Extended Evolutionary Synthesis

扩展演化综论

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Contents

What is EES?

Key concepts

Focal topics

How the EES differs from MS/SET?

What is EES?

An alternative way to think about and understand evolutionary phenomena

Key Concepts Topics

What is EES?

- **扩展演化综论**（EES）是关于生物演化现象的新思考和新理解。虽然与主流的演化理论不同，例如标准演化理论（SET）和现代演化综论（MS）。但是EES并不寻求取代它们，而是可以与它们共存，以刺激演化生物学研究领域的发展。

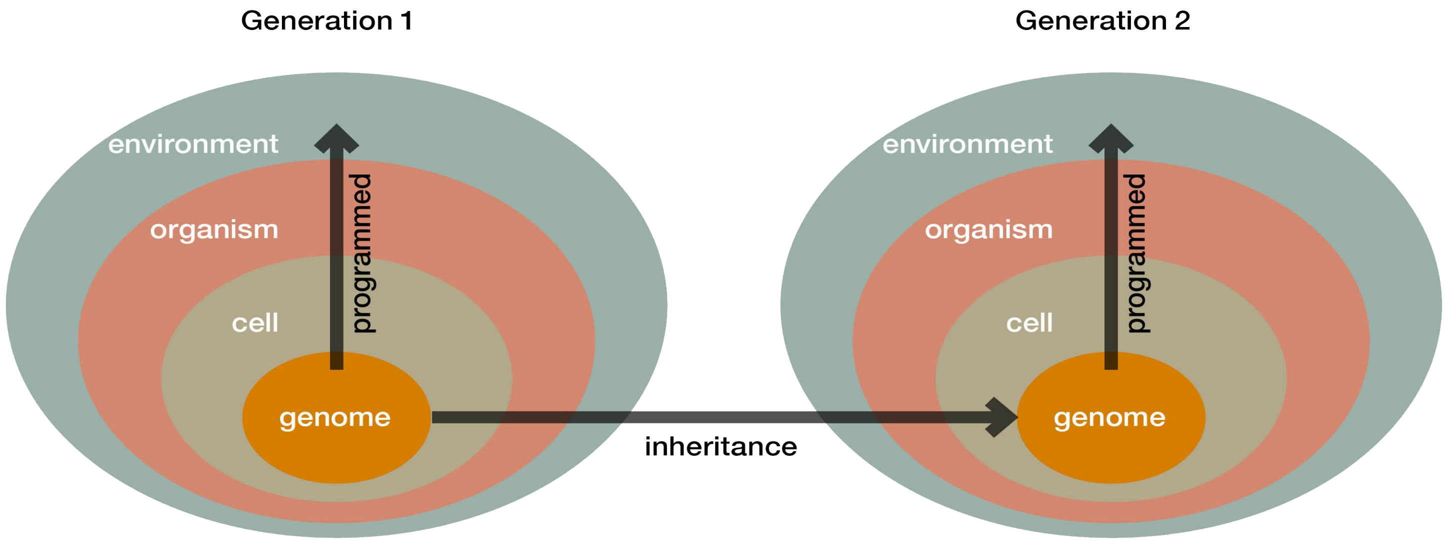
Key Concepts

Constructive development

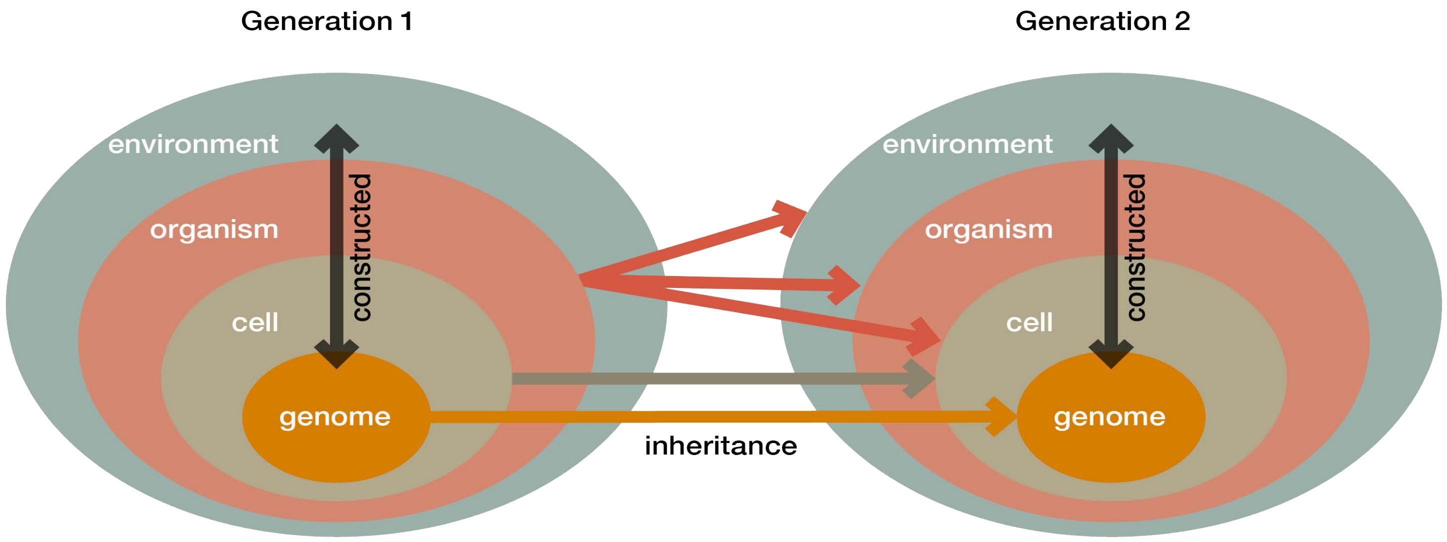
Reciprocal causation

Constructive development — Key Concept

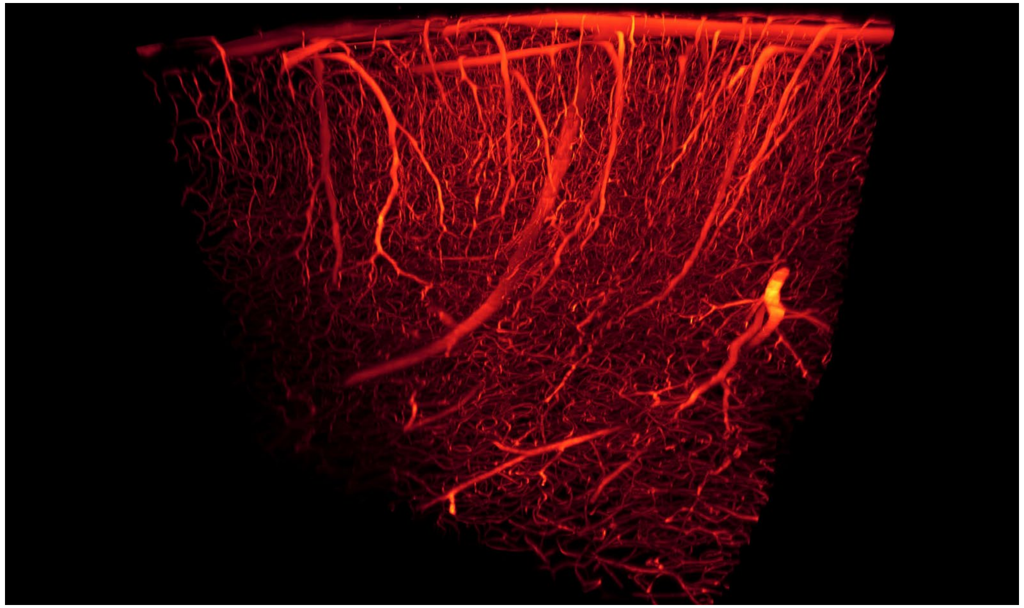
