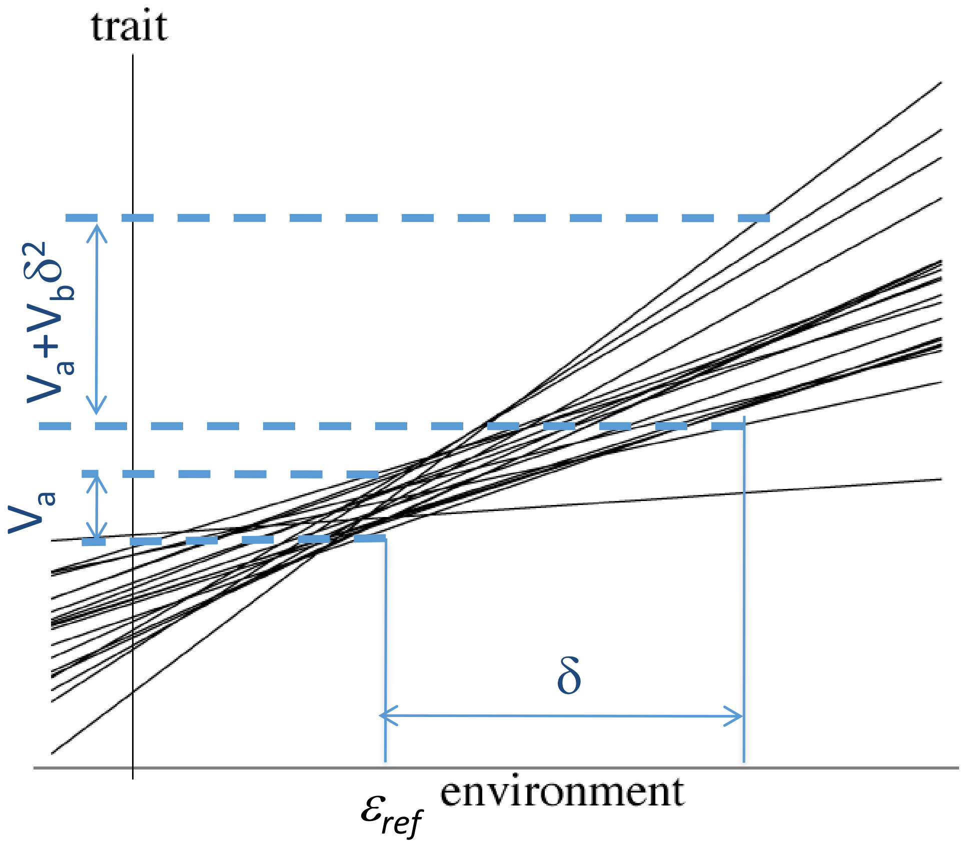


Linear reaction norms:

- Slope and elevation uncorrelated in a reference environment ε_{ref}

Gavrilets & Scheiner 1993;
Lande 2009, JEB

Genetic (co)variance of reaction norm traits



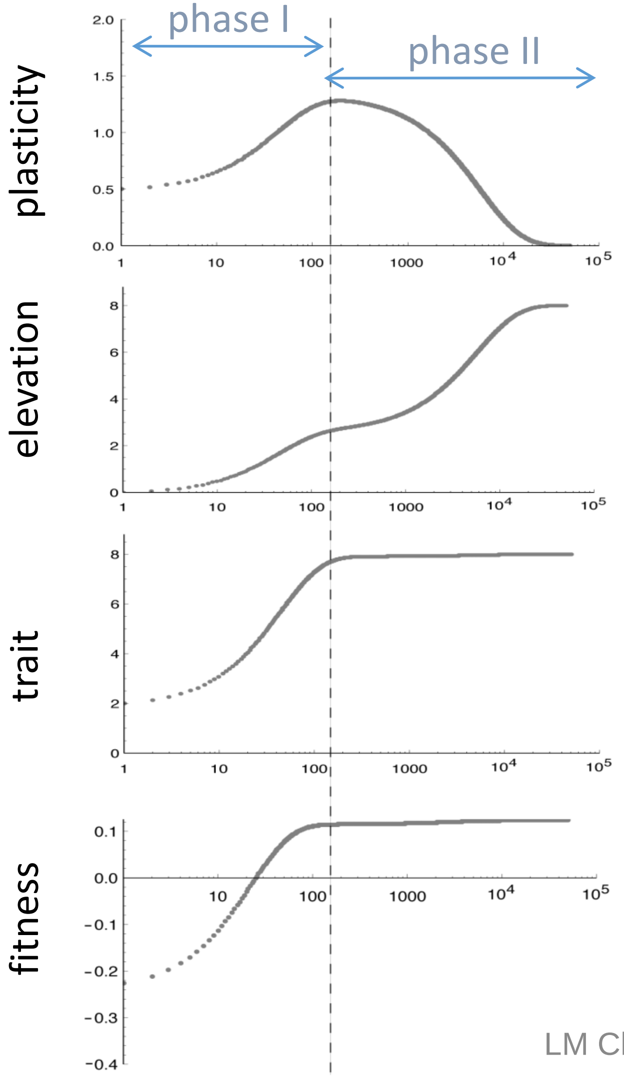
Linear reaction norms:

