

# **Natural Selection in Variable Environments**

Henrique Teotónio

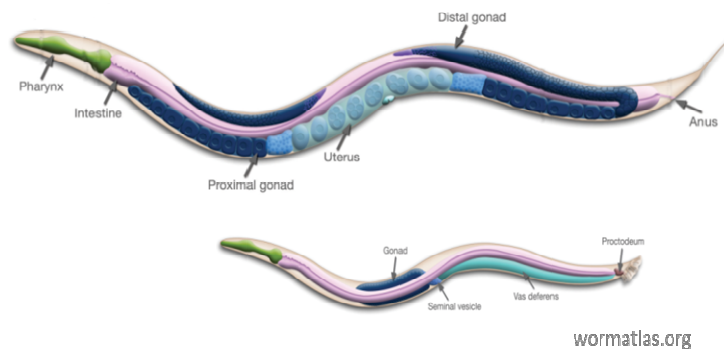
Snigdhadip Dey, Thiago Guzella, Stephen Proulx (UCSB)



## **NS in Variable Environments**

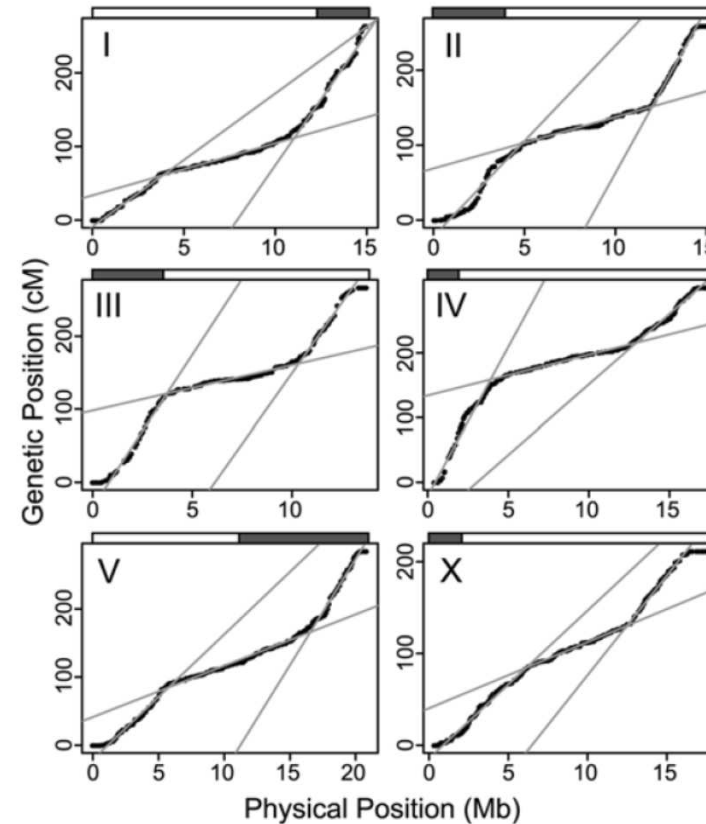
- . Temporal versus spatial variation
- . Within- versus between-generation variation
- . Continuous versus discrete variation
- . Rates of environmental change versus environmental fluctuations
  
- . Environmental dimensionality (information, cue reliability)
  
- . Evolution by mutation accumulation
- . Evolution from pre-existing genetic diversity
- . Evolution from standing genetic variation

## *Caenorhabditis elegans*



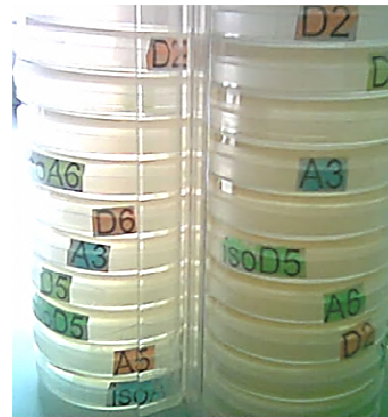
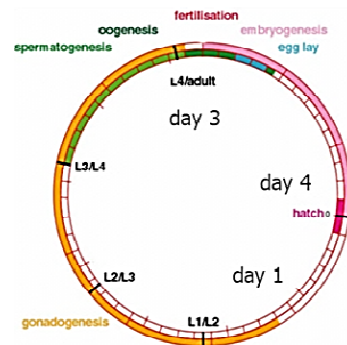
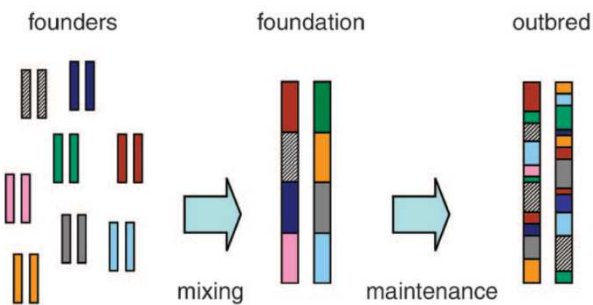
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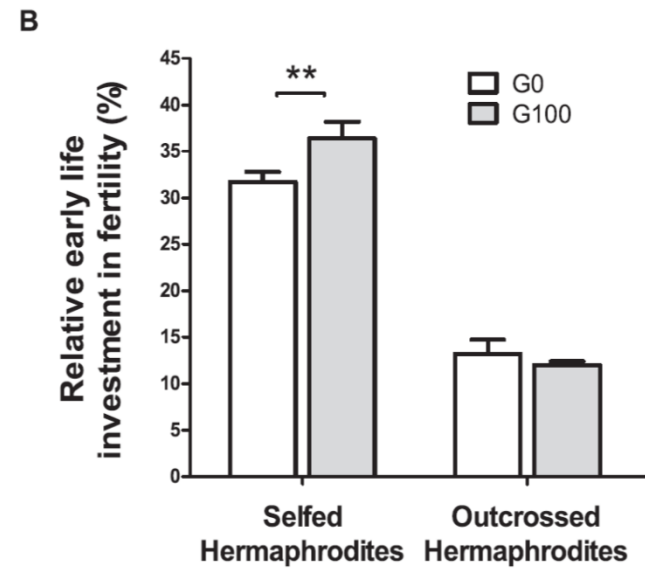
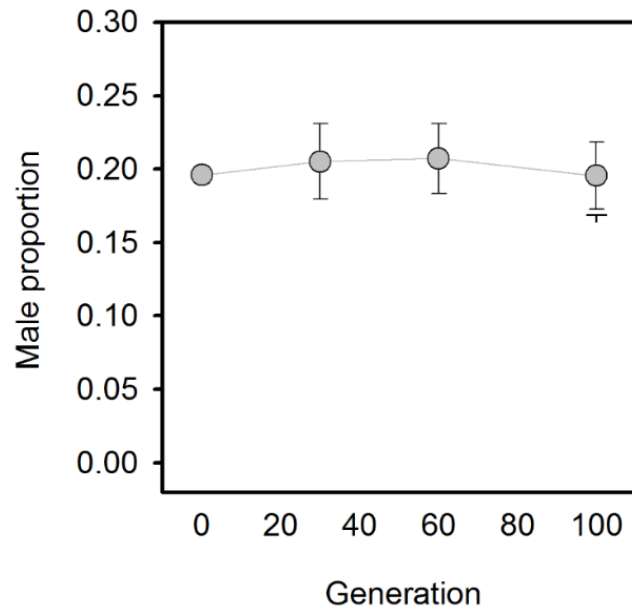
- bacteriofagous androdioecious nematode (ancestral dioecy)
- hermaphrodites can only mate with males: analogous to pollen discounting in angiosperms
- protandrous hermaphrodites (spermatogenesis is followed by oogenesis): self-sperm limited
- sex determination is chromosomal (X0 males; XX hermaphrodites)
- predominant selfing in ephemeral environments (boom and burst dynamics)
- 100 Mb genome size; 1 SNP/kb; recent “whole-genome” sweeps and background selection

## *C. elegans* Experimental Evolution



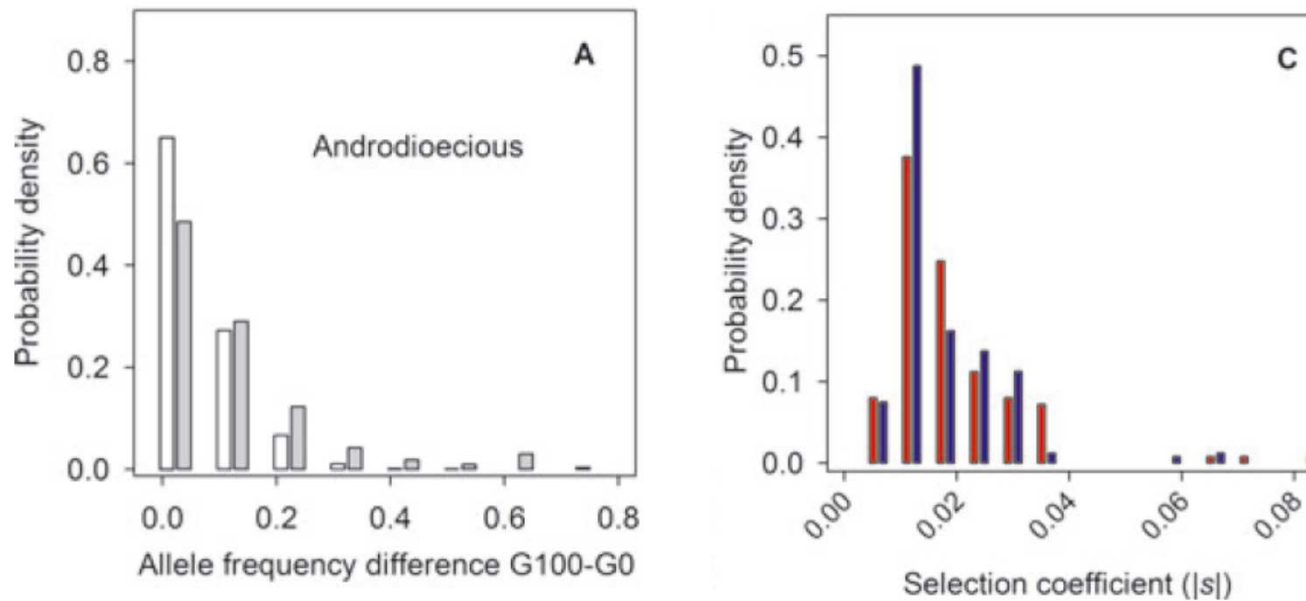
- ancestor population with standing genetic diversity: hybrid from 16 wild isolates
- 4-day discrete non-overlapping generations, constant L1 to adult density of  $N=10^4$
- ancestral and derived populations compared in "common garden" assays

# Domestication to the Lab Environment



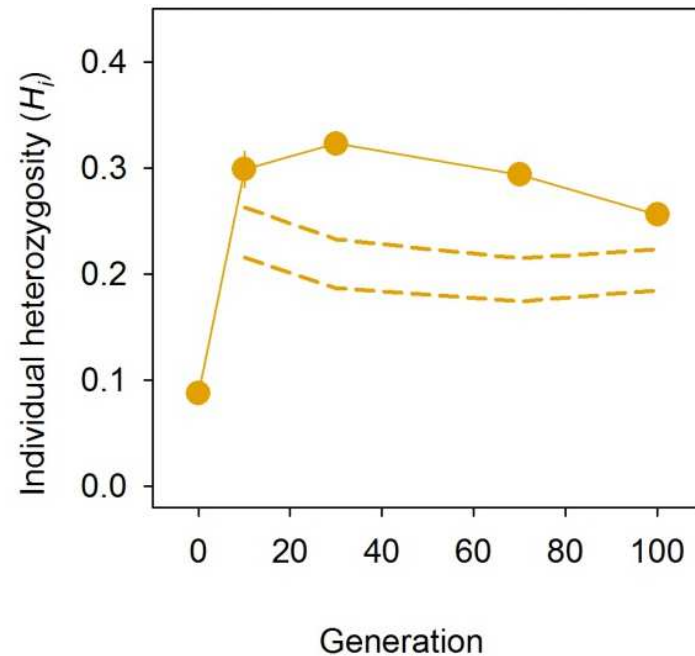
Teotónio et al. PlosOne (2012)  
Carvalho et al. BMC Evol Biology (2013a,b)  
Poullet et al. Evolution (2016)

## Domestication to the Lab Environment



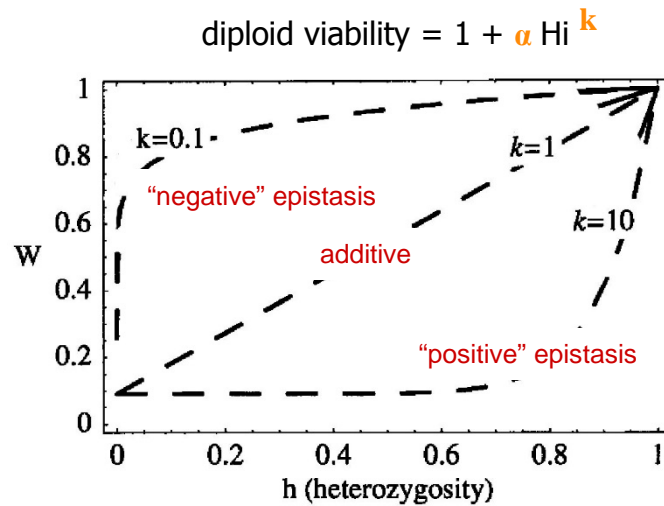
- ~350 SNPs across 2 chromosomes, ~200k genotypes across 4 time points
- empty bars: expected binomial sampling; filled bars: observed
- 40% differentiated SNPs, 4% extinction\_fixation

## Domestication to the Lab Environment

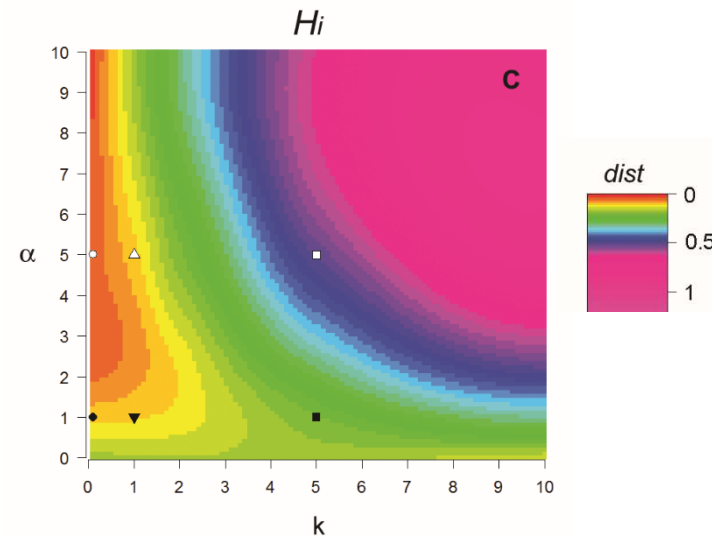


- dashed lines: expected  $H_i$  under genetic drift (numerical simulations with imposed/observed demography and expected genetic distances between SNPs; no mutation)

## Domestication to the Lab Environment



Navarro and Barton (2002)

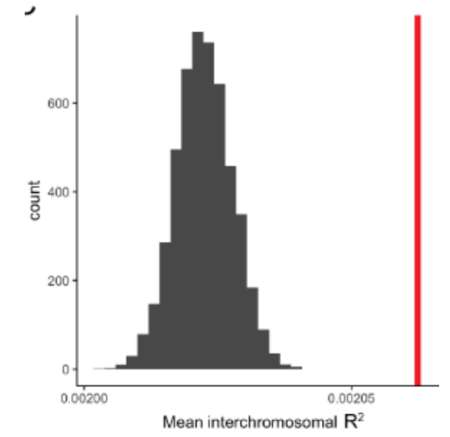
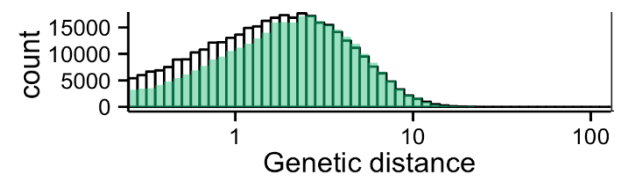
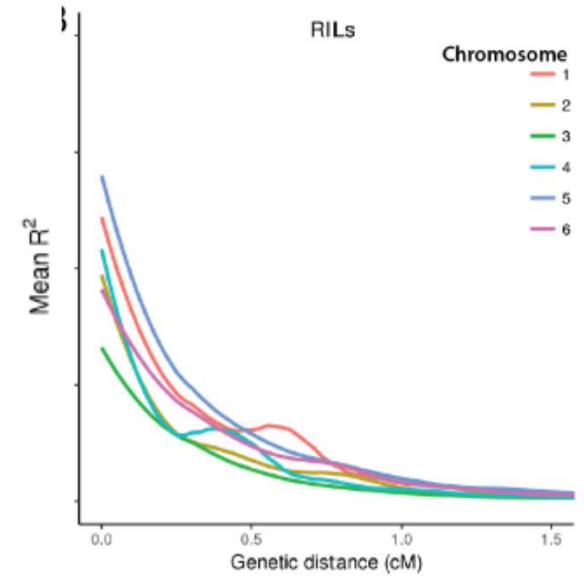
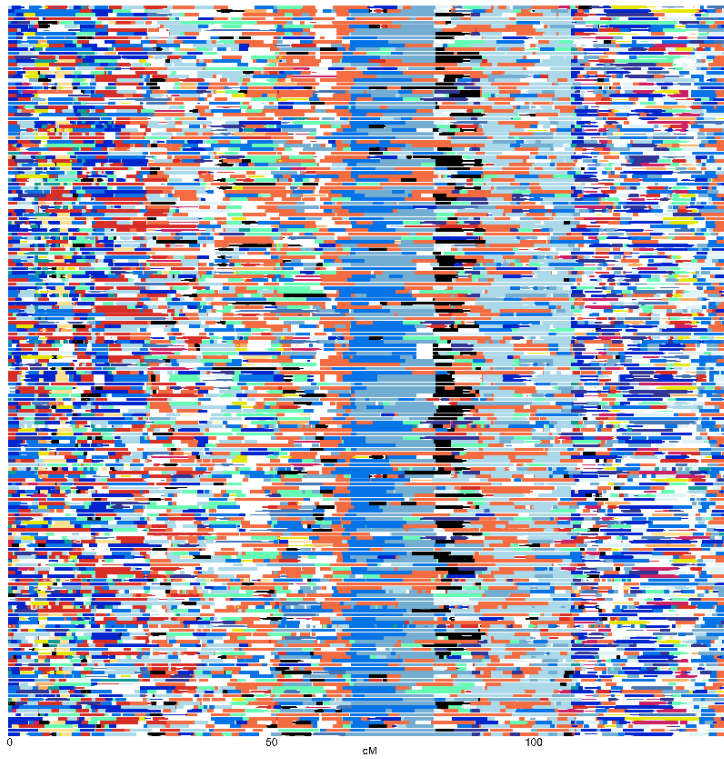


