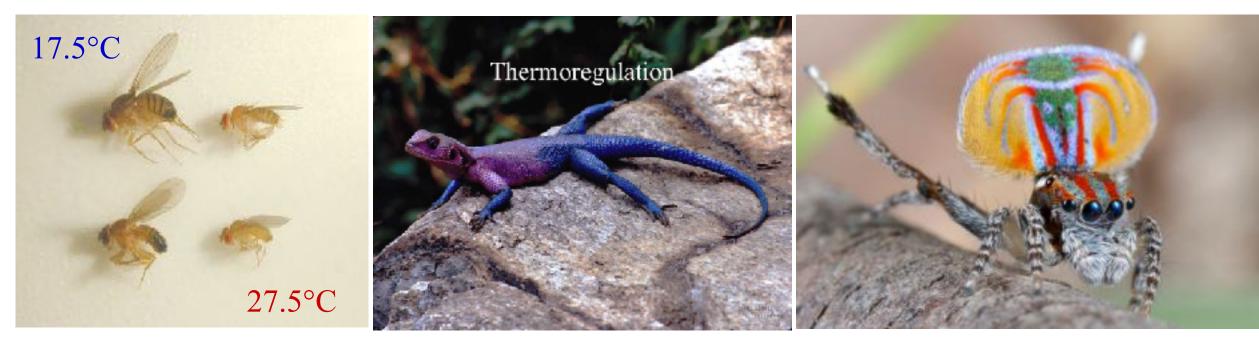
# Incorporating plasticity into studies of adaptive evolution

Development Physiology Behavior

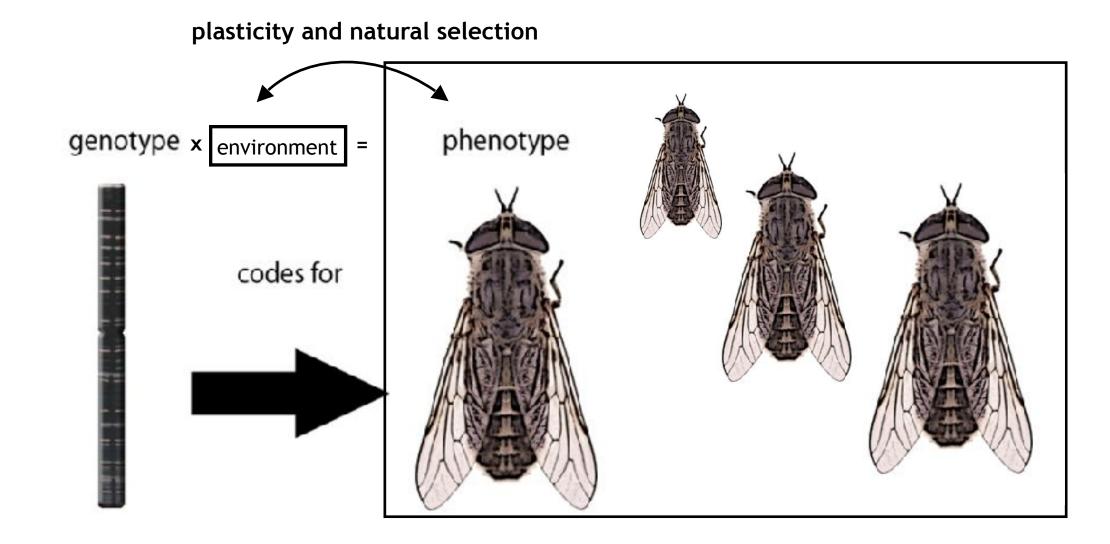


The First Response of Organisms to Environmental Change

Cameron Ghalambor Department of Biology Colorado State University

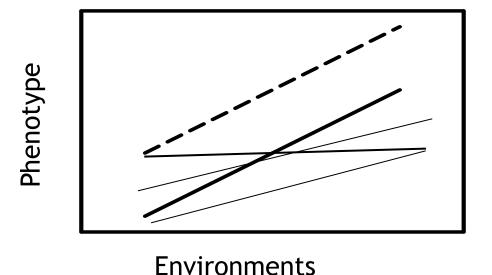
### The General Question:

Is there a relationship between environmentally induced phenotypic plasticity and genetically based adaptive evolution?