- Slope and elevation uncorrelated in a reference environment ε_{ref}
- Phenotypic and genetic variances are minimum in ε_{ref}
- Covariance between a trait and its plasticity proportional to deviations δ from ε_{ref}
  → the larger δ, the more **directional selection on the trait causes indirect selection on its plasticity**

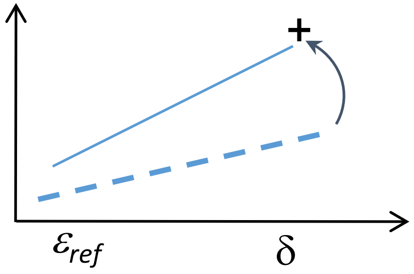
Gavrilets & Scheiner 1993;
Lande 2009, JEB

Evolution following abrupt stress

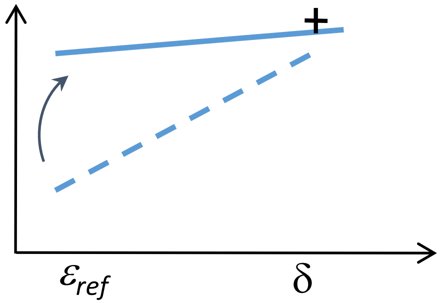
- Sudden shift of the environment from 0 to δ , causing change in optimum
- If maladaptation initially stronger than cost of plasticity: two-phase process



- **Phase I**: increase in plasticity, rapid approach to optimum phenotype



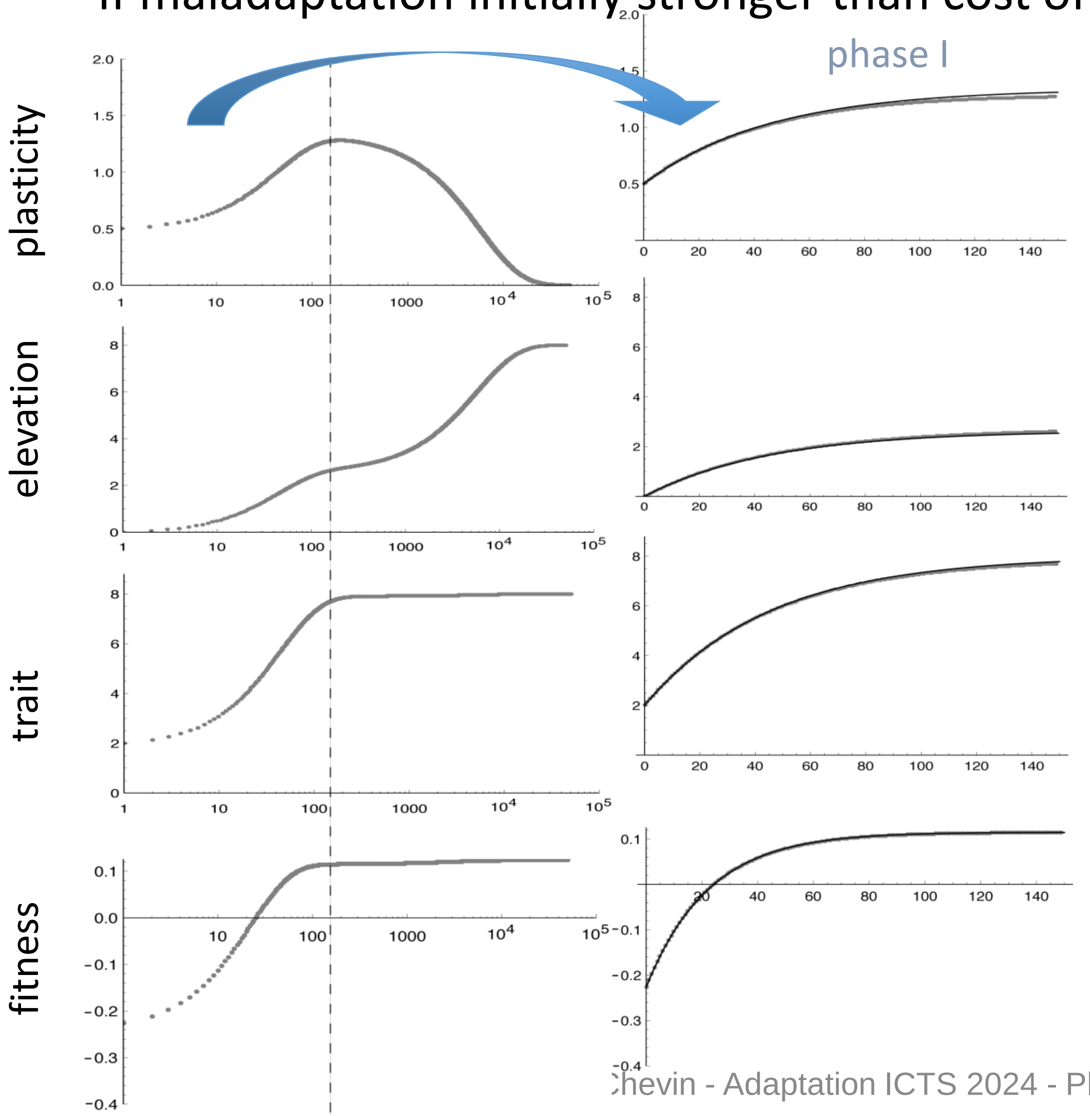
- **Phase II**: 'genetic assimilation', plasticity decreases, compensated by increase in reaction norm elevation.