Programmed Development

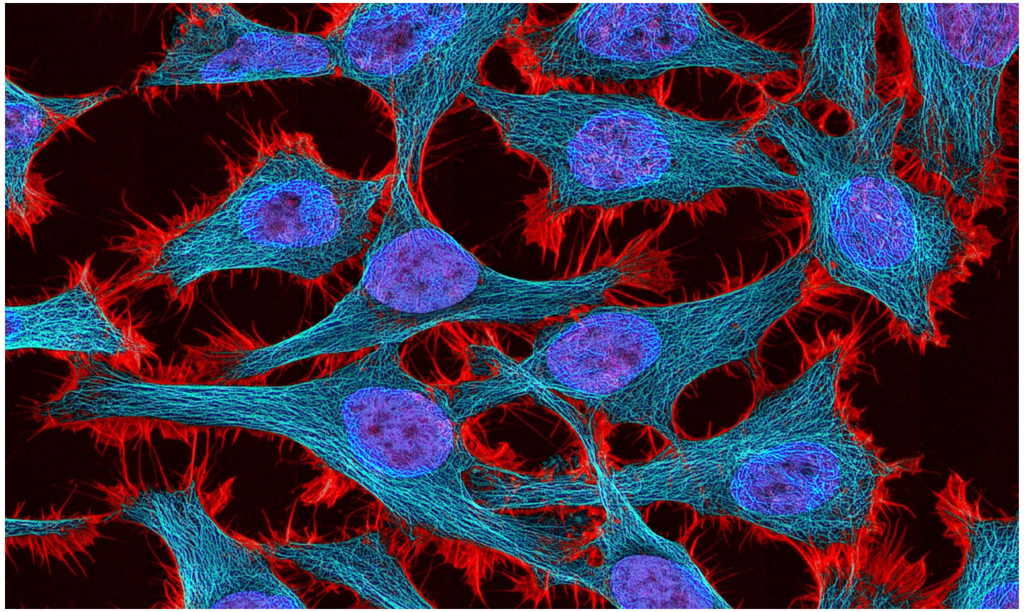


Constructive Development



Constructive development — Key Concept





For example, the 'shape' of the circulatory system is constructed according to the oxygen and nutrient needs of tissues, rather than being genetically predetermined. Likewise, the nervous system develops through axonal exploration.

Constructive Development — Key Concept

foraging

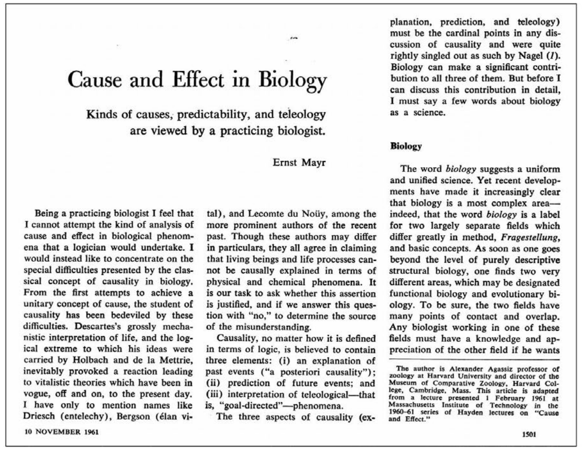
song

Figure 2. Mean (+s.e.) volume of prey items provided by (*a*) blue tit and (*b*) great tit parents in relation to the age of parent. Open bars, controls; filled bars, cross-fostered (reared by the other species). Prey volume was estimated from length and width of prey relative to bill length of parent. Sample size (number of parents) is shown above the bars.

Figure 3. Mean proportion (+s.e.) of various prey types provided by (*a*) blue tit and (*b*) great tit parents. Open bars, controls (70 blue tits, 79 great tits); filled bars, cross-fostered (reared by the other species; 67 blue tits, 65 great tits).

Constructive Development — Key Concept

Reciprocal causation — Key Concept



Cause and Effect in Biology

Kinds of causes, predictability, and teleology are viewed by a practicing biologist.