#### **Background: Terms and Definitions**

- 1. Phenotypic plasticity: the capacity for a genotype to produce different phenotypes in response to different environmental conditions
  - property of the genotype, individual, or other genetic group (clone, RIL, population)
  - phenotype is predictable depending on the environment (NOT developmental noise)
  - can be visualized as a line, curve, function, called the "reaction norm"



The reaction norm of a trait is the quantitative representation of this continuum as a line or curve that shows the particular way a genotype's phenotype varies as a function of the environment: (can be adaptive or non-adaptive). A flat reaction norm (slope = 0) is canalized trait.

2. Genotype x Environment Interaction (GxE): Variation among genotypes in how they respond across environments (population level)

## Is plasticity an overlooked and major component of adaptive evolution?









J. M. Baldwin

I.I. Schmalhausen

C. H. Waddington

M. J. West-Eberhard

If so, why has it been so challenging to incorporate into traditional neo-Darwinian thinking?

#### A Problem of Terminology?

J. M. Baldwin - "The Baldwin Effect"

I.I. Schmalhausen - "Theory of Stabilizing Selection"

C. H. Waddington - "Genetic Assimilation"

M. J. West-Eberhard - "Genetic Accommodation"

Instead Let's Use The Accepted Terminology and Theory to Understand the Problem



#### Standard Theory: Variance Components of a Quantitative Trait

$$V_P = V_G + V_E + V_{G*E}$$

 $V_P$  = total phenotypic variation of the segregating population

V<sub>G</sub> = genetic variation that contributes to the total phenotypic variation

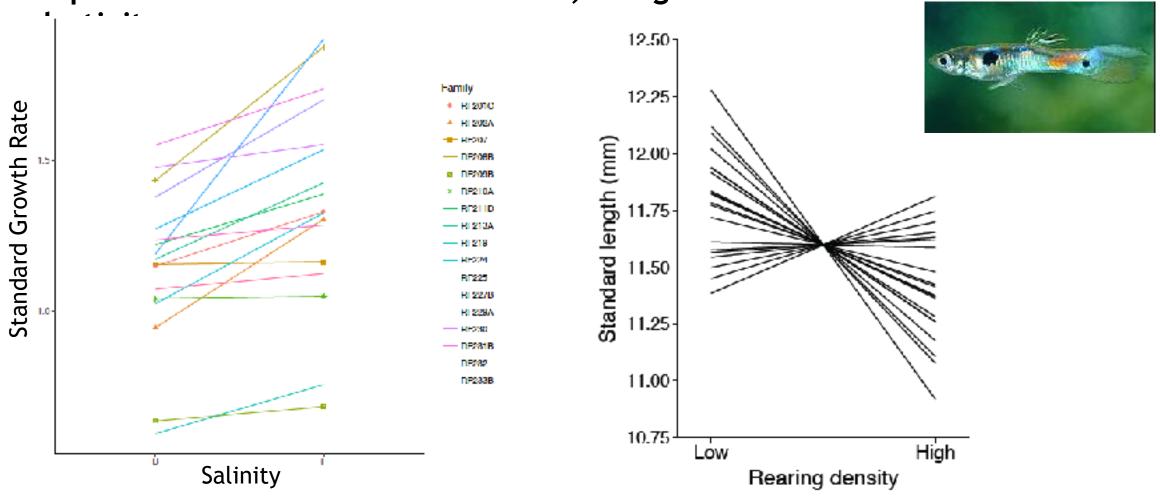
 $V_E$  = environmental contribution to the total phenotypic variation (random, family, maternal effects)  $V_{G^*E}$  = variation associated with the genetic and environmental factor interactions

$$H^2 = \frac{V_G}{V_D} =$$
 Heritability (the percent of the total variance explained by relatedness)