- "ABC" methods on  $H_e$ ,  $F_{is}$ ,  $H_i$  and  $CV(H_i)$  support balancing selection during lab domestication
- associative overdominance [  $w = (1-s)^x * (1-hs)^y$  ] does not fit the data after 30 generations

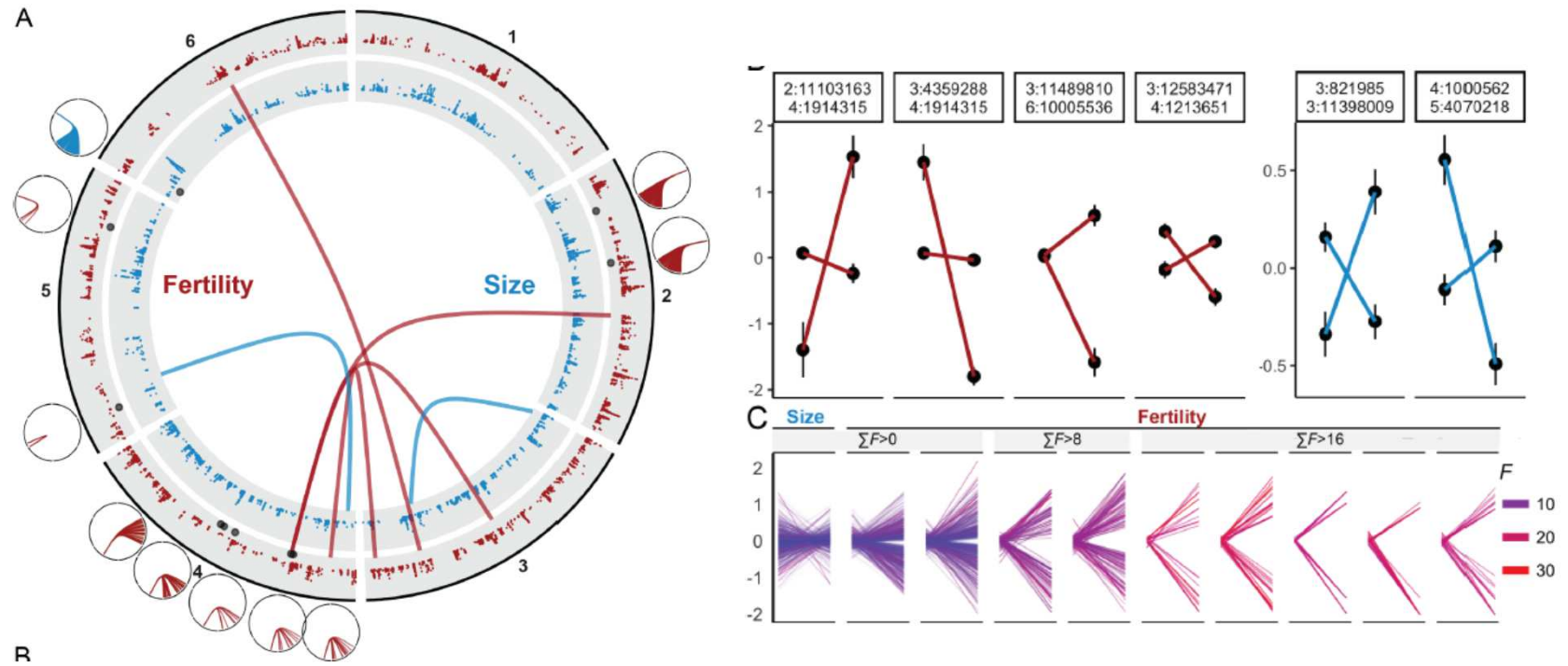
Chelo and Teotónio Evolution (2013)  
Chelo et al. Heredity (2013)



# Domestication to the Lab Environment

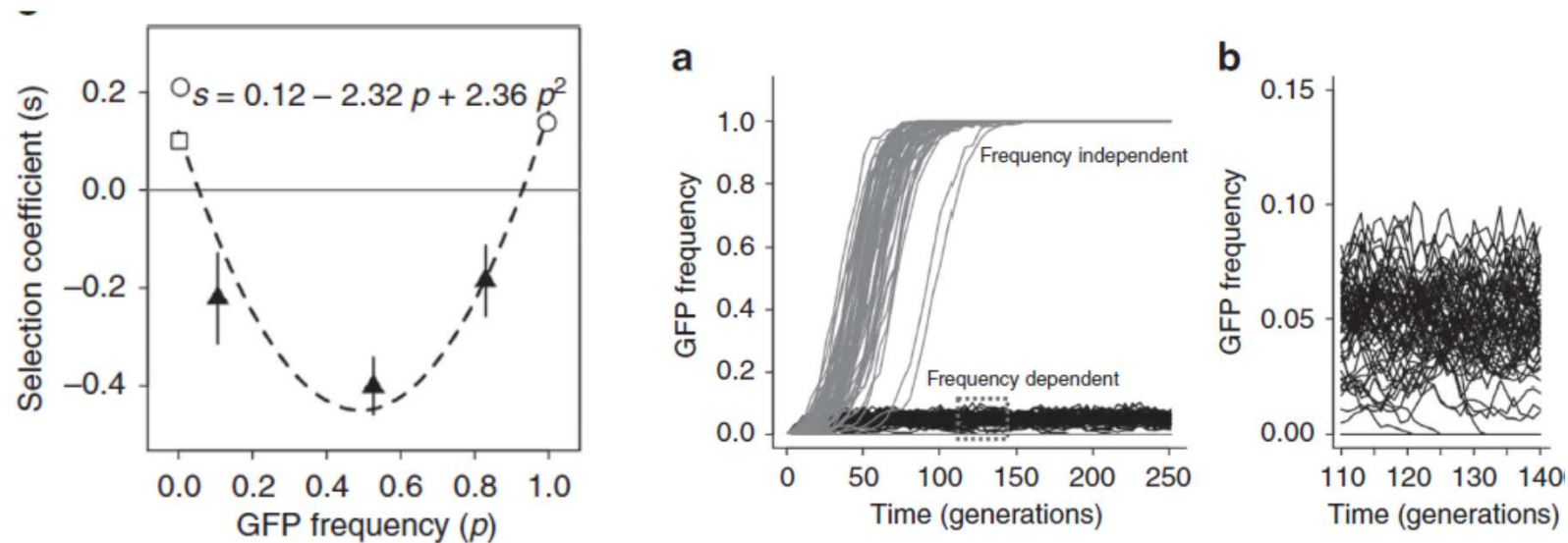


# Domestication to the Lab Environment



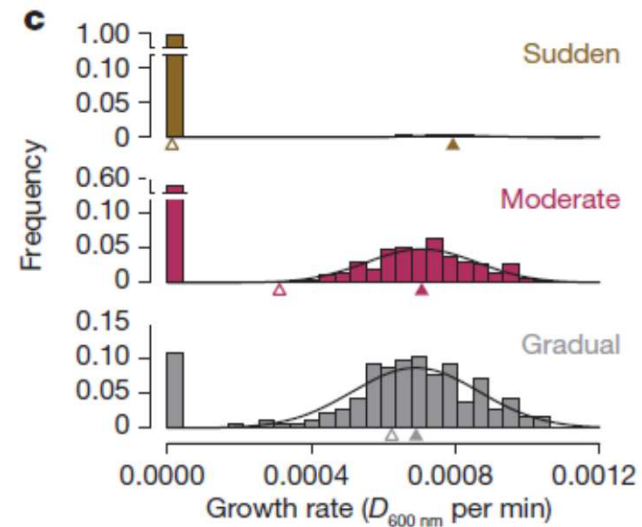
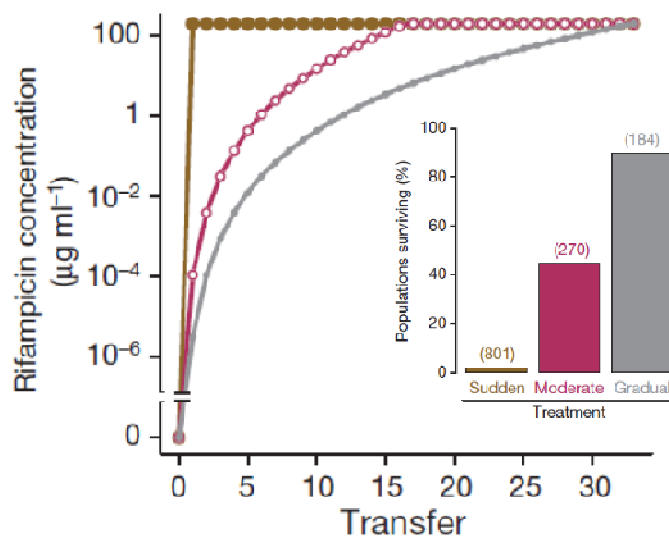
- additive by additive (polygenic) epistasis, without main single locus additive effects

## NS in Constant Environments



- head-to-head competitions between two inbred lines derived from the domesticated population
- right plots: not only polymorphism can be maintained, but the prob of extinction may increase

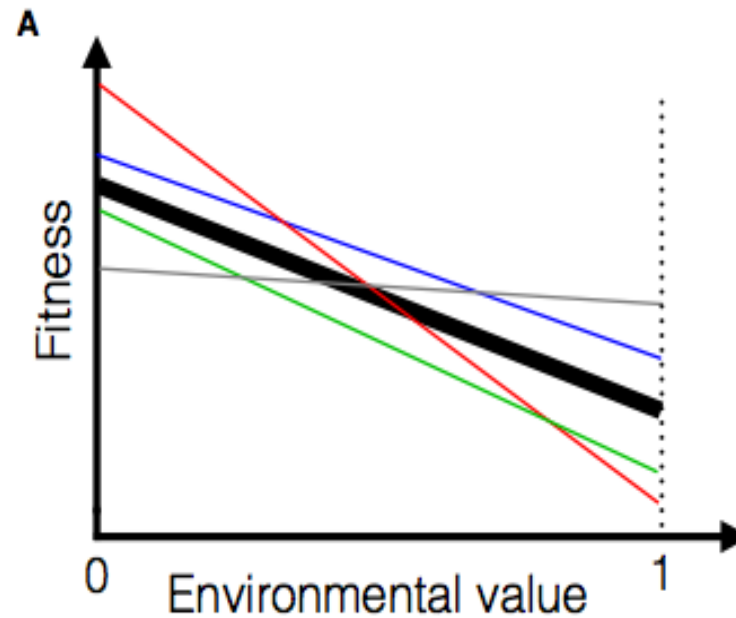
## Population genetics and adaptation to changing environments



- population survival and adaptation depend on the order of mutation accumulation and time to “explore” the fitness landscape

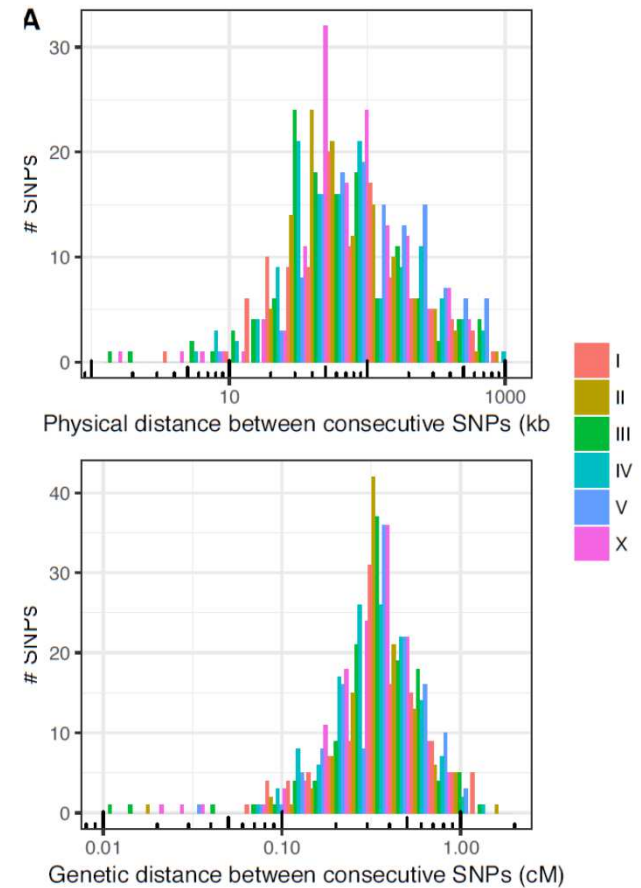
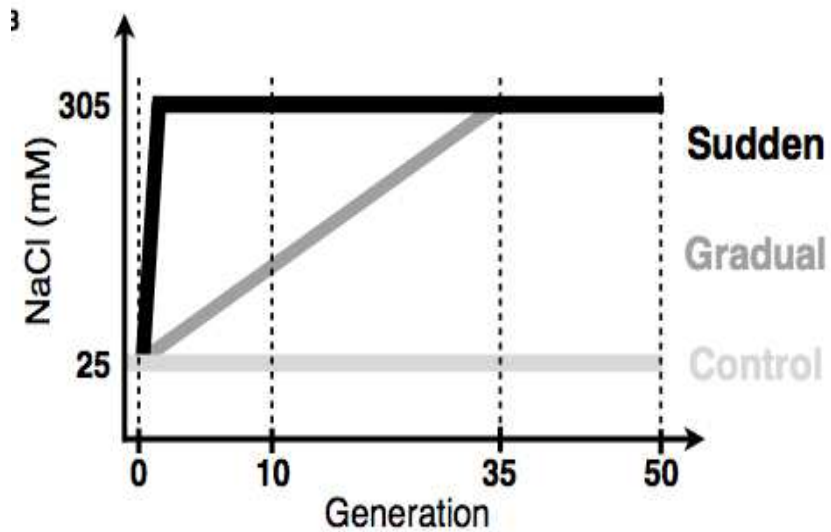
Lindsey et al. Nature (2013)  
see also Gorter et al. AmNat (2015)