Gavrilets & Scheiner 1993; Lande 2009, JEB

Reaction norm evolution under abrupt stress

- Sudden shift of the environment from 0 to δ , causing change in optimum
- If maladaptation initially stronger than cost of plasticity: two-phase process



Phase I

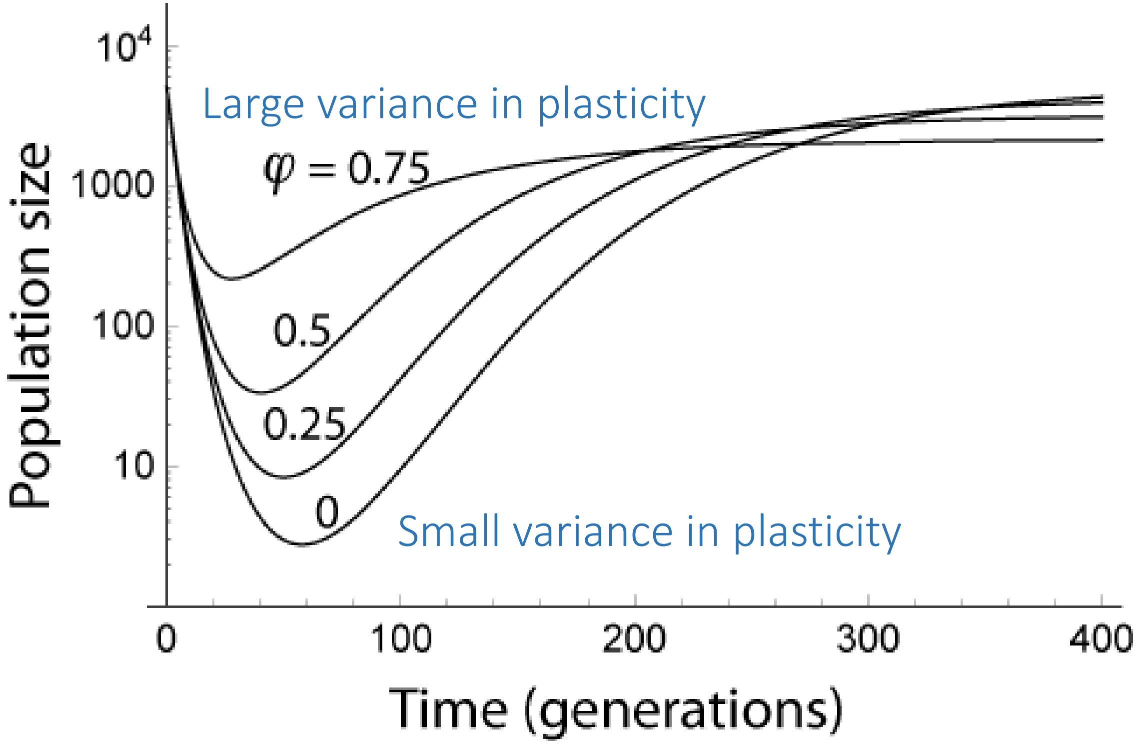
- Determines extinction risk
- Simple exponential evolutionary dynamics
- Evolving plasticity makes rate of adaptation faster by factor $(1-\phi)^{-1}$