 $V_{G^*E}$  = Genetic variation in the plastic response to the environment

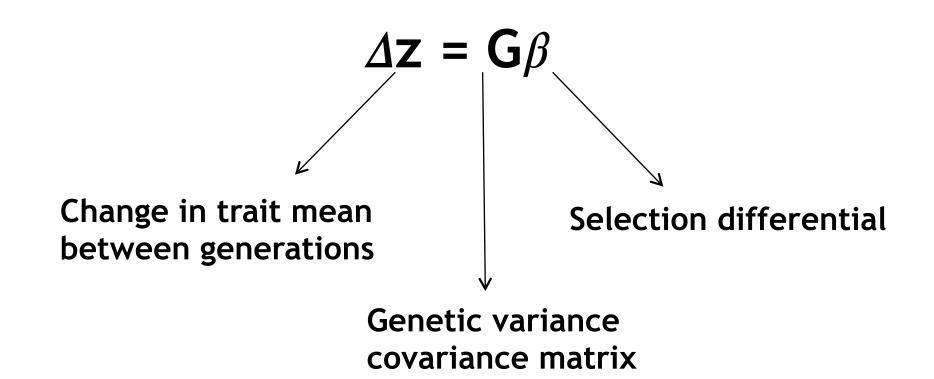
#### Genotype x Environment Interactions

Typically not all genotypes produce the same phenotype in response to environmental variation, i.e. genetic variation for

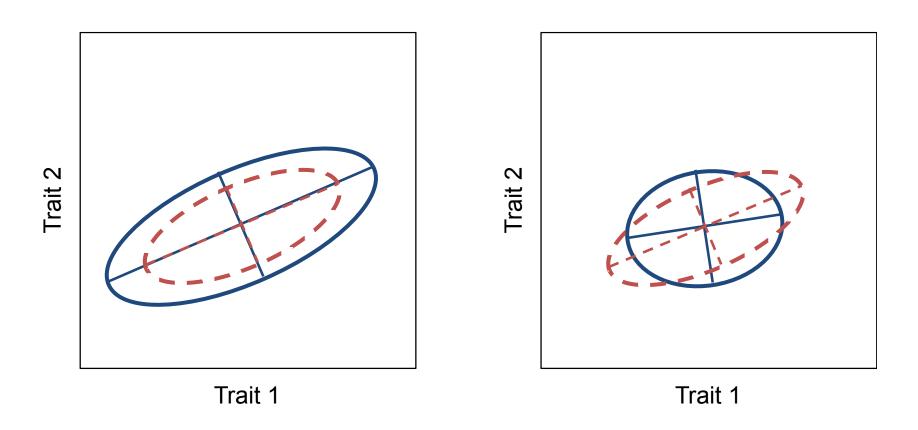


So, if plasticity can evolve, what role does it play in adaptive evolution?

## How Might Plasticity Influence Adaptive Evolutionary Responses?

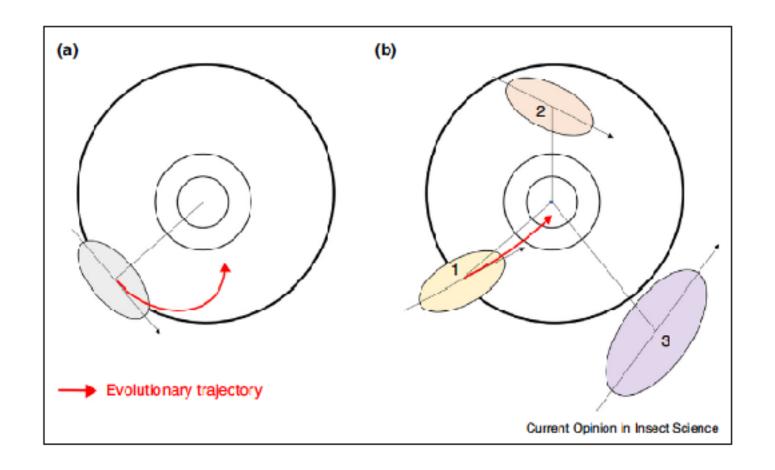


## Heritability and Genetic Correlations Between Traits Can Constrain or Bias the Evolution of Traits; How Plastic Are They?