## Evolution From Pre-Existing Diversity: Fitness Reaction Norms



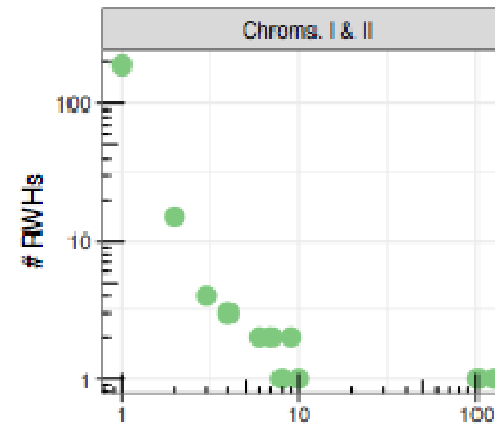
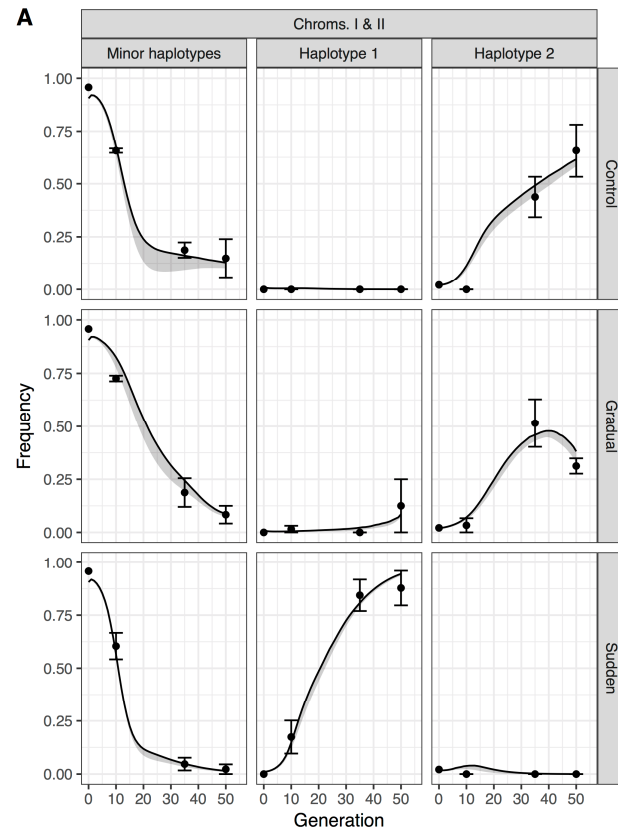
- genetic drift might lead to the loss of the best genotypes in the most extreme environment under slower environmental change
- adaptation can also be compromised the slower the environmental change because similarly fit genotypes can be maintained for longer

# Experimental Evolution Design

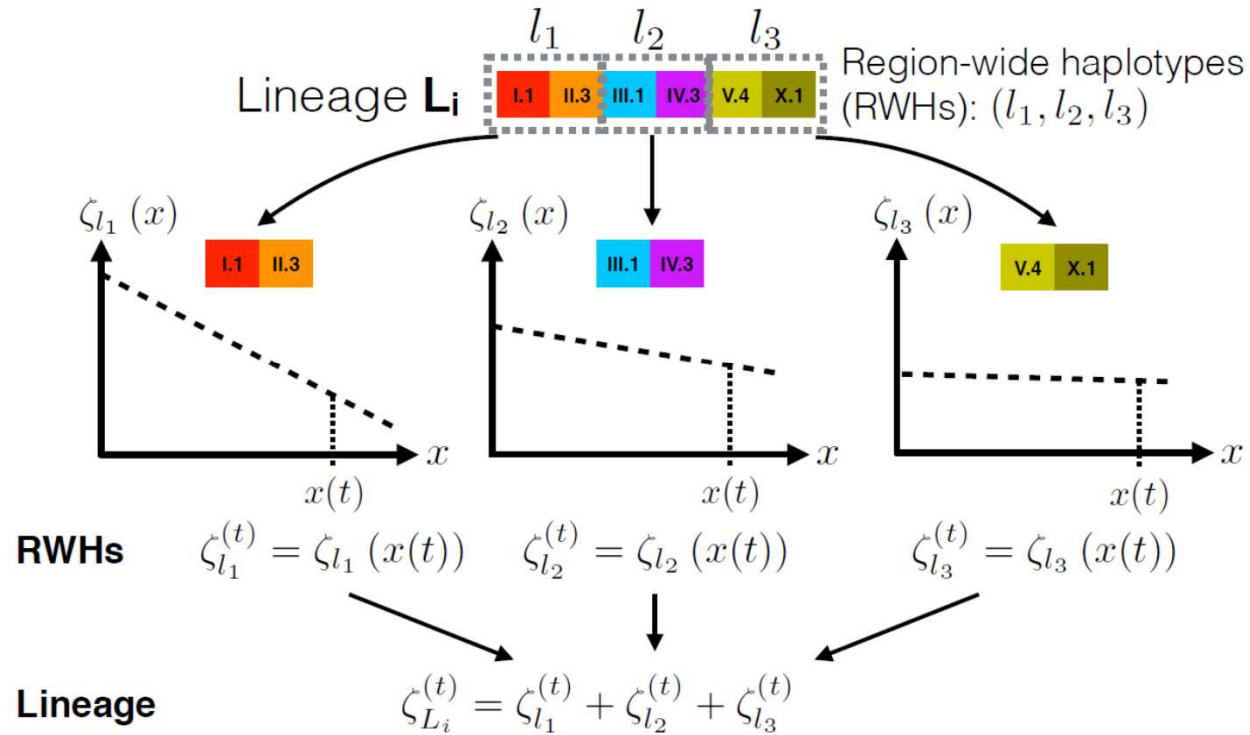


- ancestor population with standing genetic diversity (lab adapted population)
- reproduction exclusively by selfing (genetically-modified to kill males)
- dashed vertical lines indicate sample points for individual genotyping

# Experimental Population Genetic Dynamics

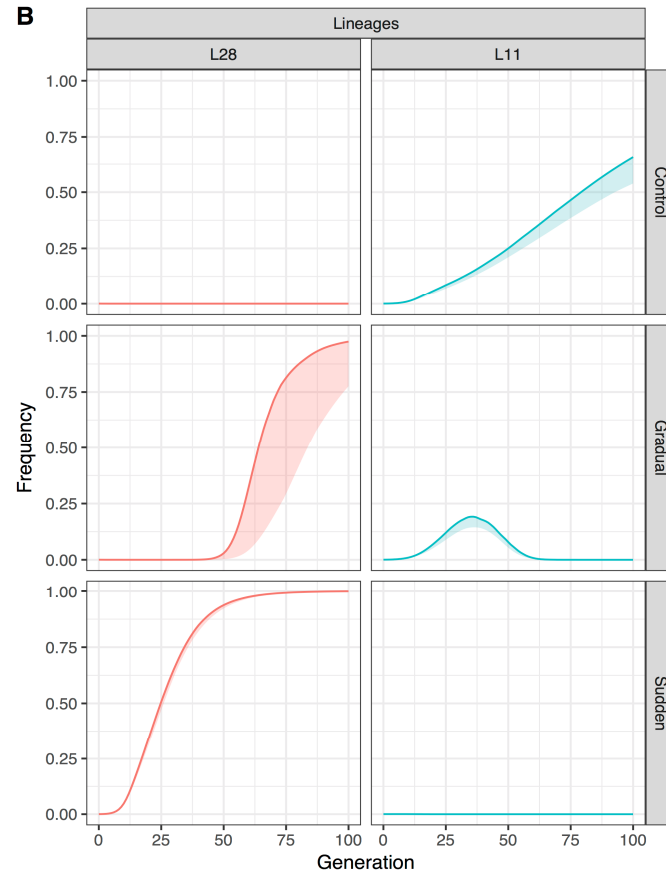


# Inference Model for Lineage ID and Frequency



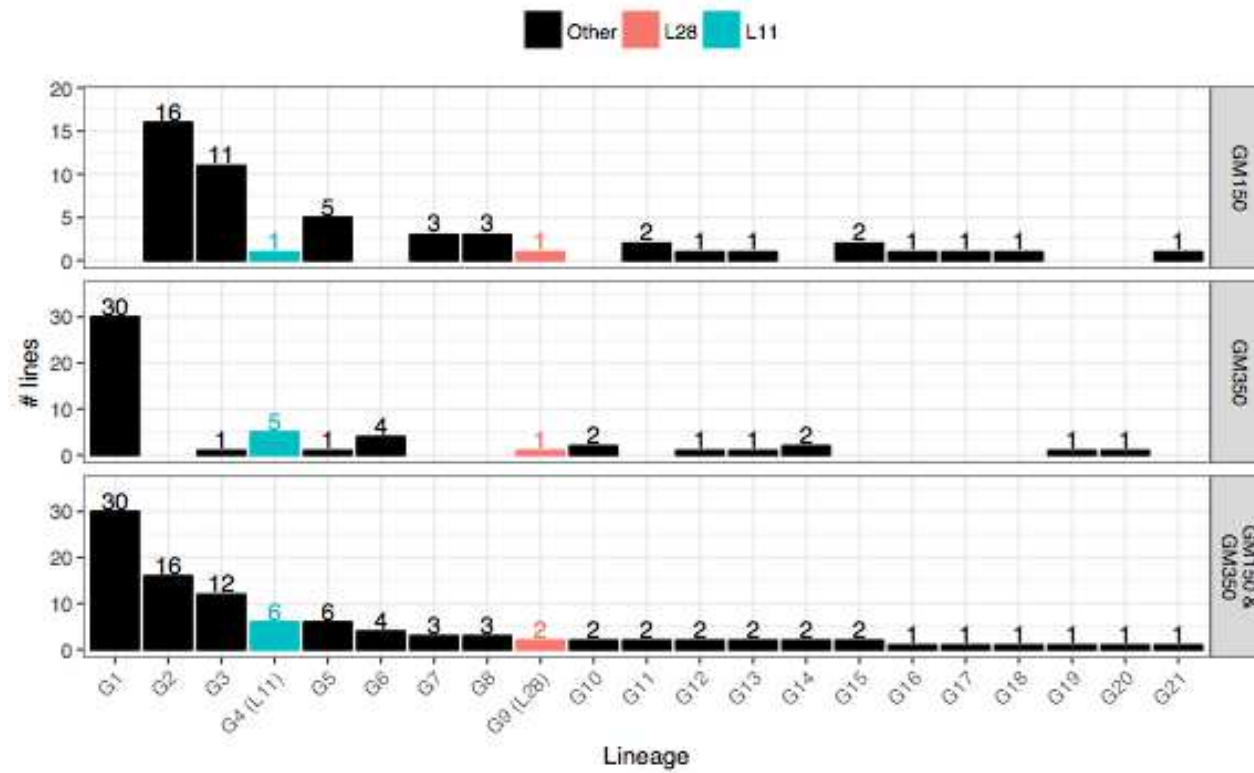


# Expected Population Genetic Dynamics

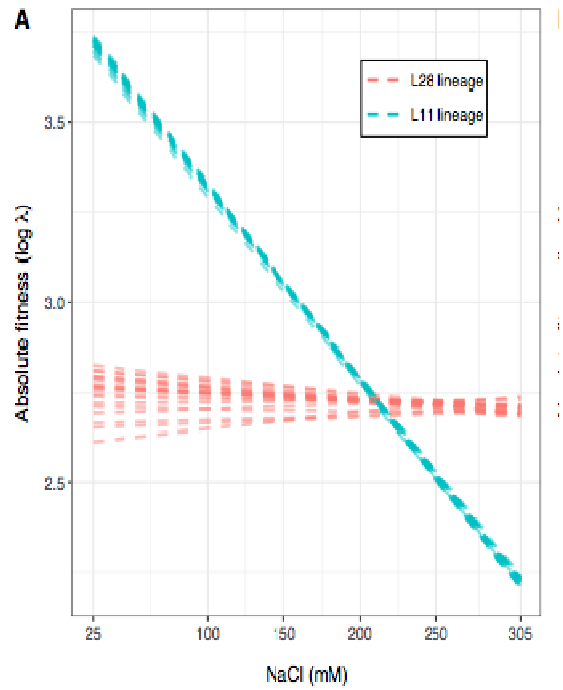


Similar dynamics with linear and quadratic fitness reaction norms

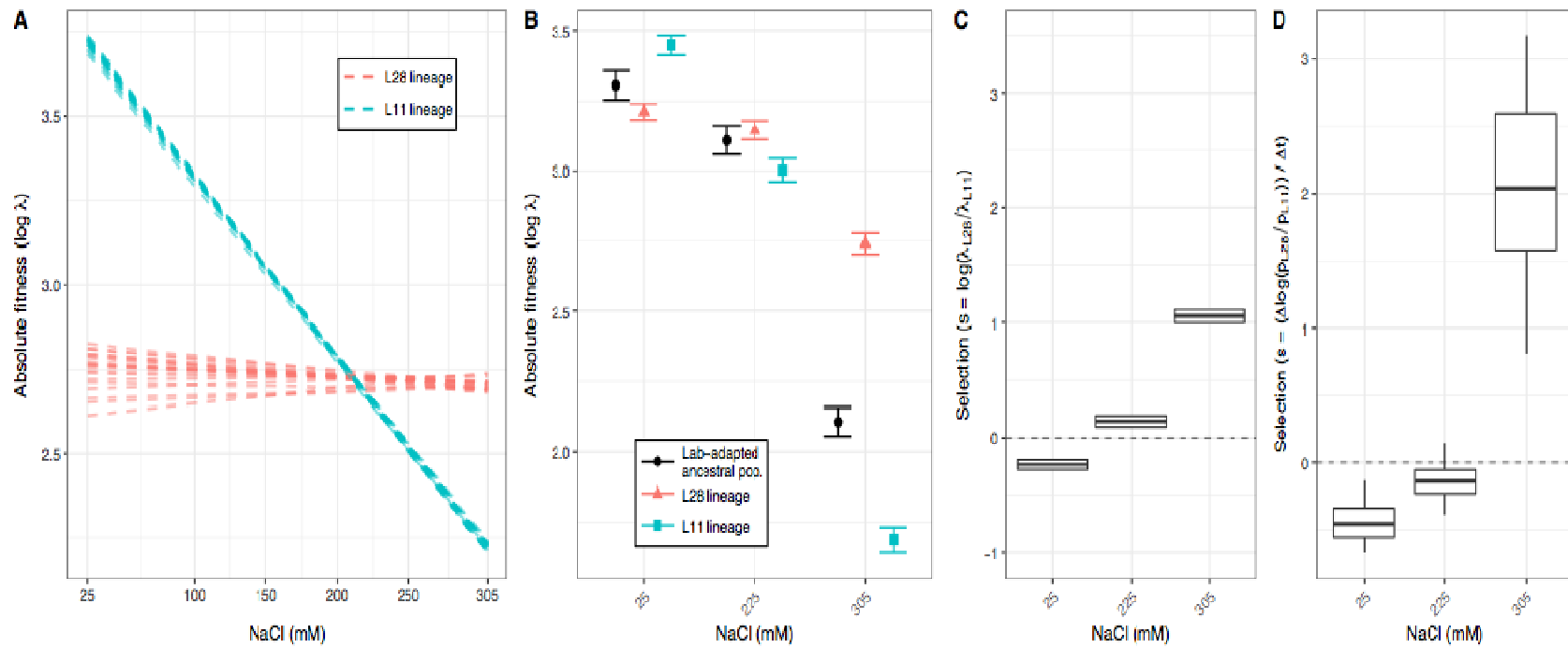
## Identifying the two adaptive lineages



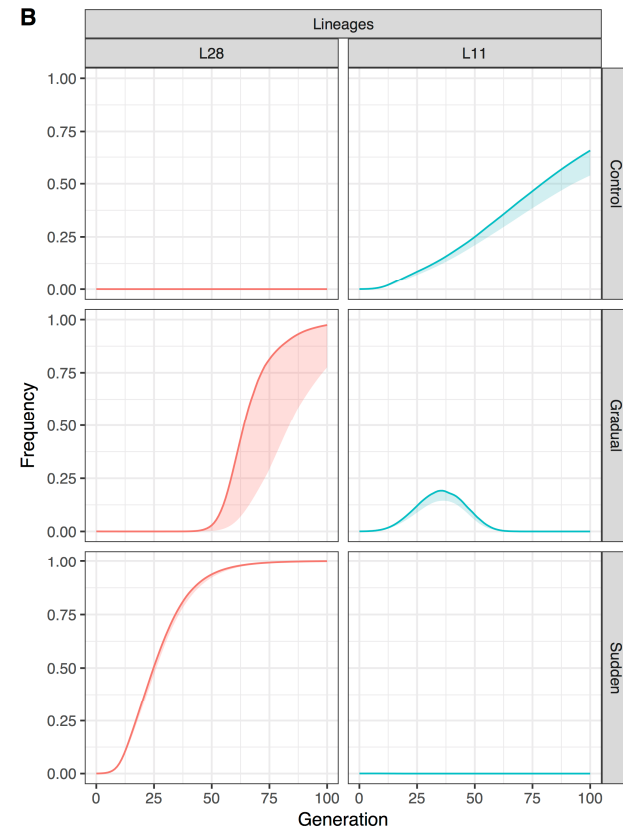
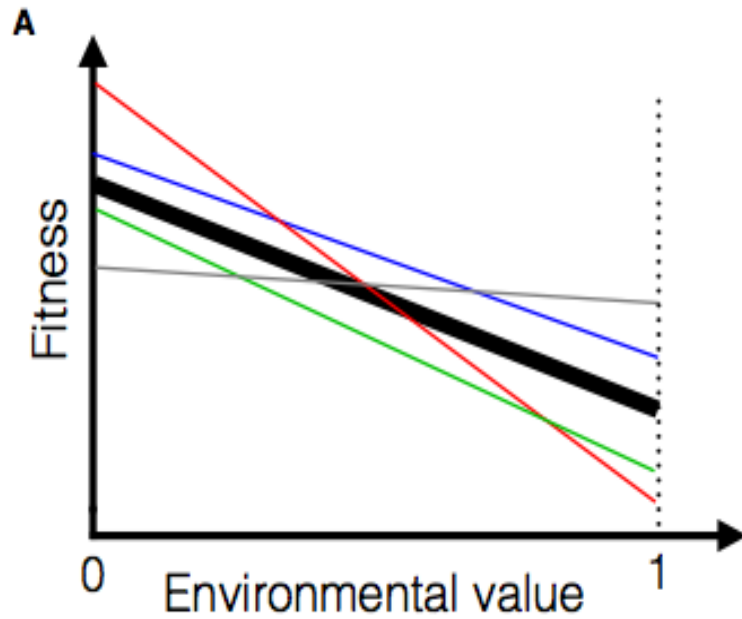
# Expected Fitness Reaction Norms