$\phi \approx$ proportion of genetic variance of trait caused by variance in plasticity

Chevin and Lande 2010, Evolution

Population dynamics

- Speed of phenotypic evolution determines minimum pop size and extinction risk[1]
- Here, mostly determined by variance in plasticity[2]



1: Gomulkiewicz & Houle 1995, Evolution
2: Chevin and Lande 2010, Evolution

Centre d'Ecologie Fonctionnelle & Evolutive

erc European Research Council

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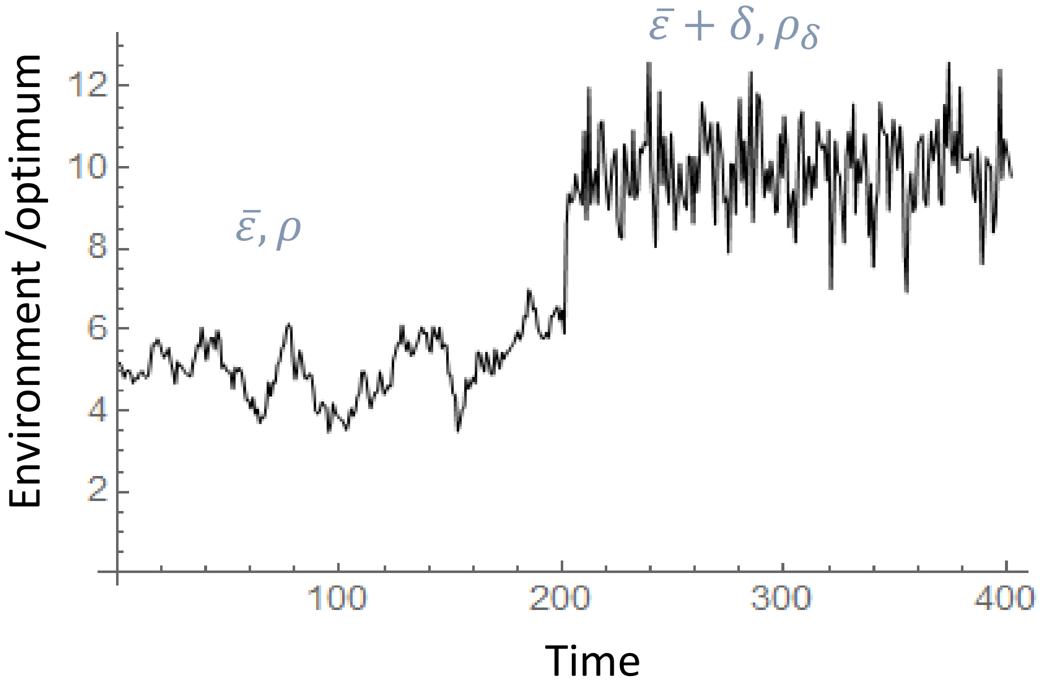
Thanks!

Questions?

ER with evolving plasticity in stochastic environment

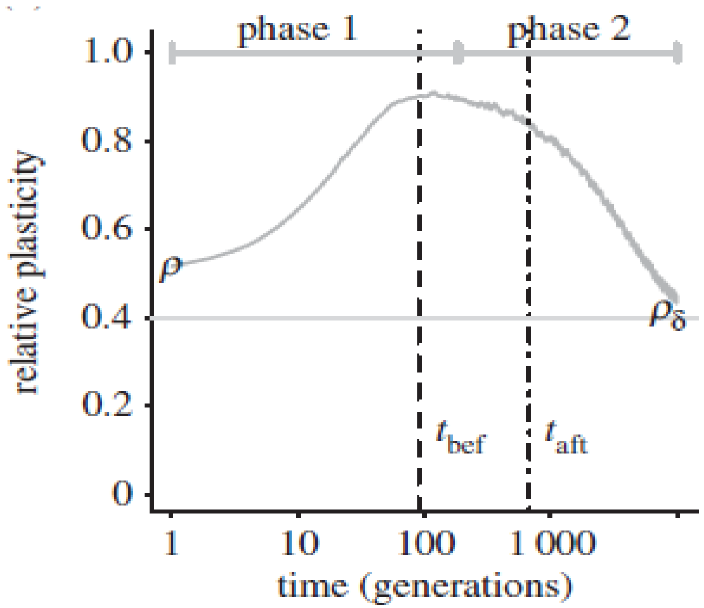
- Climate change alters environmental (auto)correlations and predictability
- Model where environmental shift modifies the **mean** (δ) and **autocorrelation** (ρ_δ) **of random fluctuations** in environment