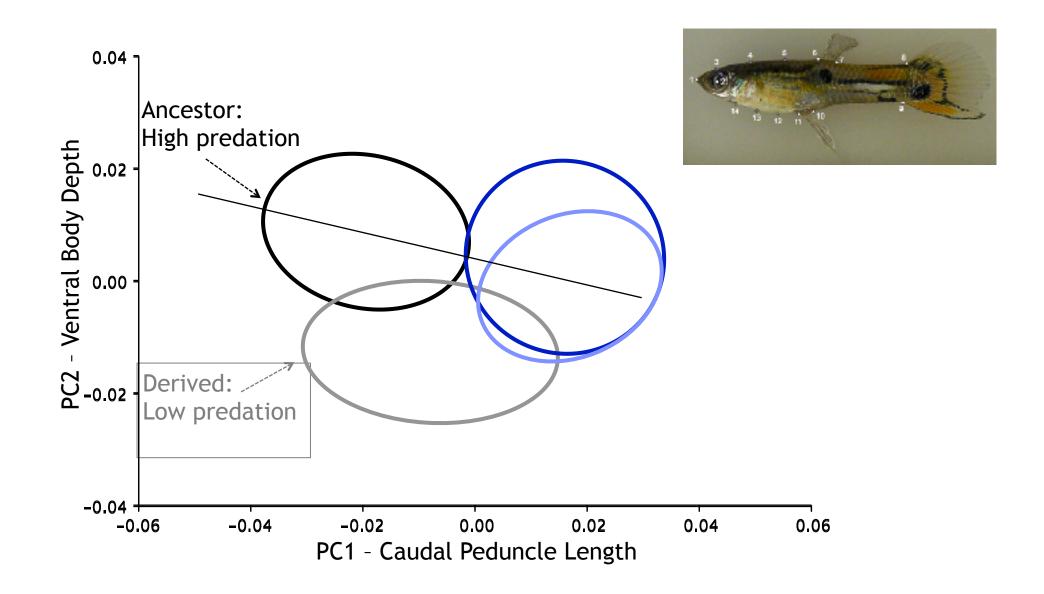


Schluter 1996 Evolution Sgro & Hoffmann 2004 Heredity Hansen & Houle 2008

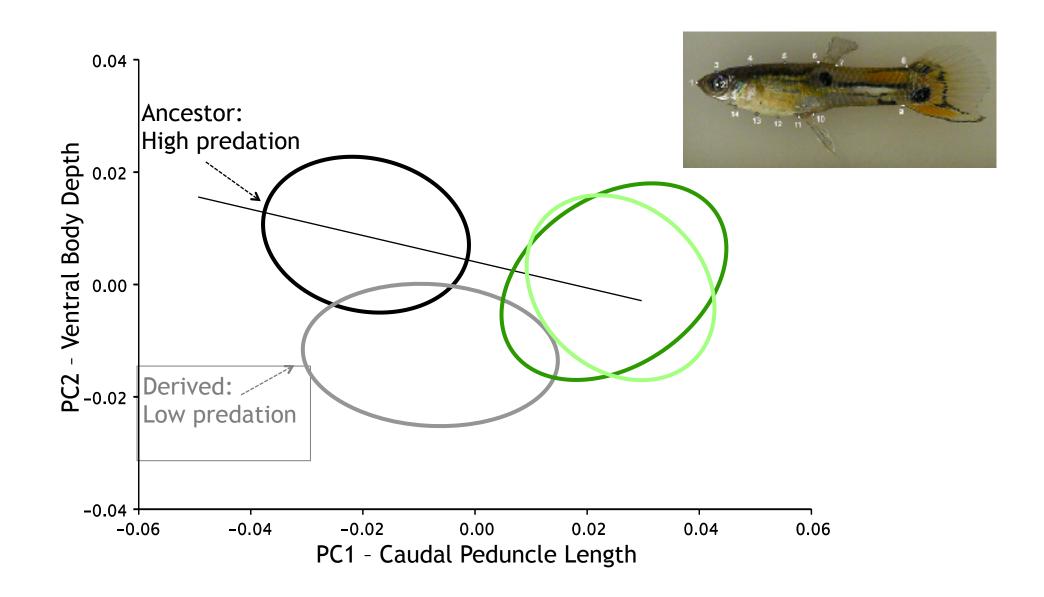
## Little Empirical Data For How Patterns of Trait Correlations Change in Response to a New Environment



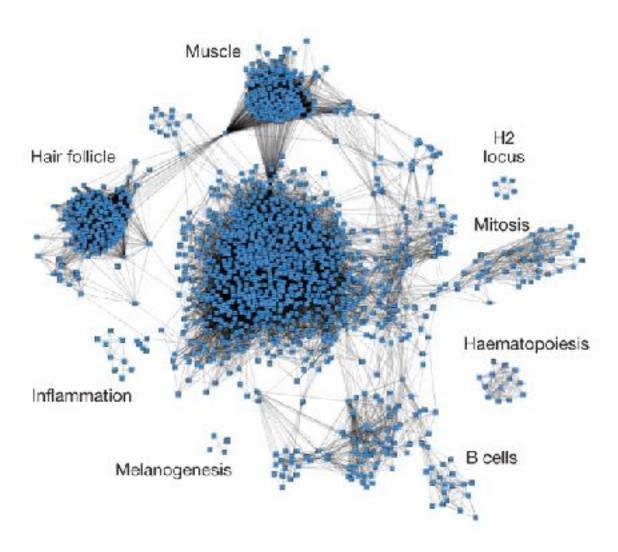
### Plasticity in Trait Correlations Following Introduction to a New Environment