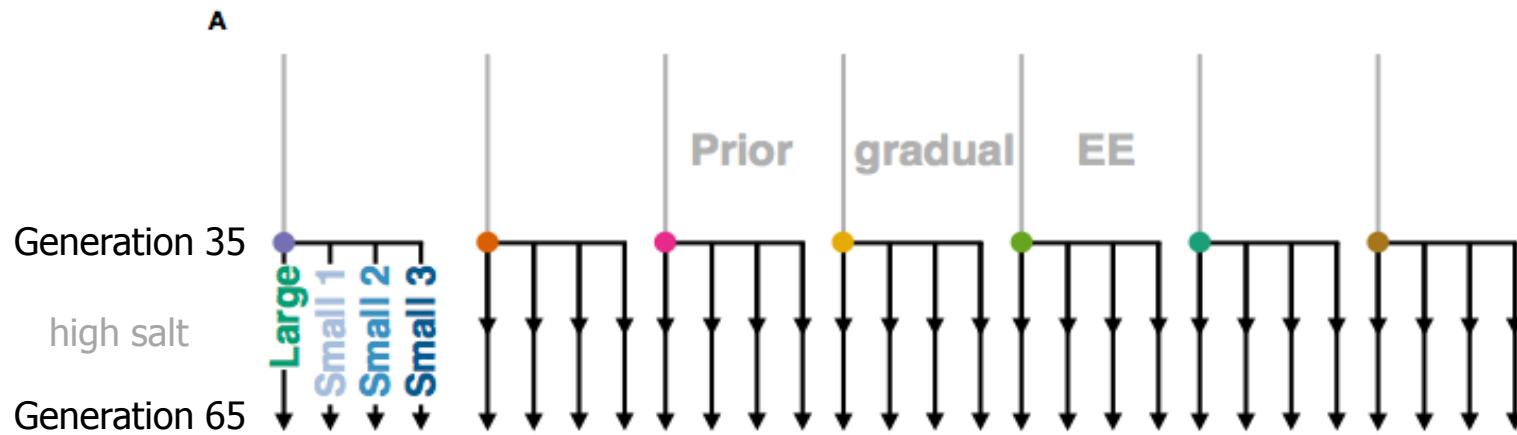
# Expected and Observed Fitness Reaction Norms



# A Role for Genetic Drift and/or Maintenance of Polymorphism?

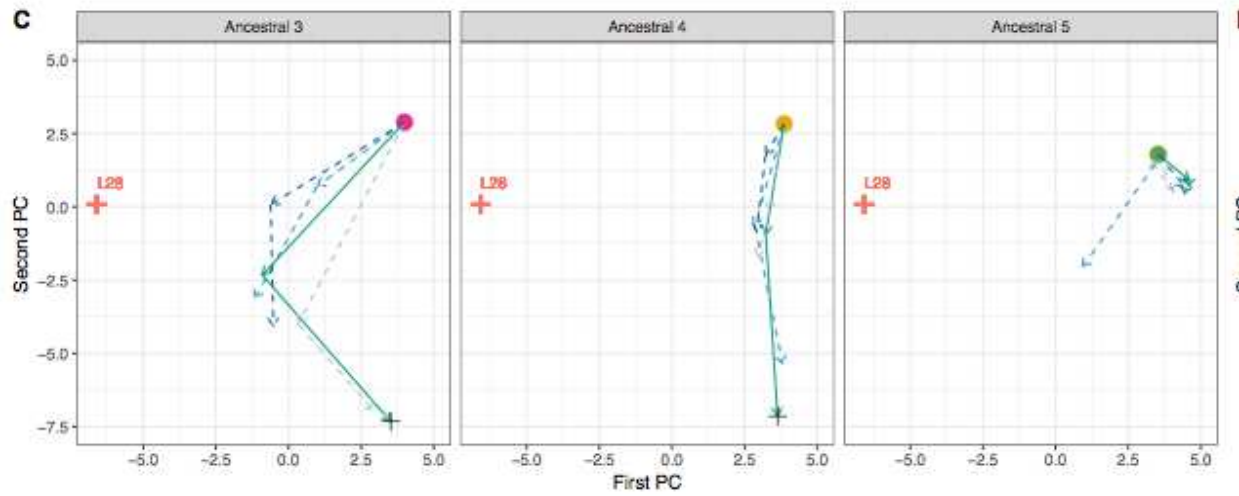
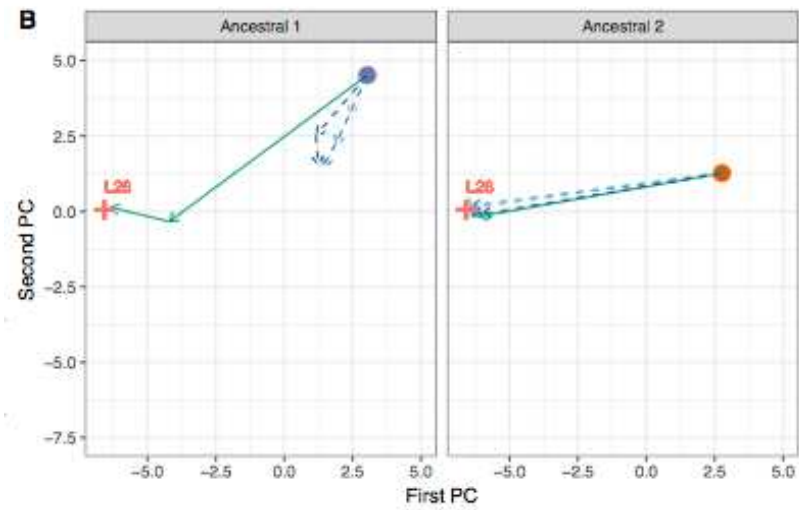


# Experimental Evolution Design

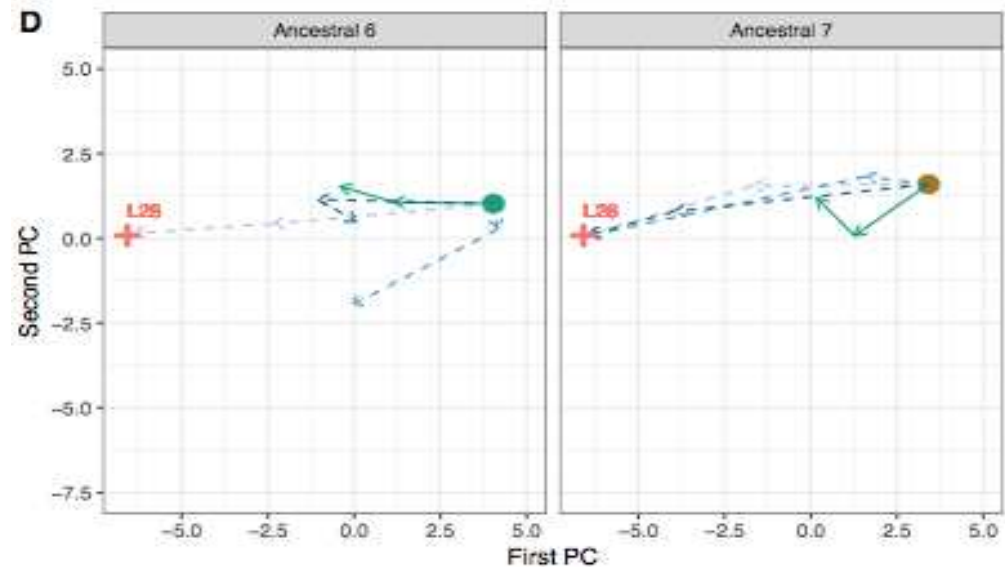


- seven gradual populations at G35 revived and high salt evolution repeated
- populations pool-genotyped at G35 and after 15 and 30 generations

# Founder Effects and Selection Efficiency

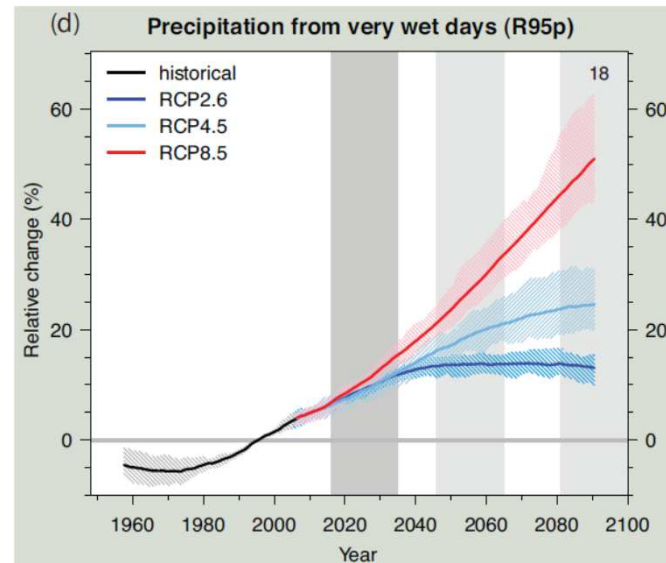


## Founder Effects and Selection Efficiency





## NS in Temporally Fluctuating Environments



Stocker et al. 2013 Intergovernmental Panel on Climate Change

- when individuals have information during development about the environment they will face at reproduction, one expects that the evolution of phenotypic plasticity underlies adaptation
- when this information about environmental change can only be provided by the mother then the selection for maternal effects should underlie adaptation

## Maternal Independent Effects

offspring phenotypes do not depend on maternal environment

Consider two discrete phenotypes in two discrete environments;  
their geometric mean fitness across all possible environmental regimes can be described by:

$$\log(\hat{w}_1) = (\alpha \log(c_1 s_{1,1}) + (1 - \alpha) \log(c_1 s_{2,1}))$$

$$\log(\hat{w}_2) = (\alpha \log(c_2 s_{1,2}) + (1 - \alpha) \log(c_2 s_{2,2}))$$

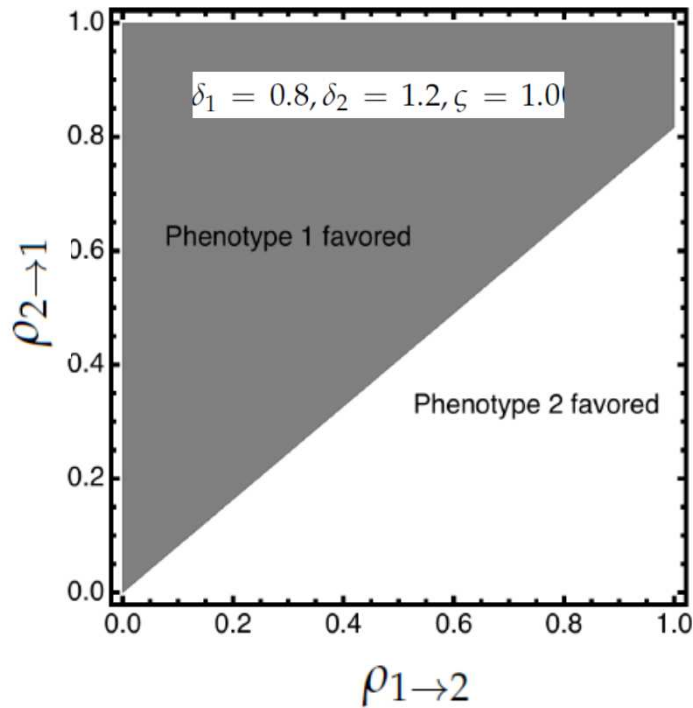
$\alpha$  is the frequency of environment 1

$c$  is the fecundity of phenotype

$s$  is the survivorship of phenotype

## Maternal Independent Effects

offspring phenotypes do not depend on maternal environment



For example, phenotype 2 is favored when:

$$\log(\hat{w}_2) - \log(\hat{w}_1) > 0$$

$$\rho_{2 \rightarrow 1} > - \frac{\rho_{2 \rightarrow 1} (\log(\delta_2) + \log(\zeta))}{\log(\delta_1) + \log(\zeta)}$$

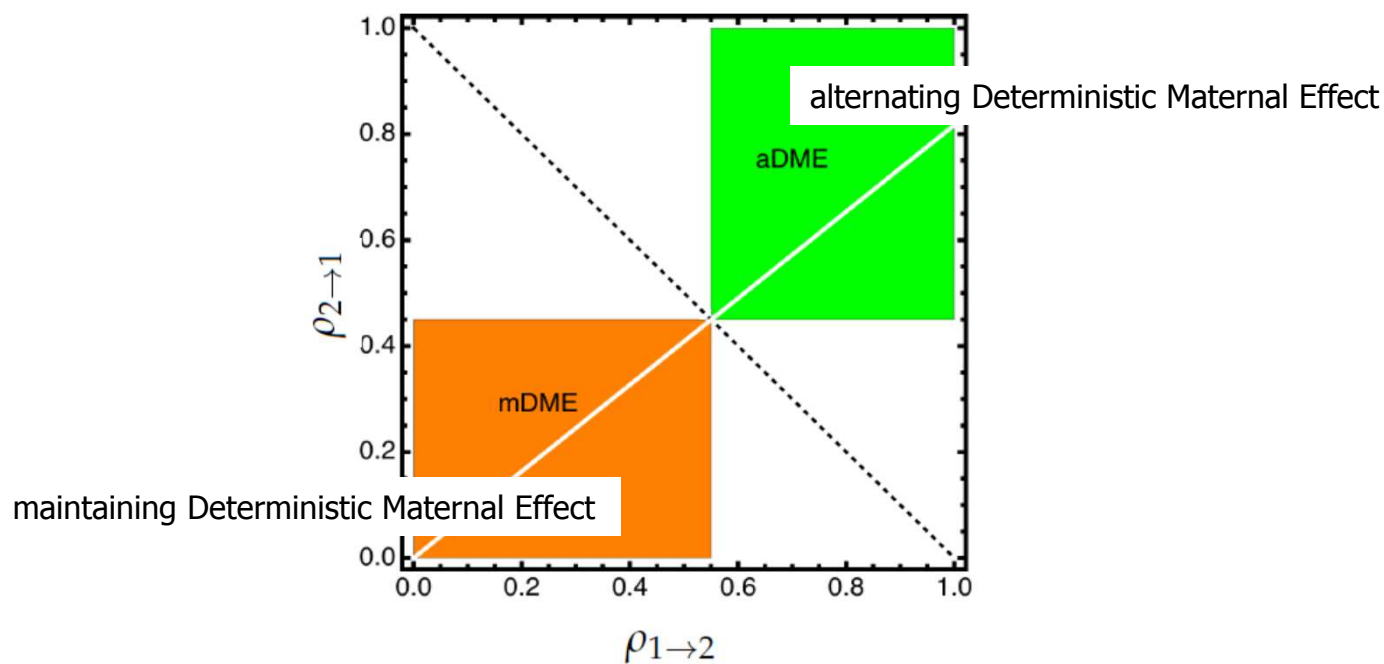
- $\rho_{i \rightarrow j}$  is the probability that environment changes from  $i$  to  $j$
- $\delta_i$  is the relative survival of phenotype 2 in environment  $i$
- $\zeta$  is the relative fecundity of phenotype 2