Ernst Mayr

Being a practicing biologist I feel that I cannot attempt the kind of analysis of cause and effect in biological phenomena that a logician would undertake. I would instead like to concentrate on the special difficulties presented by the classical concept of causality in biology. From the first attempts to achieve a unitary concept of cause, the student of causality has been bedeviled by these difficulties. Descartes's grossly mechanistic interpretation of life, and the logical extreme to which his ideas were carried by Holbach and de la Mettrie, inevitably provoked a reaction leading to vitalistic theories which have been in vogue, off and on, to the present day. I have only to mention names like Driesch (entelechy), Bergson (élan vital), and Lecomte du Noüy, among the more prominent authors of the recent past. Though these authors may differ in particulars, they all agree in claiming that living beings and life processes cannot be causally explained in terms of physical and chemical phenomena. It is our task to ask whether this assertion is justified, and if we answer this question with "no," to determine the source of the misunderstanding.

Causality, no matter how it is defined in terms of logic, is believed to contain three elements: (i) an explanation of past events ("a posteriori causality"); (ii) prediction of future events; and (iii) interpretation of teleological—that is, "goal-directed"—phenomena.

The three aspects of causality (explanation, prediction, and teleology) must be the cardinal points in any discussion of causality and were quite rightly singled out as such by Nagel (1). Biology can make a significant contribution to all three of them. But before I can discuss this contribution in detail, I must say a few words about biology as a science.

Biology

The word *biology* suggests a uniform and unified science. Yet recent developments have made it increasingly clear that biology is a most complex area—indeed, that the word *biology* is a label for two largely separate fields which differ greatly in method, *Fragestellung*, and basic concepts. As soon as one goes beyond the level of purely descriptive structural biology, one finds two very different areas, which may be designated functional biology and evolutionary biology. To be sure, the two fields have many points of contact and overlap. Any biologist working in one of these fields must have a knowledge and appreciation of the other field if he wants

The author is Alexander Agassiz professor of zoology at Harvard University and director of the Museum of Comparative Zoology, Harvard College, Cambridge, Mass. This article is adapted from a lecture presented 1 February 1961 at Massachusetts Institute of Technology in the 1960–61 series of Hayden lectures on "Cause and Effect."

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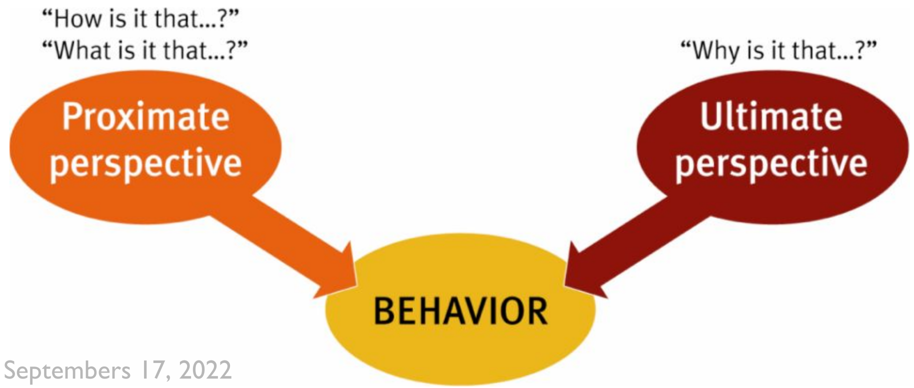
Proximate Causes

Other biologist
Chemist
Physicist
Engineers

vs

Ultimate Causes

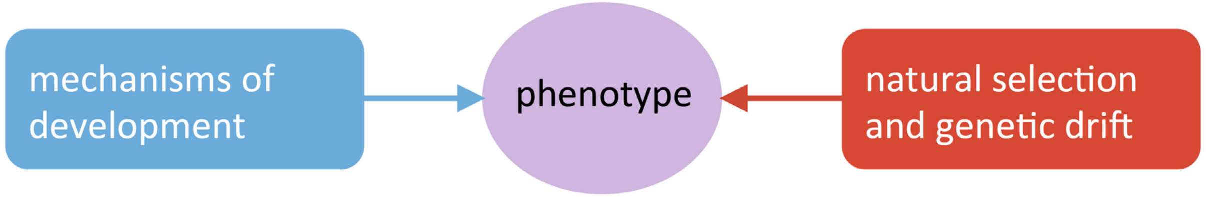
Evolutionary biologist



Traditional view

proximate causes
(decoding of genetic program)

ultimate causes
(building a genetic program)