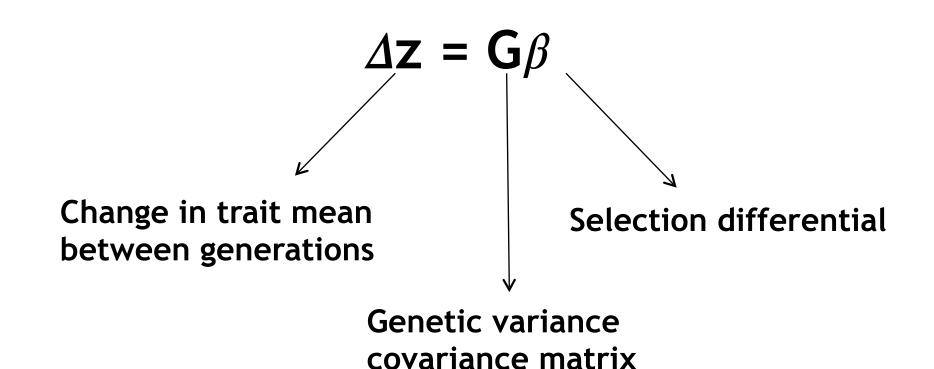
### Plasticity in Trait Correlations Following Introduction to a New Environment



### Visual Representation of a Gene Network: Plastic and Under Selection



## How Might Plasticity Influence Adaptive Evolutionary Responses?



### Adaptive Phenotypic Plasticity Phenotypic Change in the Same Direction Favored by Selection



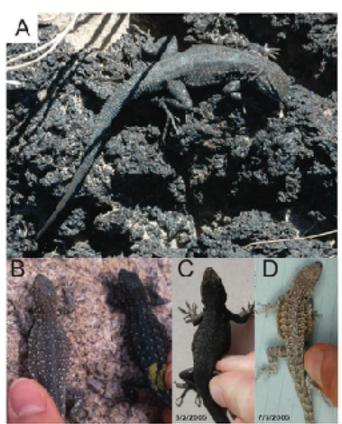
Limb length in *Anolis* Losos et al. 2000