## Deterministic Maternal Effects

offspring phenotypes depend on maternal environment in a consistent manner

$$\log(\hat{w}_{\text{aDME}}) = \left( (1 - \rho_{1 \rightarrow 2})\alpha \log(c_2 s_{1,2}) + \rho_{1 \rightarrow 2}\alpha \log(c_2 s_{2,2}) + \dots \right)$$

$$\log(\hat{w}_{\text{DME}}) - \log(\hat{w}_{\text{MIE}}) > 0$$



$\alpha$  is the frequency of environment 1

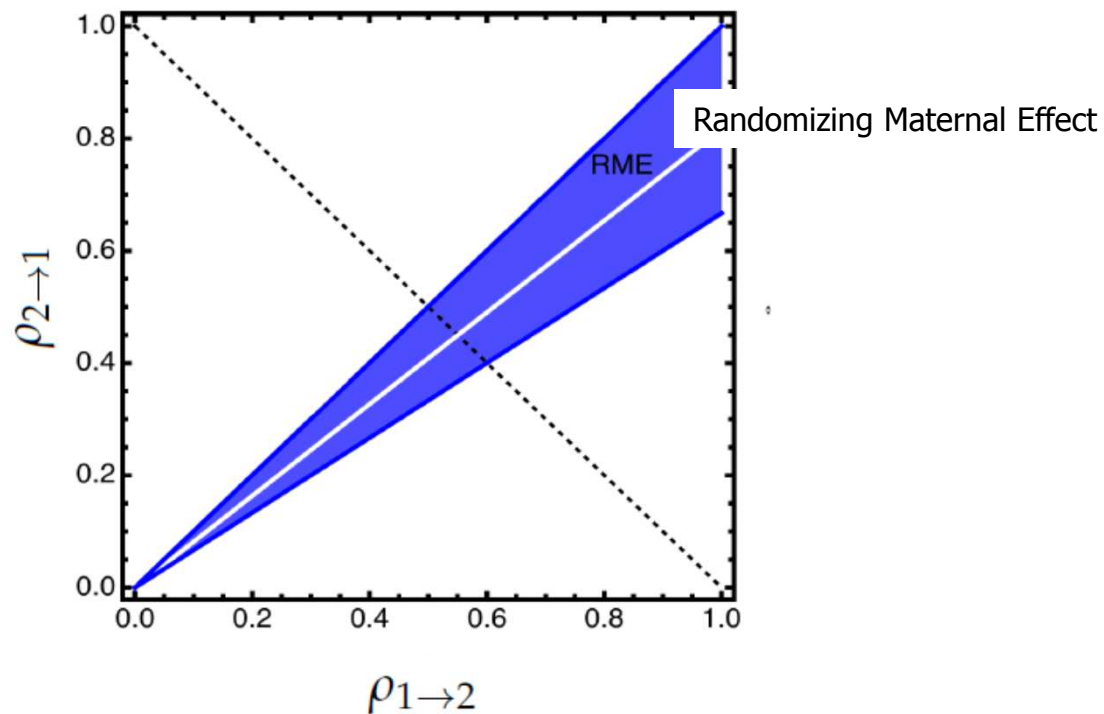
$\rho_{i \rightarrow j}$  is the probability that environment changes from  $i$  to  $j$

## Randomizing Maternal Effects

mothers randomize offspring phenotypes, but the probability of producing a given phenotype does not depend on maternal environment

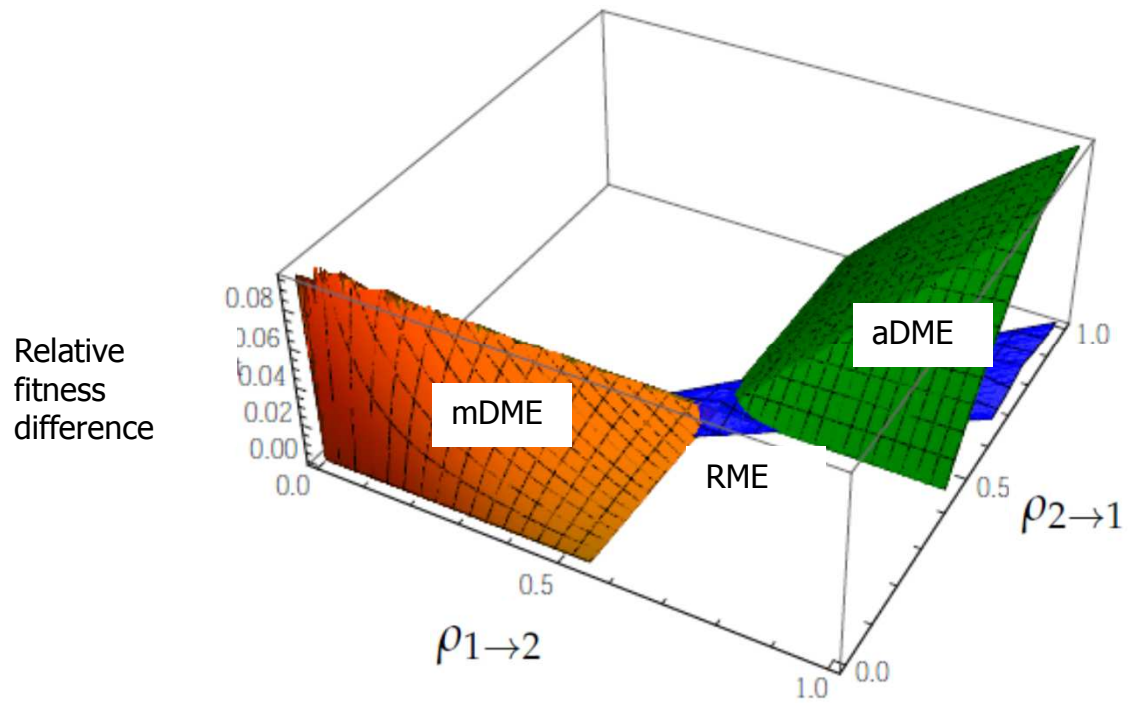
$$\log(\hat{w}_{\text{RME}}) = \alpha \log(\gamma c_1 s_{1,1} + (1 - \gamma) c_2 s_{1,2}) + \dots$$

$$\log(\hat{w}_{\text{RME}}) - \log(\hat{w}_{\text{MIE}}) > 0$$

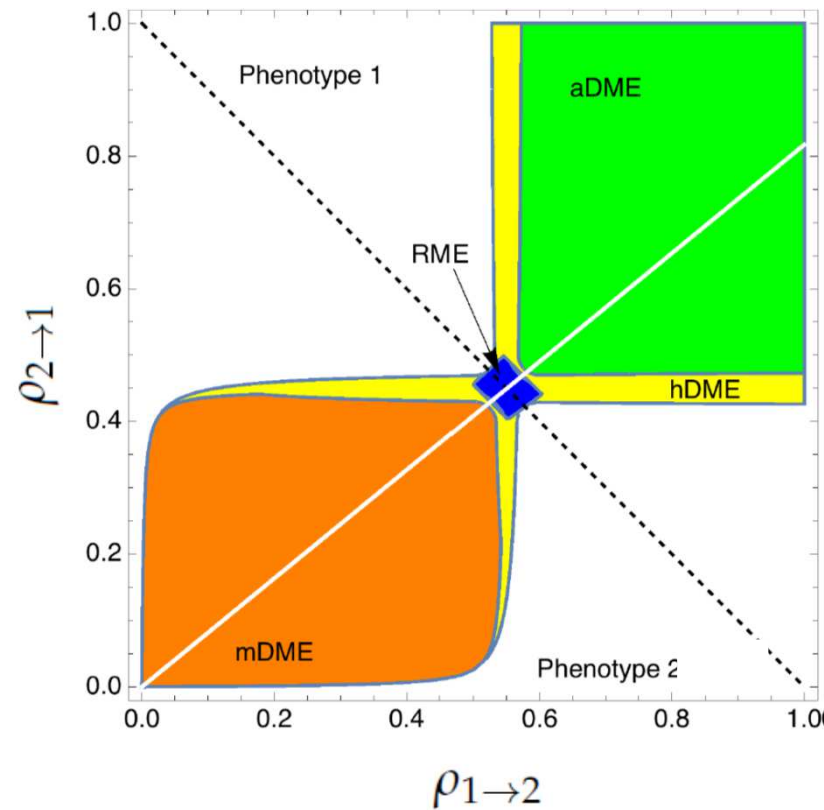


$\rho_{i \rightarrow j}$  is the probability that environment changes from  $i$  to  $j$   
 **$\gamma$  is the probability of producing phenotype 1**

## Deterministic and Randomizing ME Relative Fitness Difference to Maternal Independent Effects



## Selection for Maternal Effects in Fluctuating Environments



Plotted: Fitness difference between maternal effects and maternal independent effects larger than  $10^{-3}$

hDME: “hybrid deterministic maternal effects”, when the probability of randomizing offspring phenotypes depends on the maternal environment

# Maternal Effects in *C. elegans*

Current Biology 19, 859–863, May 26, 2009 ©2009 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2009.03

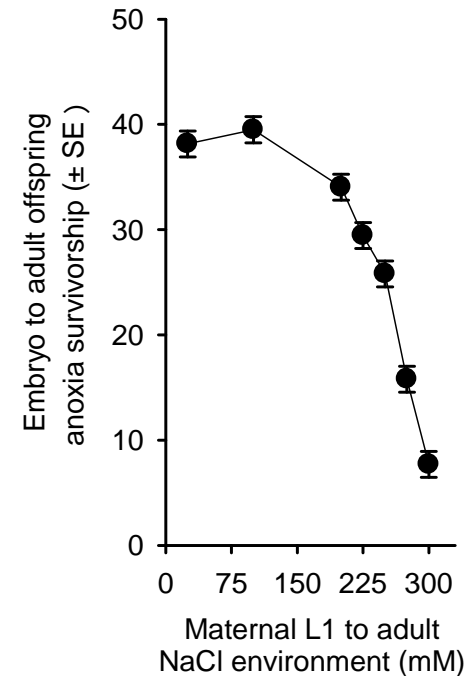
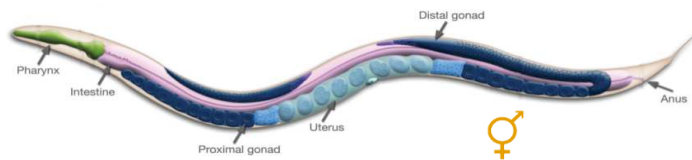
## Adaptive Sugar Provisioning Controls Survival of *C. elegans* Embryos in Adverse Environments

Harold N. Frazier III<sup>1</sup> and Mark B. Roth<sup>2,\*</sup>

<sup>1</sup>Molecular and Cellular Biology Graduate Program  
University of Washington  
Seattle, WA 98195  
USA

<sup>2</sup>Basic Science Division  
Fred Hutchinson Cancer Research Center  
Seattle, WA 98109  
USA

embryos are not generally  
sure to hyperosmotic con  
the salt in a way that mak  
We next tested *daf-2(e*  
which carry a hypomorpl  
insulin-like growth factor  
engage in OPC and found  
adapt their embryos to s  
No embryos from OPC e  
salt ubiquitously 20% of



Dey et al. (not published)

Hermaphrodites challenged with high NaCl concentrations since larval stages have broods with poor survivorship in anoxia



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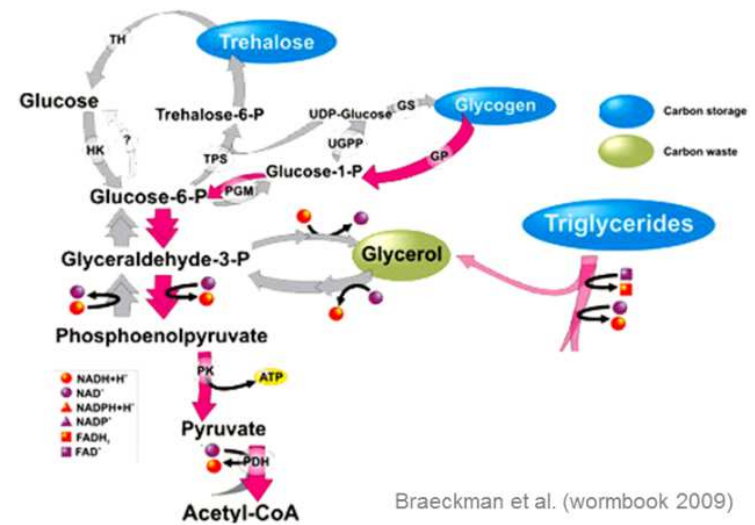
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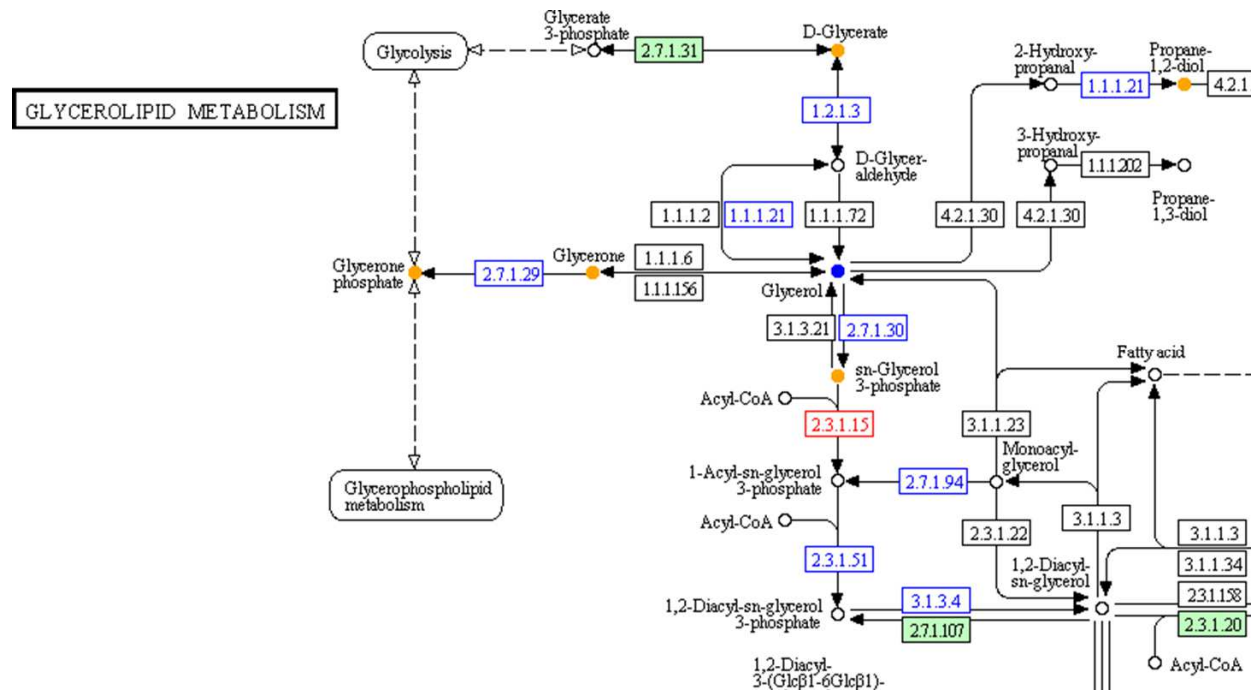
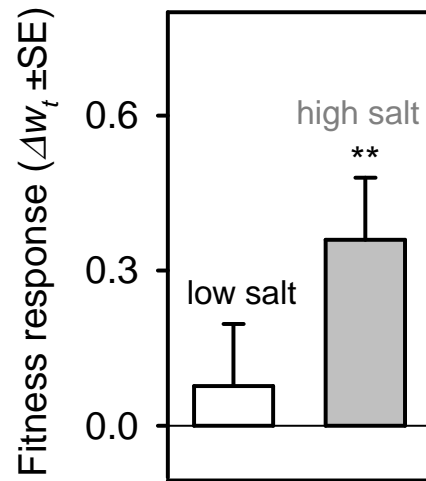
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We next tested *daf-2(e* which carry a hypomorph insulin-like growth factor engage in OPC and found adapt their embryos to s  
No embryos from OPC e  
salt, whereas 20% of



Hermaphrodites trade-off glycerol production necessary for their survival in high salt conditions with glycogen provisioning of their embryos

# Adaptation to High Salt Conditions

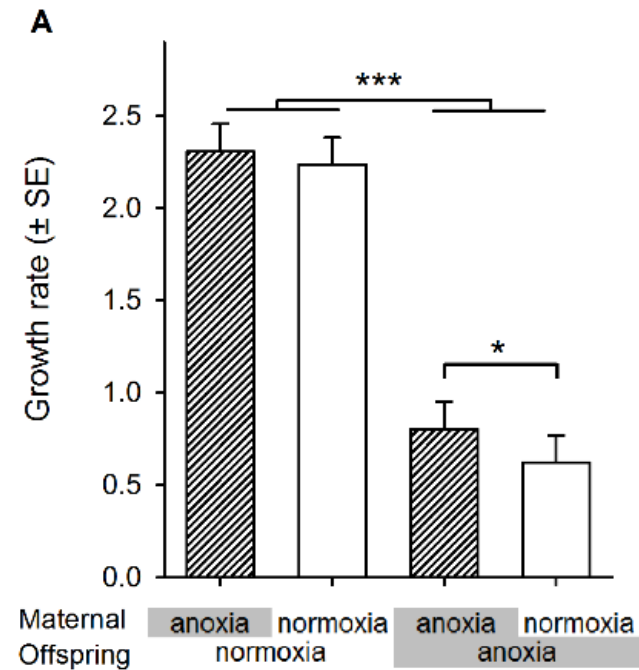
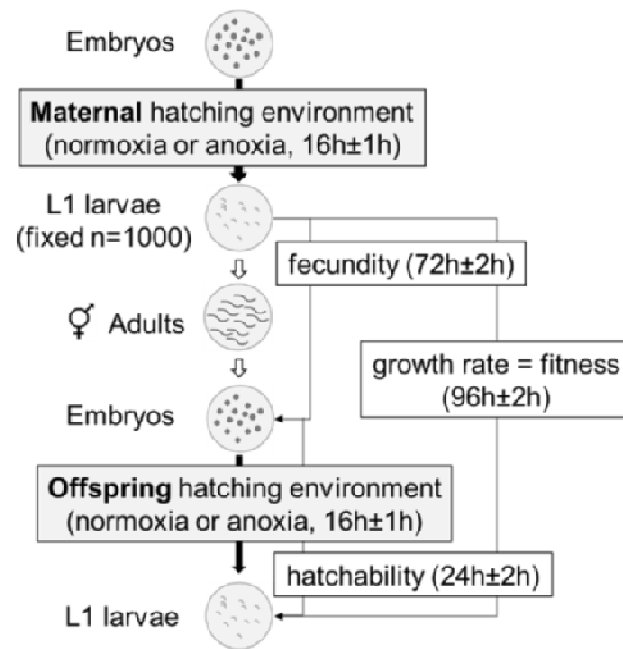