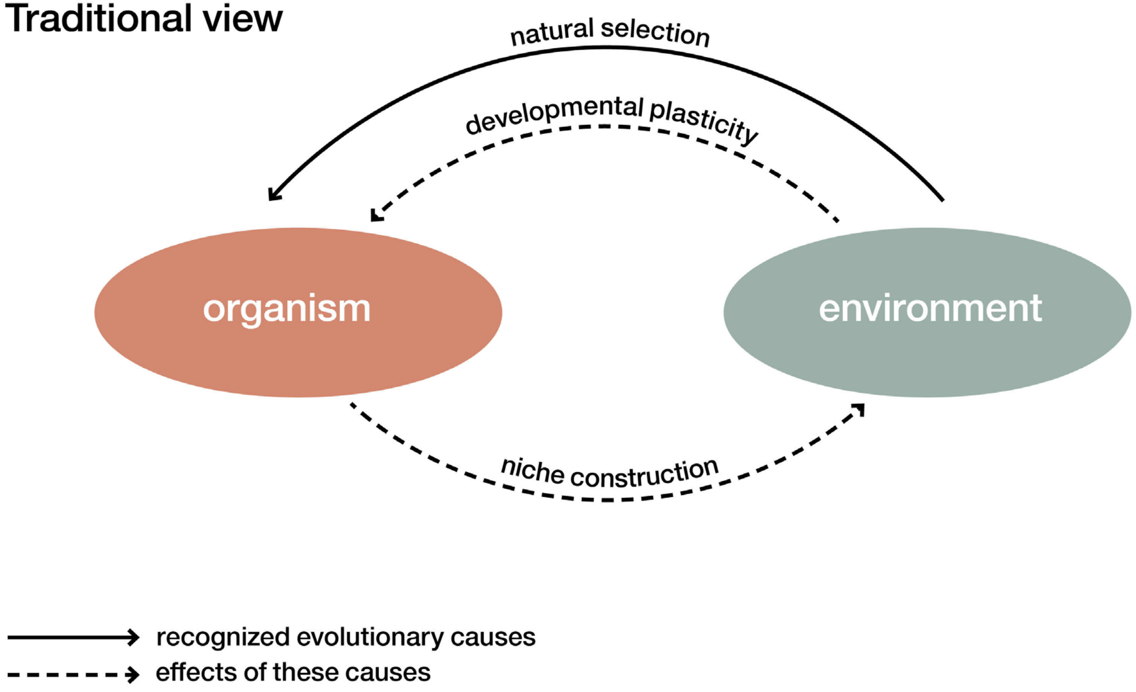


non-evolutionary science

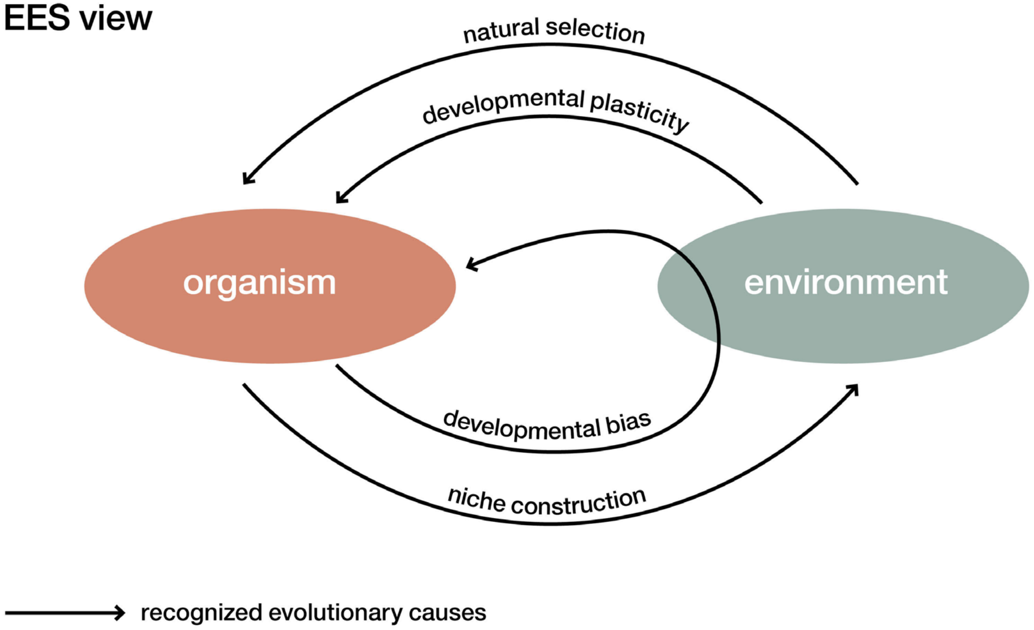
evolutionary science

Reciprocal causation — Key Concept

Traditional view

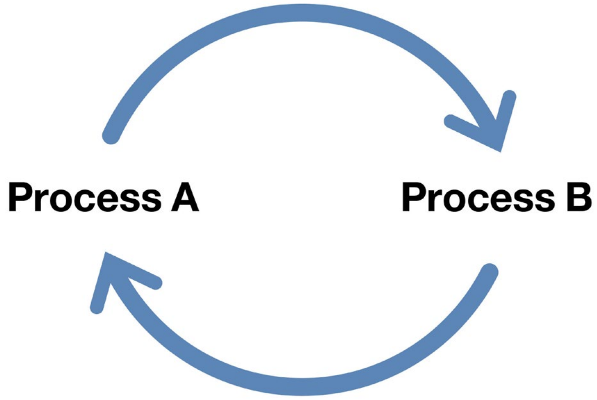


EES view