Body shape in Stickleback Wund et al. 2008



Thermal acclimation Angiletta 2009

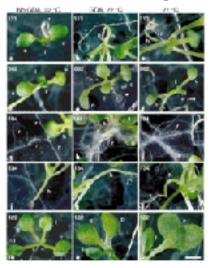


Color in *Uta* lizards Corl et al. 2018

### Non-Adaptive Phenotypic Plasticity Phenotypic Change Opposing the Direction Favored by Selection



Sexual coloration in Salmon Craig and Foote 2001

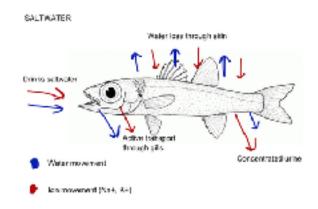




Temperature stress on development Queitsch et al. 2002, Avila et al. 2008

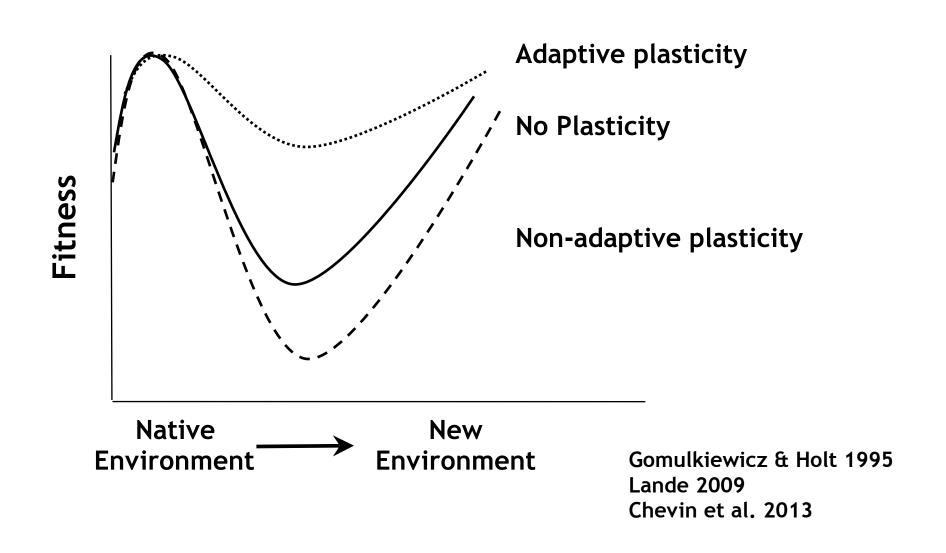


Body Temperature in *Anolis* Huey et al. 2003

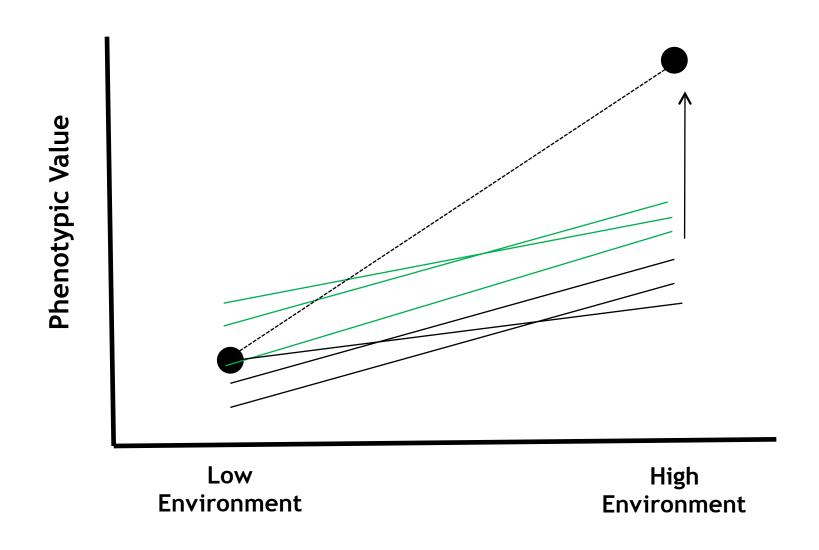


Challenge of homeostasis
Schulte 2014

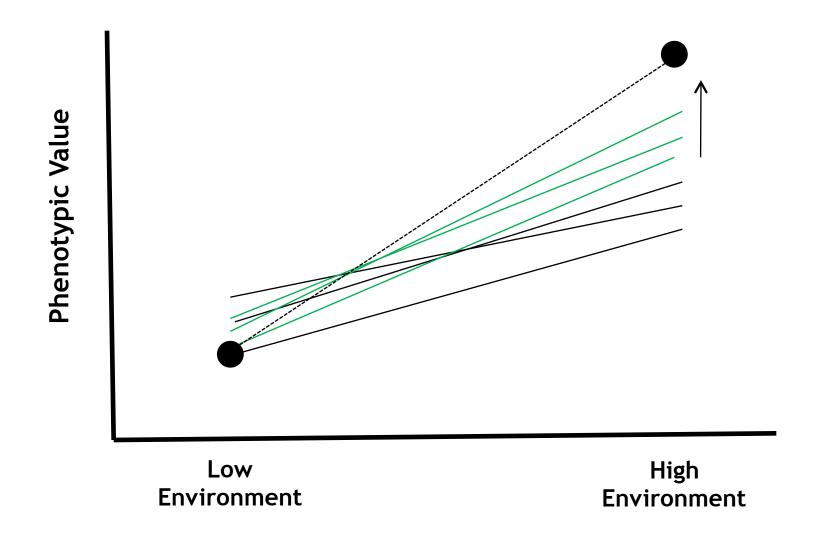
## How Plasticity Can Alter the Strength of Selection Following a Sudden Change in Environment