KEGG analysis :

↑ reg ↓ reg no change

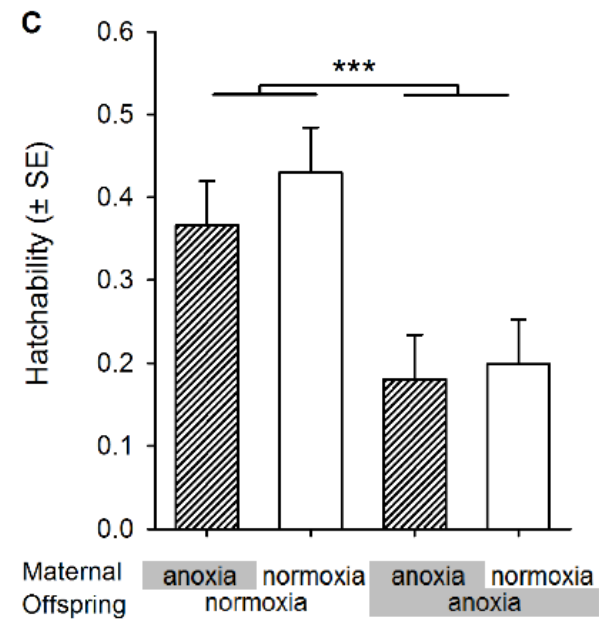
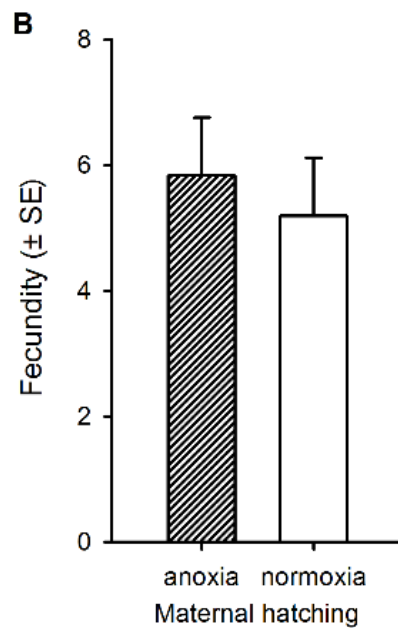
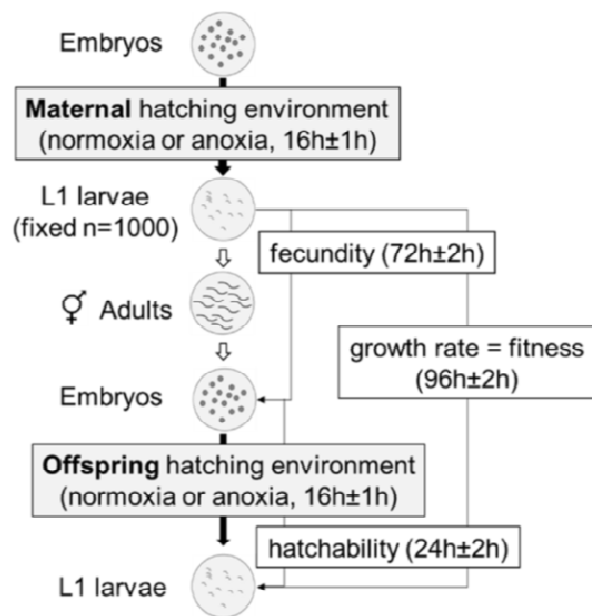
# Ancestral Adaptive State

life-cycle and high salt adapted population

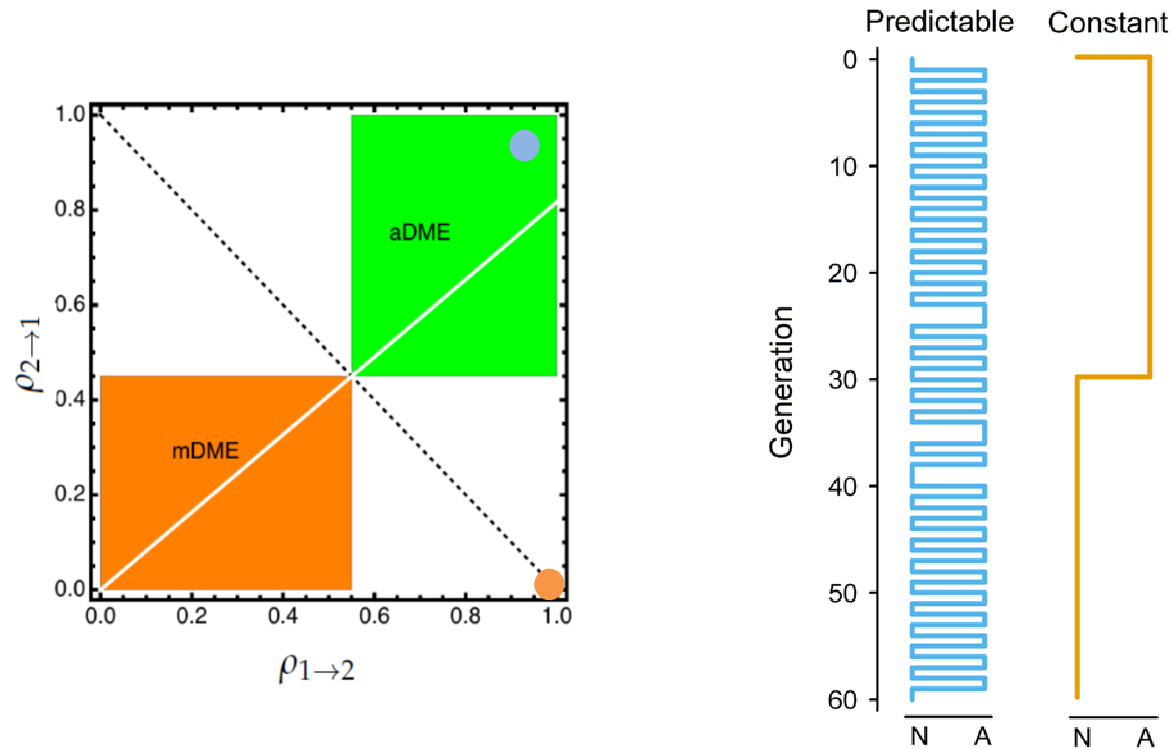


# Ancestral Adaptive State

life-cycle and high salt adapted population

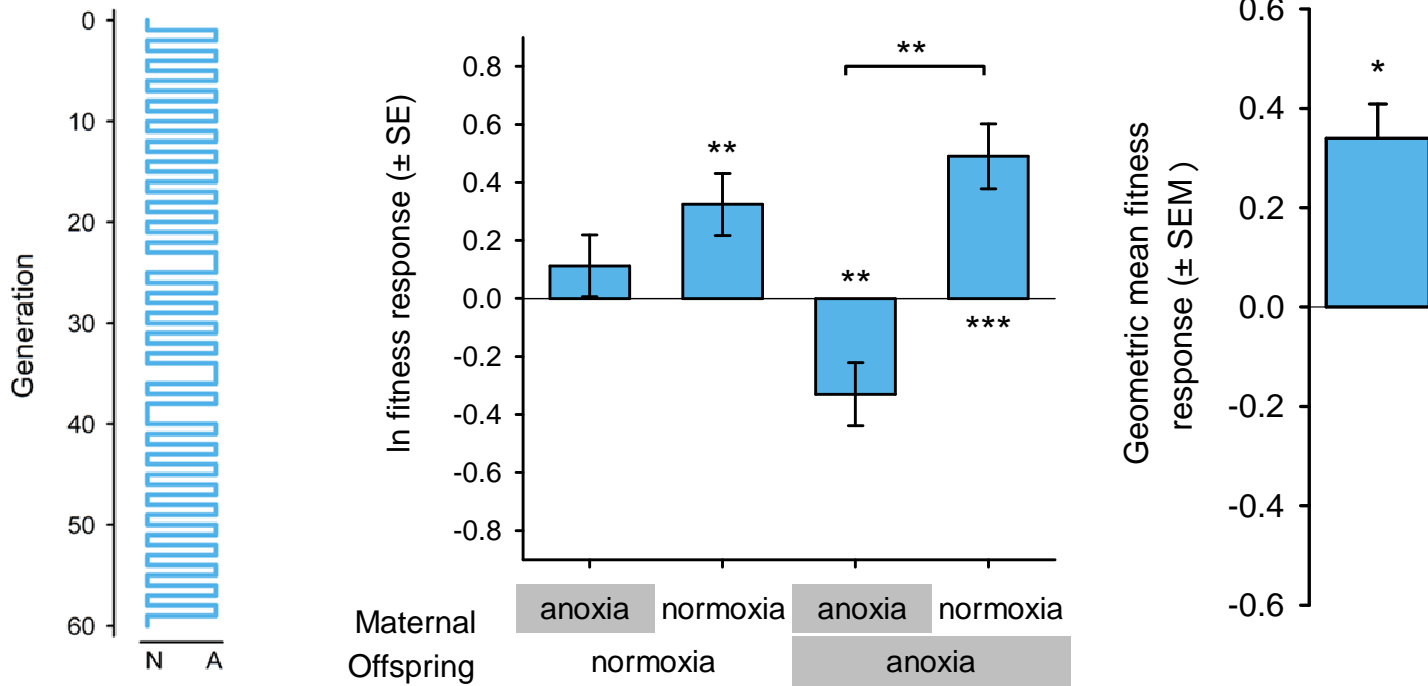


# Experimental Evolution in Correlated Environments

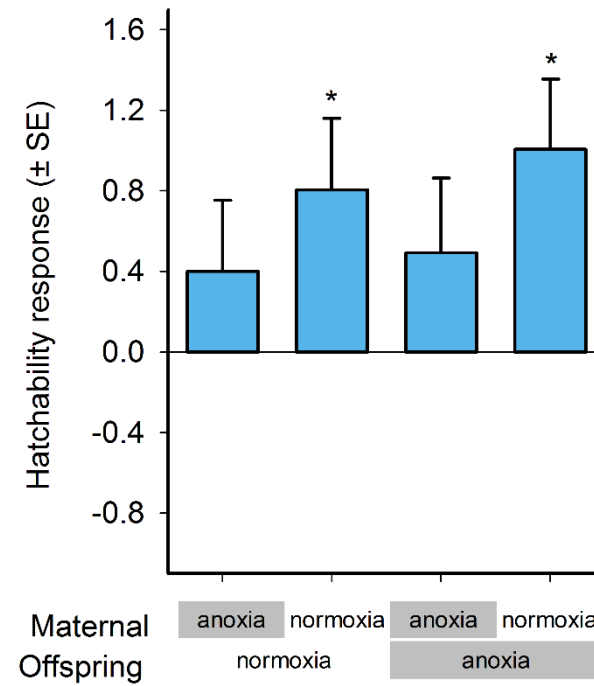
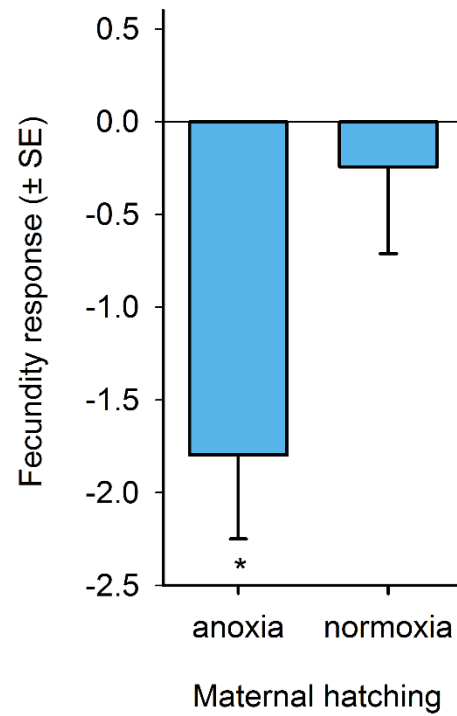
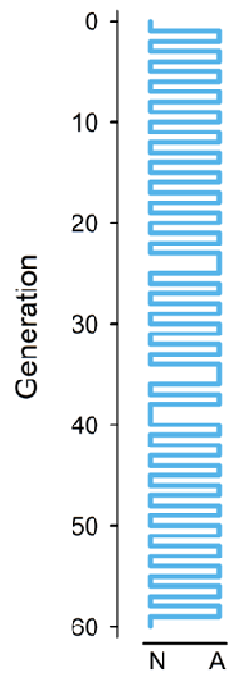


Predictable: probability of changing environments of 0.95 across 60 generations  
Constant: probability of changing environments of 0.02 across 60 generations  
Both regimes: frequency of anoxia generations of 50%

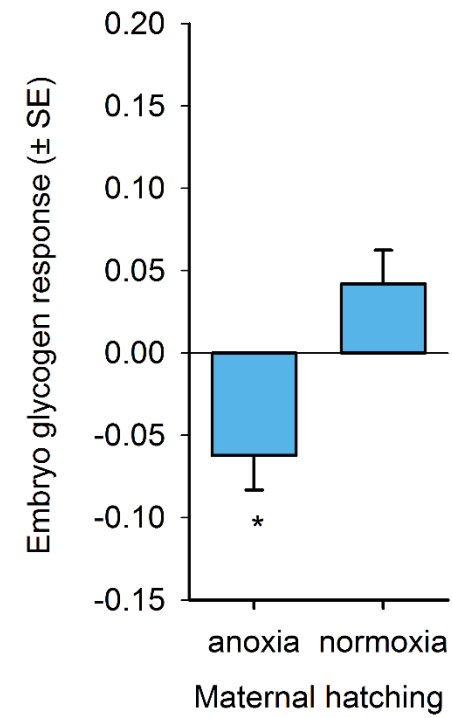
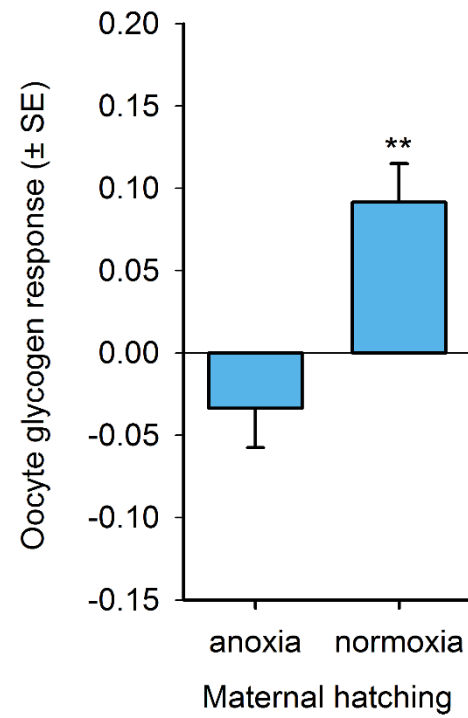
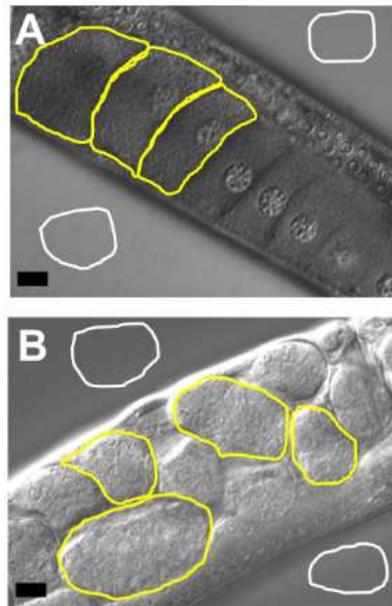
# Adaptation to Predictably Alternating Environments