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

ER with evolving plasticity in stochastic environment

- Evolutionary dynamics of plasticity: same as in Lande (2009), except that final plasticity in the long run depends on new environmental autocorrelation

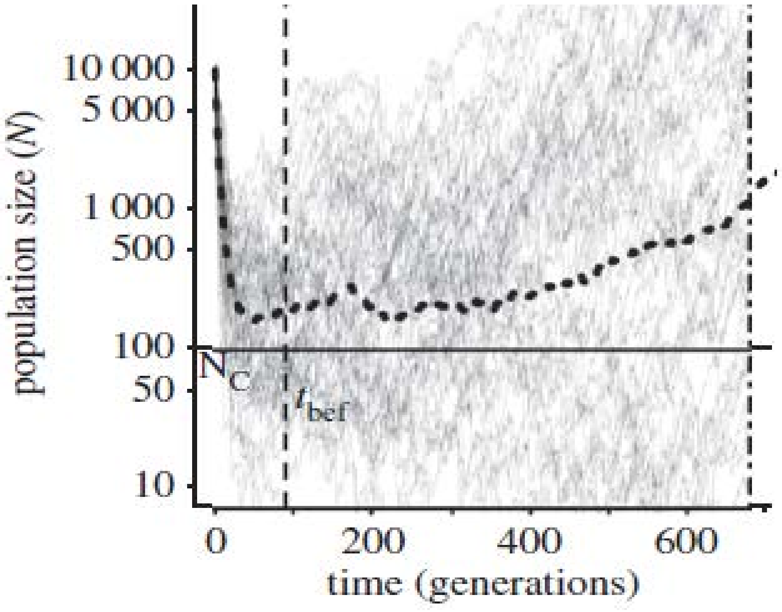


- **Transient increase in plasticity in phase I causes increased stochastic lag load** (caused by variance of mismatch with optimum)

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

ER with evolving plasticity in stochastic environment

- The expectation and variance of mismatch with optimum can be used to derive the distribution of pop size through time[1]
- Stochasticity in deviations from optimum causes *N* to span several orders of magnitude, largely contributing to extinction risk[1]

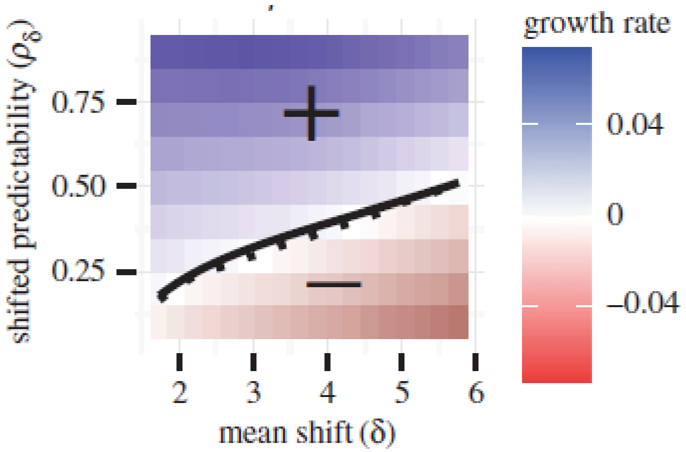


1: Chevin et al (2017 Am Nat)

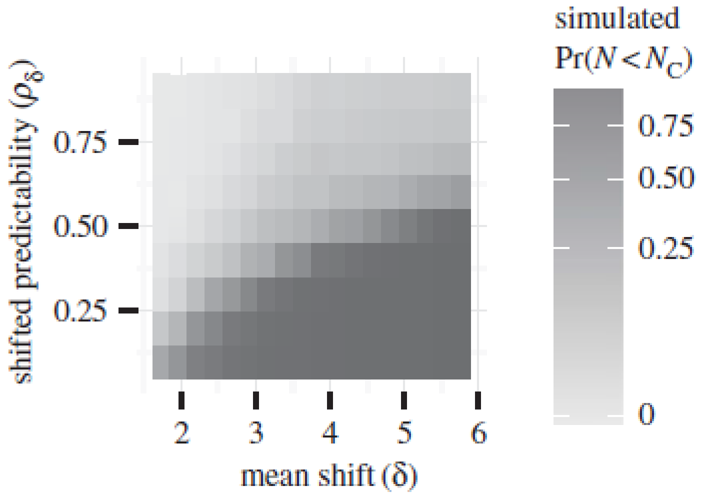
ER with evolving plasticity in stochastic environment

- **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)