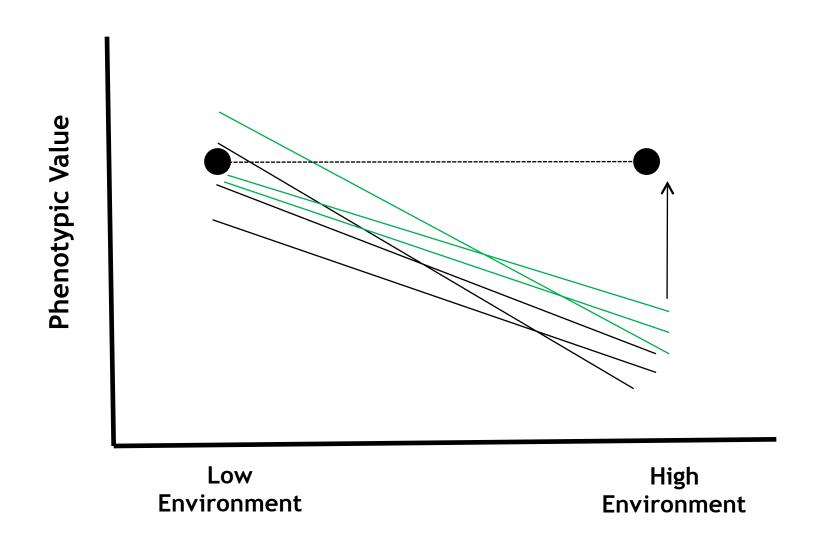
#### Adaptive Plasticity and The Evolution of Reaction Norms: The Environment as a Cue For Changing Phenotypes