# Evolution of Deterministic Maternal Effects

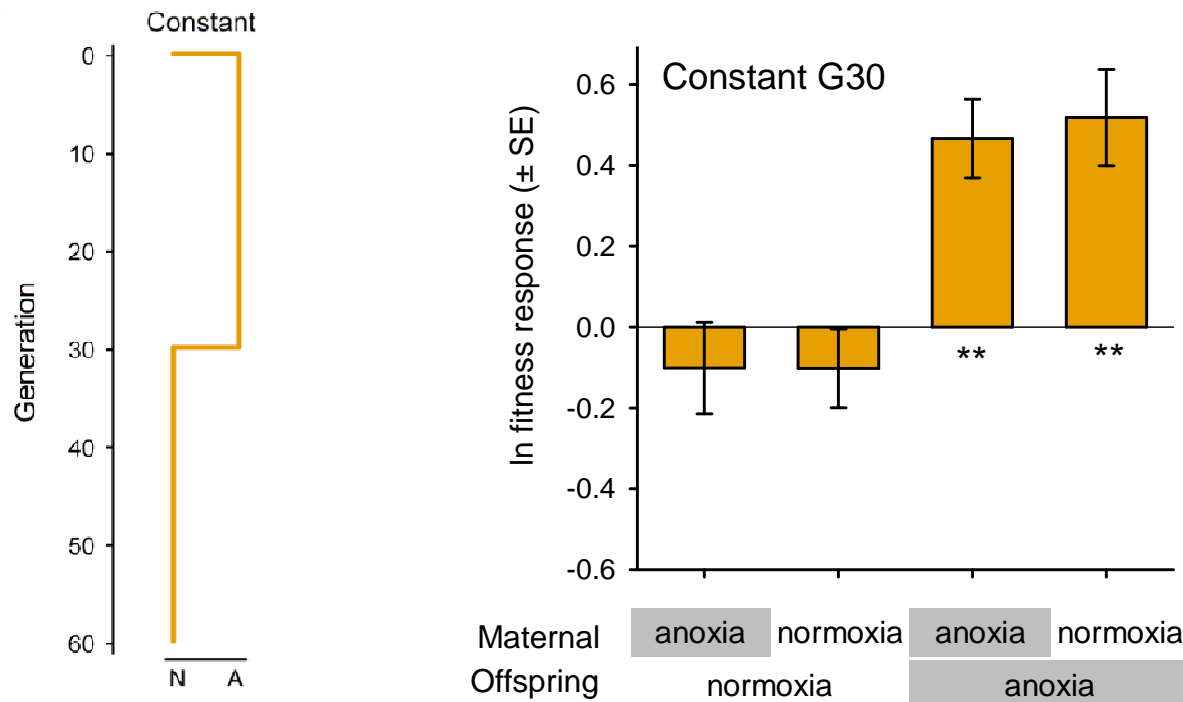


## Evolution of Glycogen Provisioning

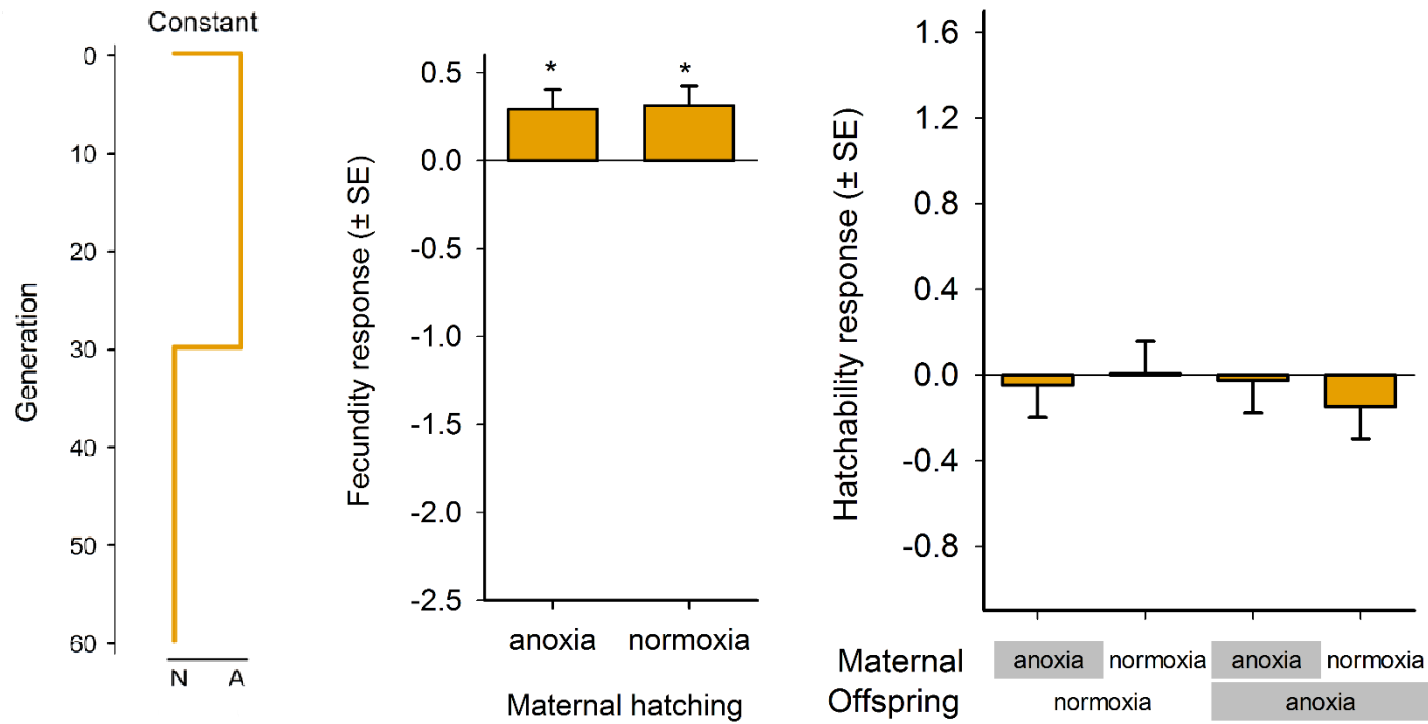




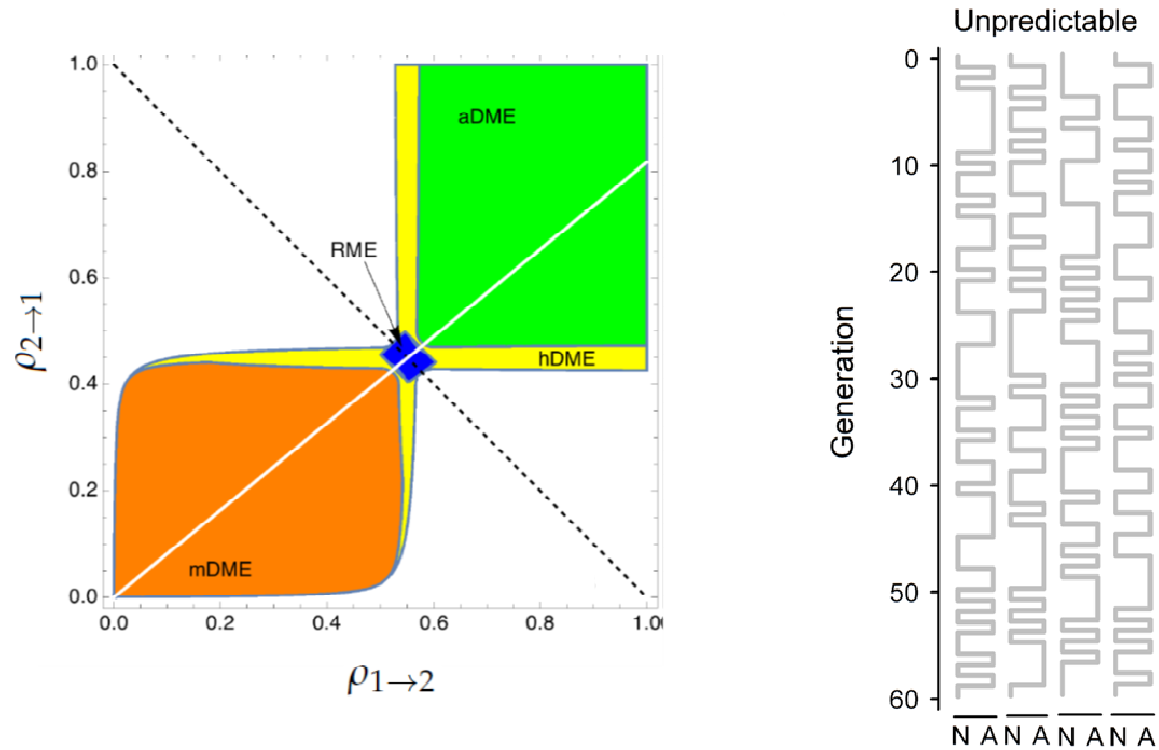
## Adaptation to (Predictably) Constant Environments



## Adaptation to Constant Environments

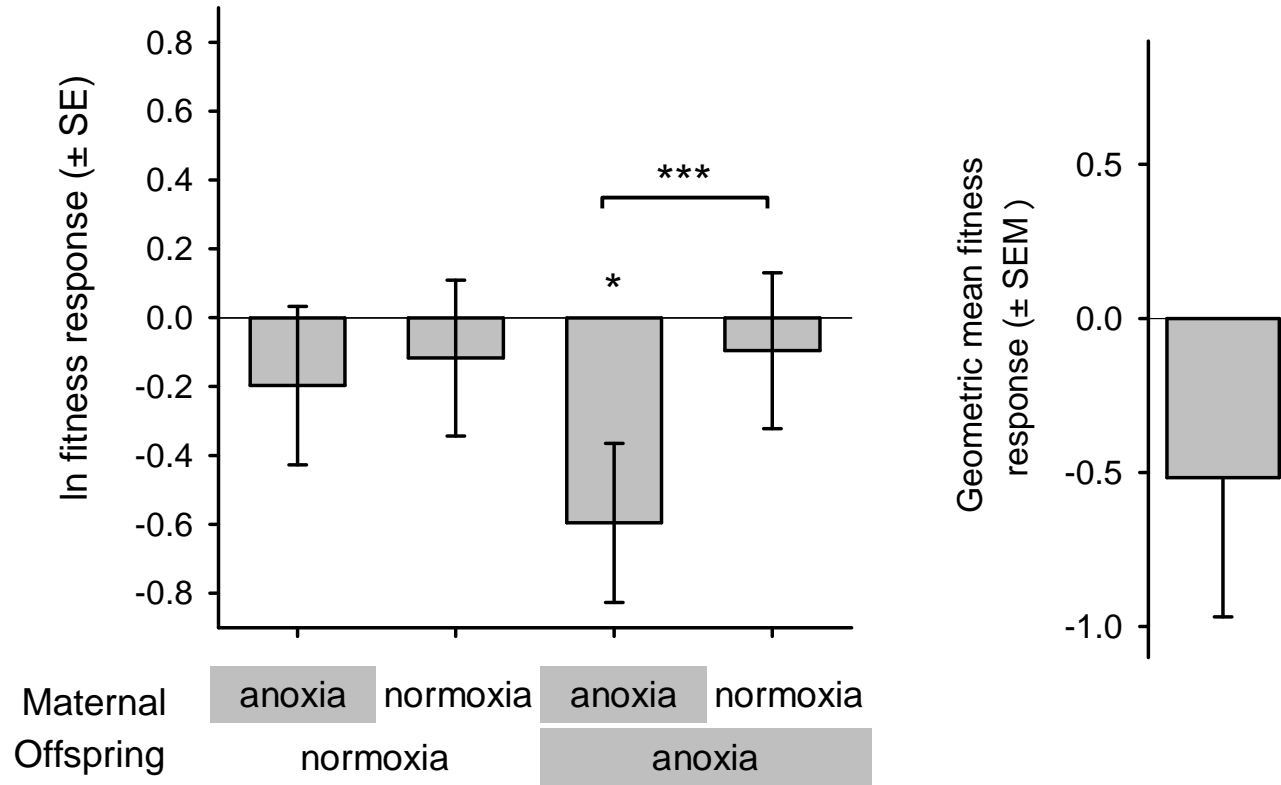


## Evolution in Uncorrelated Environments



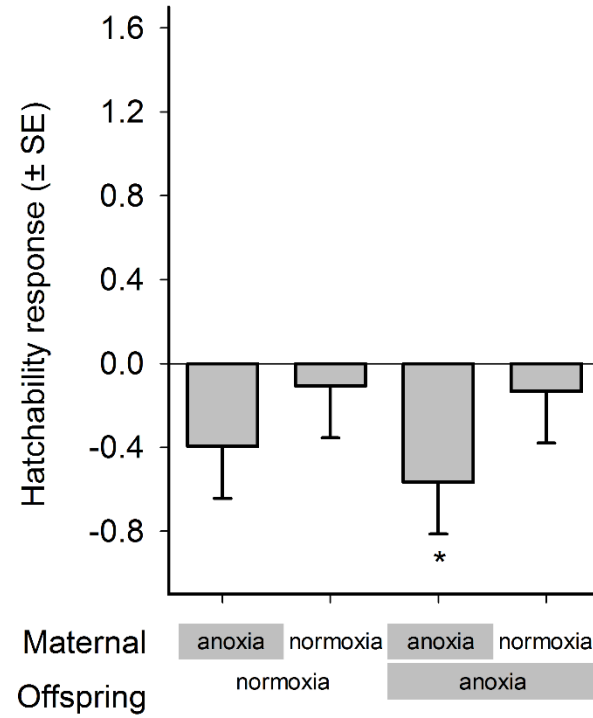
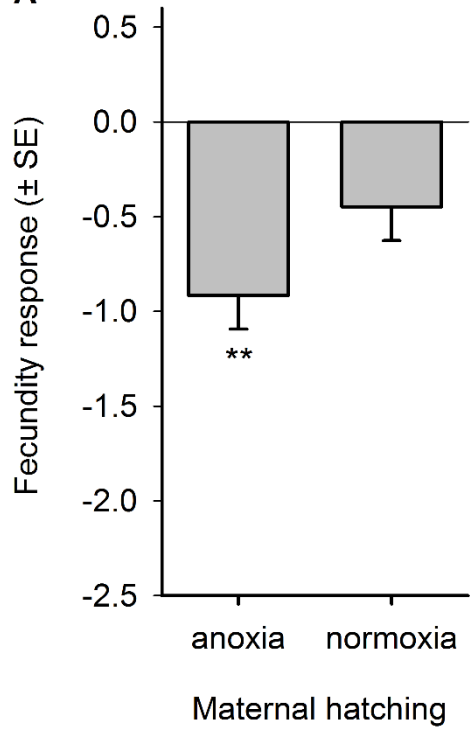
Unpredictable: probability of changing environments of 0.45 across 60 generations  
as in the other regimes: frequency of anoxia generations of 50%