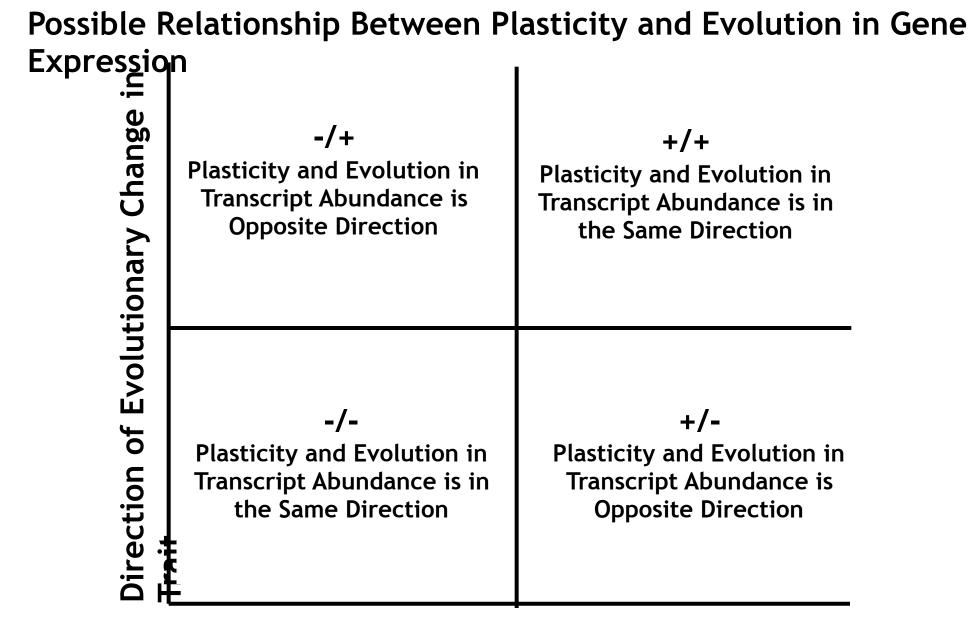


#### Adaptive Plasticity and The Evolution of Reaction Norms: The Environment as a Cue For Changing Phenotypes



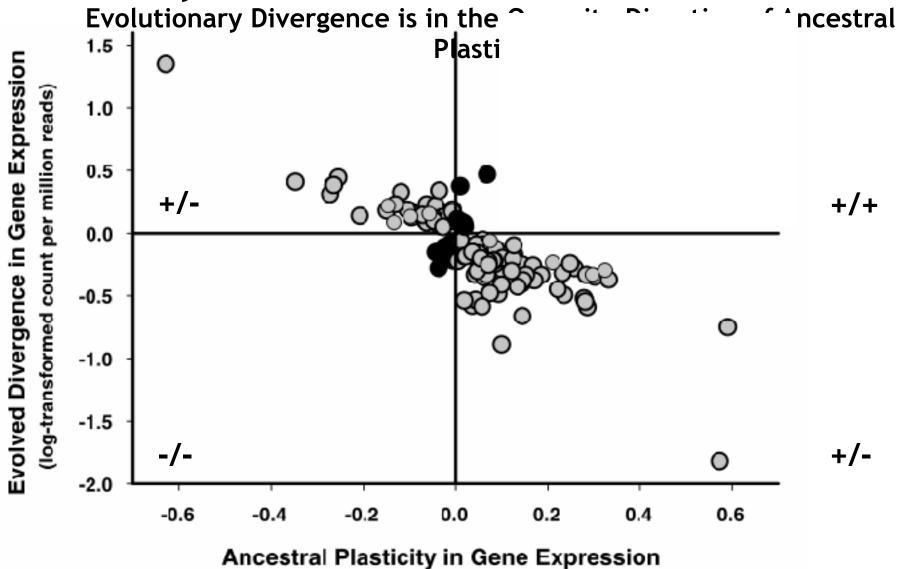
### Non-Adaptive Plasticity and Selection for Homeostasis: Selection to Buffer Phenotypes From the Environment





Direction of Plasticity in the Trait

### 135 Genes That Rapidly Evolve Exhibit Non-Adaptive Plasticity



(log-transformed count per million reads)

## Most Traits Appear to Show Adaptive Plasticity But the Traits Showing Non-Adaptive Plasticity Evolve More Quickly

Adaptive Plasticity co-gradient or synergistic selection selection

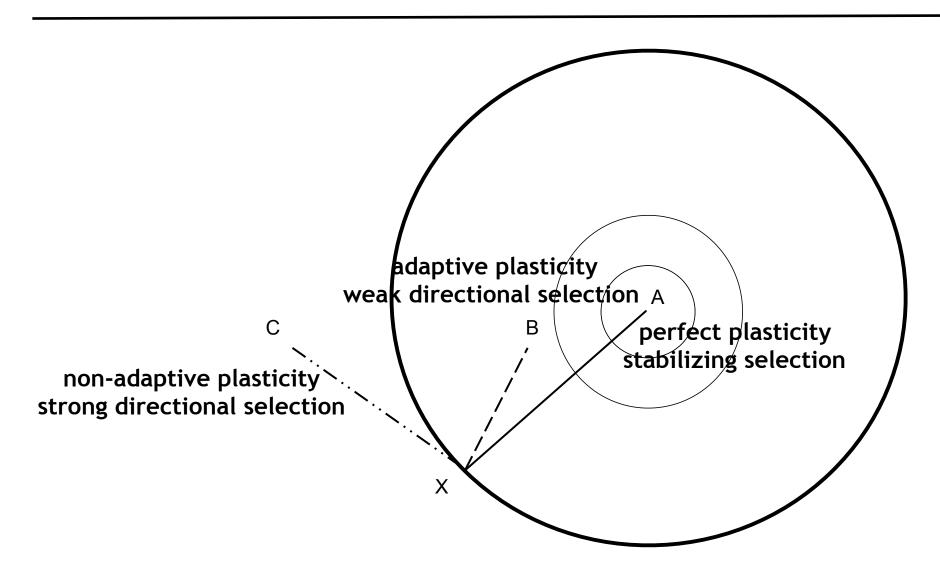
- shoaling behavior
- size at maturity
- head shape
- color patterns
- resting metabolic rate
- some aspects of body shape
- number of facial neuromasts

Non-Adaptive Plasticity counter gradient or antagonistic

growth rate some aspects of body shape initial patterns of gene expression



#### Does Plasticity Facilitate or Constrain Adaptive Evolution? It Depends on the Type of Plasticity and the Strength of Selection



#### Incorporating Phenotypic Plasticity into Evolutionary Studies

Should we avoid using terms like genetic assimilation, genetic accommodation, and the Baldwin Effect?

Will a role for plasticity in adaptive evolution be more commonly embraced if we strive to demonstrate that many evolutionary mechanisms are context or environmentally dependent?

$$\Delta \overline{z} = GB$$

Recombination rate plasticity: revealing mechanisms by design

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2}$$

Plasticity of Animal Genome Architecture Unmasked by Rapid Evolution of a Pelagic Tunicate



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