# Adaptation to Unpredictable Environments

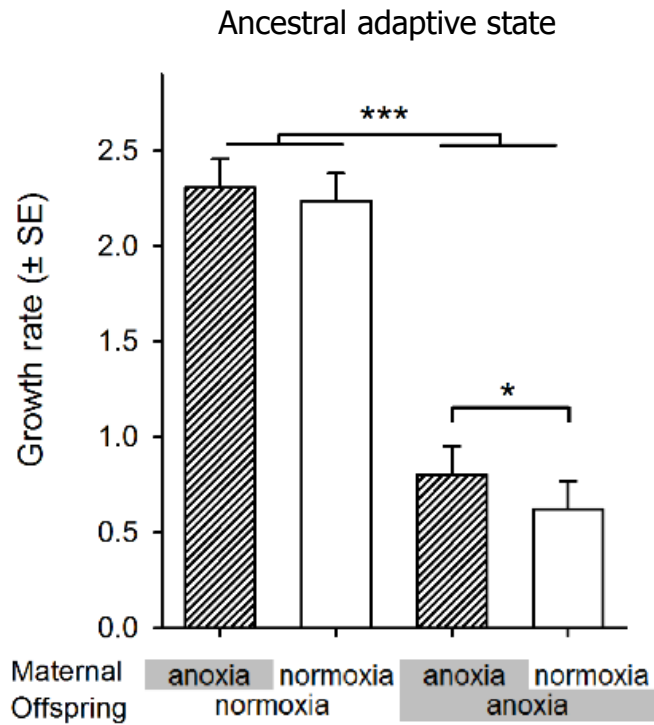


# Evolution of Maternal Effects

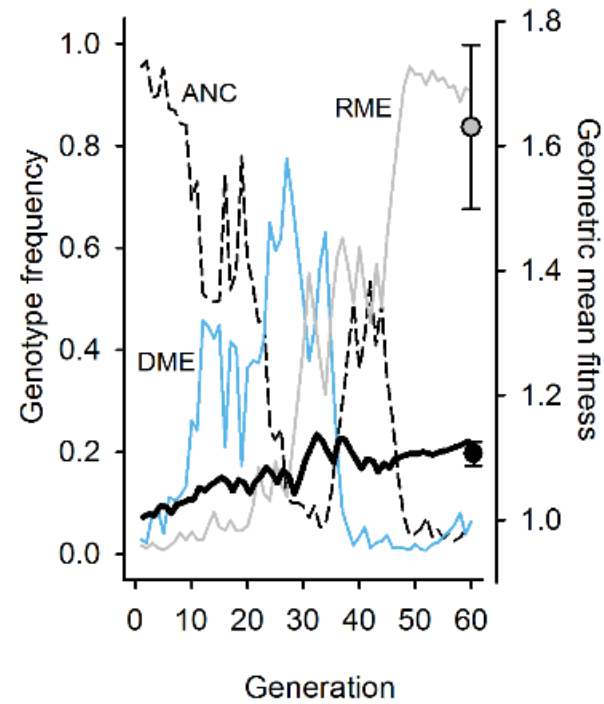
**A**



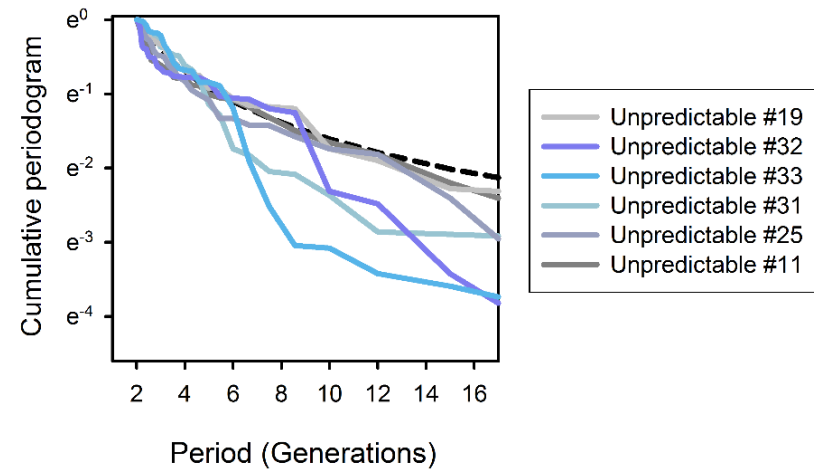
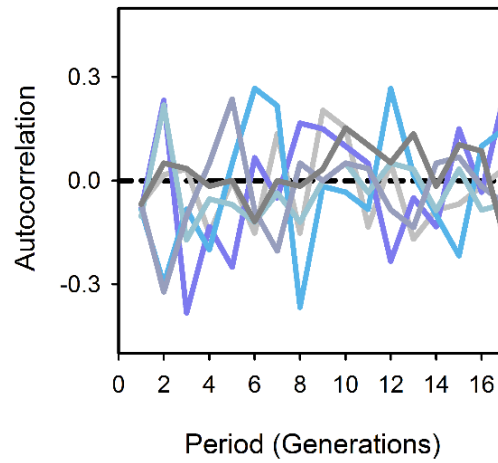
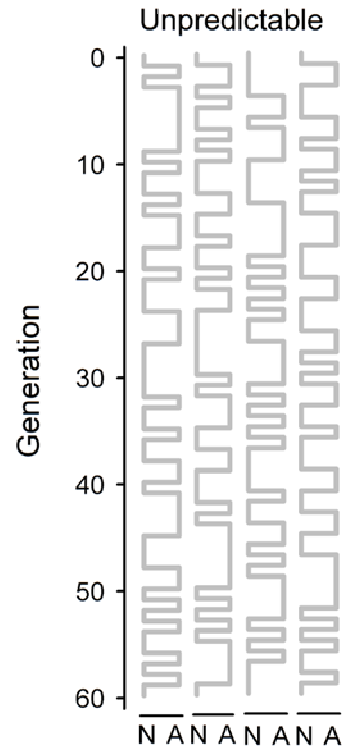
## Expected Evolution of Randomizing Maternal Effects



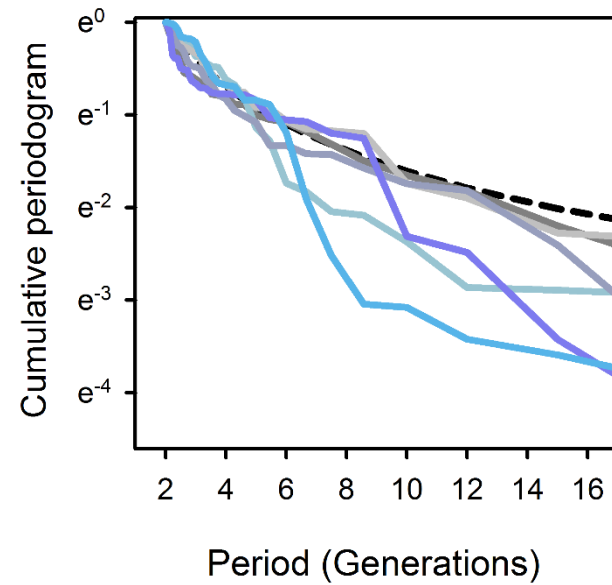
Wright-Fisher numerical simulations under the unpredictable environmental sequences



# Correlated Environmental Sequences



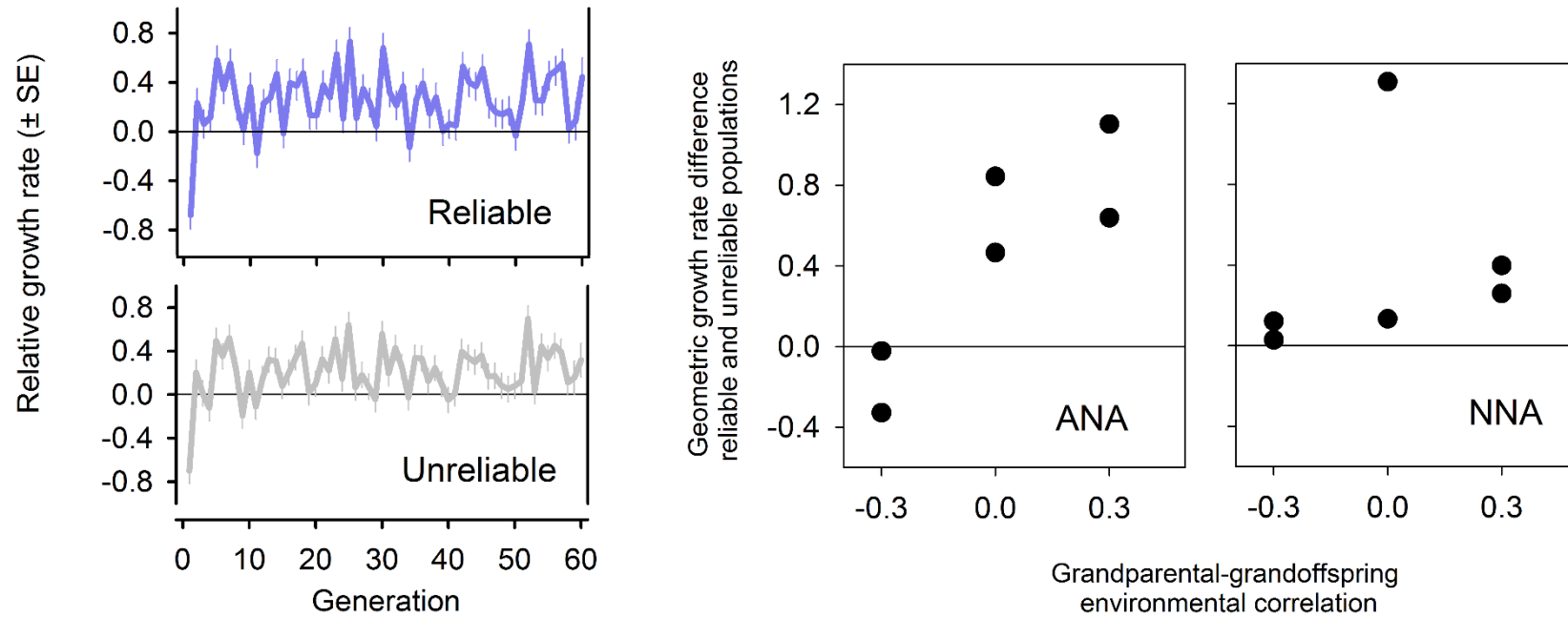
## Information and Transgenerational Effects



Unpredictable Reliable: light cue reliably given to mothers during oogenesis whenever their offspring will face anoxia

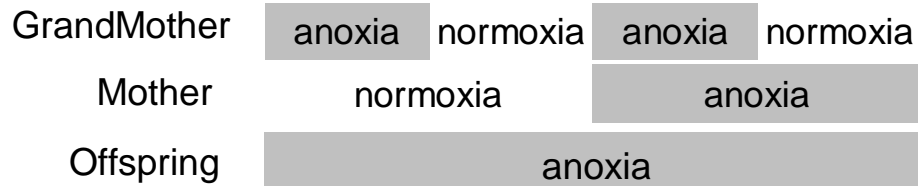
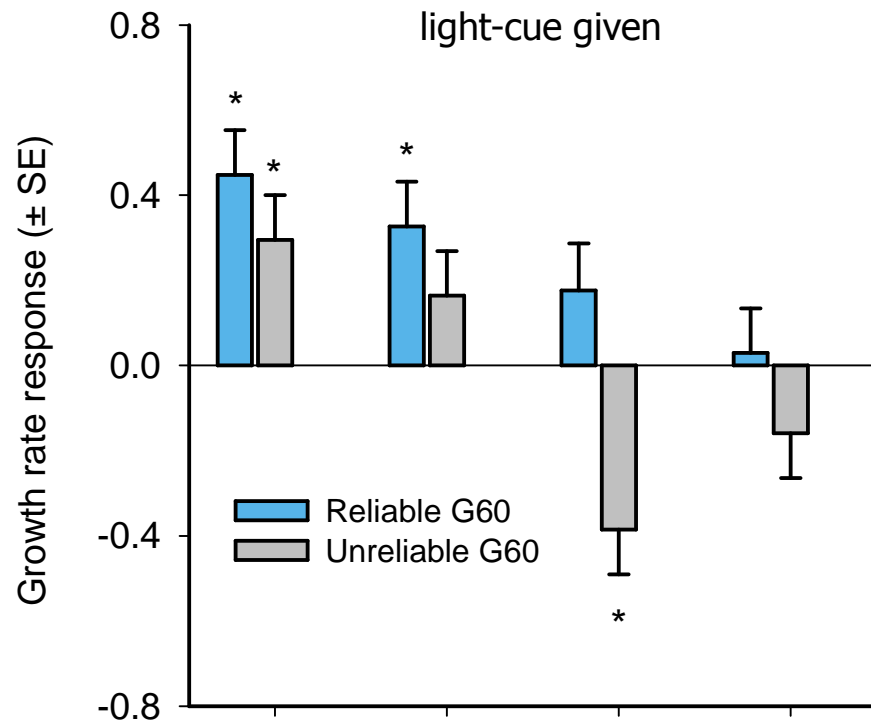


# Population Dynamics

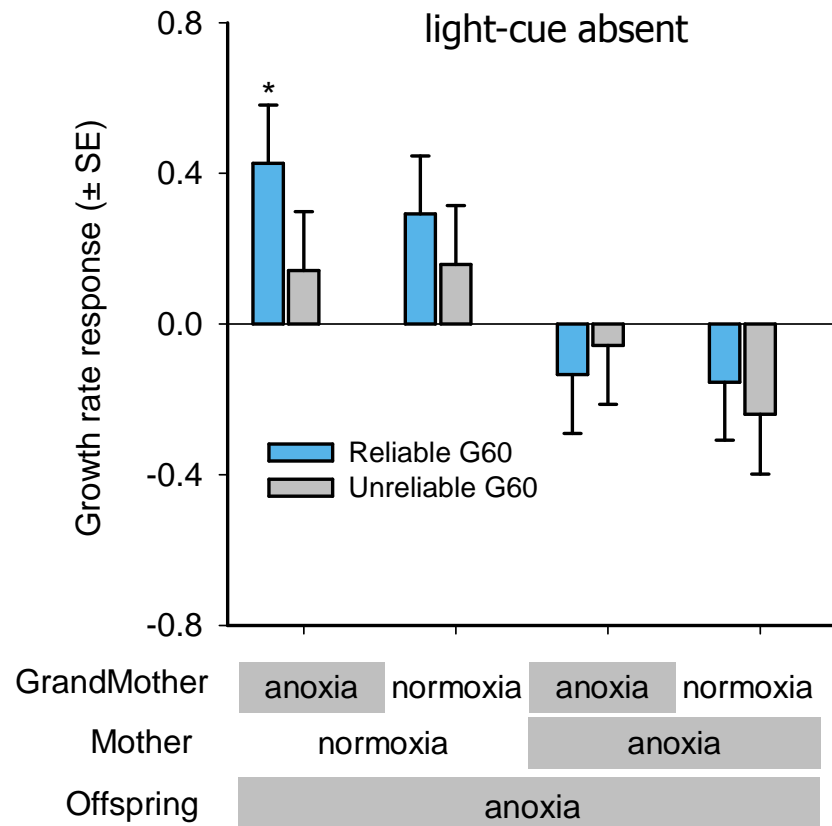
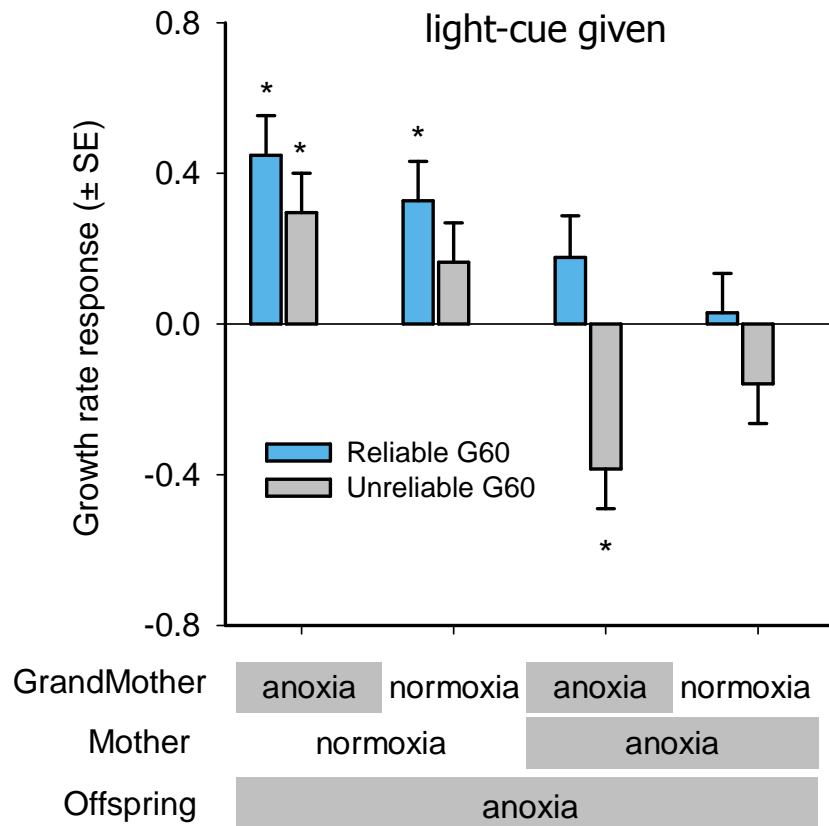


?? Grandmothers exposed to anoxia prepare their offspring to perceive the cue in order for them to provision in turn their offspring ??

# Adaptation to Unpredictably Fluctuating Environments?



# Adaptation to Unpredictably Fluctuating Environments?



## **NS in Variable Environments**

- . Temporal versus spatial variation
- . Within- versus between-generation variation
- . Continuous versus discrete variation
- . Rates of environmental change versus environmental fluctuations
  
- . Environmental dimensionality (information, cue reliability)
  
- . Evolution by mutation accumulation
- . Evolution from pre-existing genetic diversity
- . Evolution from standing genetic variation

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**Lab Support:**

Bruno Afonso, Sara Carvalho, Ivo Chelo, Anna Crist, Hervé Gendrot, Christine Goy, Pablo Ibáñez, Sofia Nunes, Veronica Pereira, Ania Pino, Sara Santos

**Funding:**



**FCT** Fundação para a Ciência e a Tecnologia  
MINISTÉRIO DA CIÊNCIA, TECNOLOGIA E ENSINO SUPERIOR

# Epigenetic Inheritance Model

$$B_i = \begin{array}{c} \begin{array}{cc} & \begin{array}{c} 1 & 2 \end{array} \\ \begin{array}{c} 1 - \beta_{i,1} & \beta_{i,1} \\ \beta_{i,2} & 1 - \beta_{i,2} \end{array} \end{array} \end{array}$$

Matrix determining probability that offspring have phenotype 1 or 2

$$S_i = \begin{array}{c} \begin{array}{cc} & \begin{array}{c} 1 & 2 \end{array} \\ \begin{array}{c} s_{i,1} & 0 \\ 0 & s_{i,2} \end{array} \end{array} \end{array}$$

Offspring survivorship in environment  $i$

One generation iteration is:

$$N_1 = N_0 S_J B_A$$

# Long-run growth of population

For constant reproductive factor:

$$\lambda = \exp [1/T (T \log [\lambda_{\text{fixed}}])]$$

If per generation multiplier is a random variable then –

$$\lambda = \exp \left[ 1/T \left( \sum_t \log [\lambda_t] \right) \right] = \exp \left[ \sum_i p_i \log [\lambda_i] \right]$$

# Long-run growth of population : non-scalar

For constant reproductive factor:

$$\lambda = \exp [1/T (T \log [\lambda_{\text{fixed}}])]$$

$$\lambda = \exp \left[ 1/T \left( \log \left[ \begin{bmatrix} n_{1,0} & n_{2,0} \end{bmatrix} (B_{E_1} S_{E_1} B_{E_2} S_{E_3} B_{E_3} \dots) \cdot (1, 1) \right] \right) \right]$$

For a specific “genotype” that has a pair of B matrices. We can calculate the growth by multiplying together the matrices over time. The lambda that is equivalent to the fixed multiplier is the Lyapunov exponent.