Developing organisms are not solely products, but are also **CAUSES** of evolution

The causation in biological system is inherently reciprocal



Focal Topics

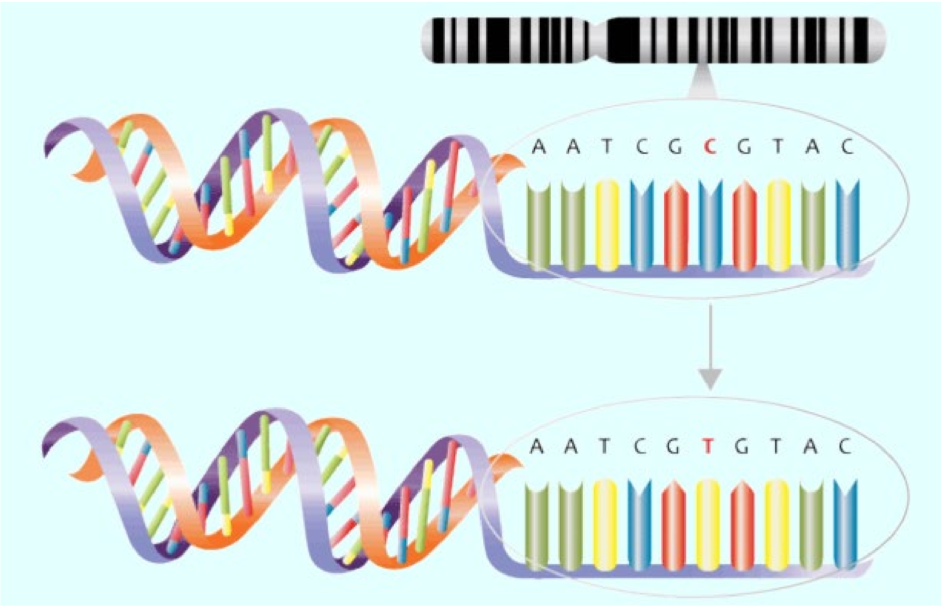
Developmental bias

Developmental plasticity

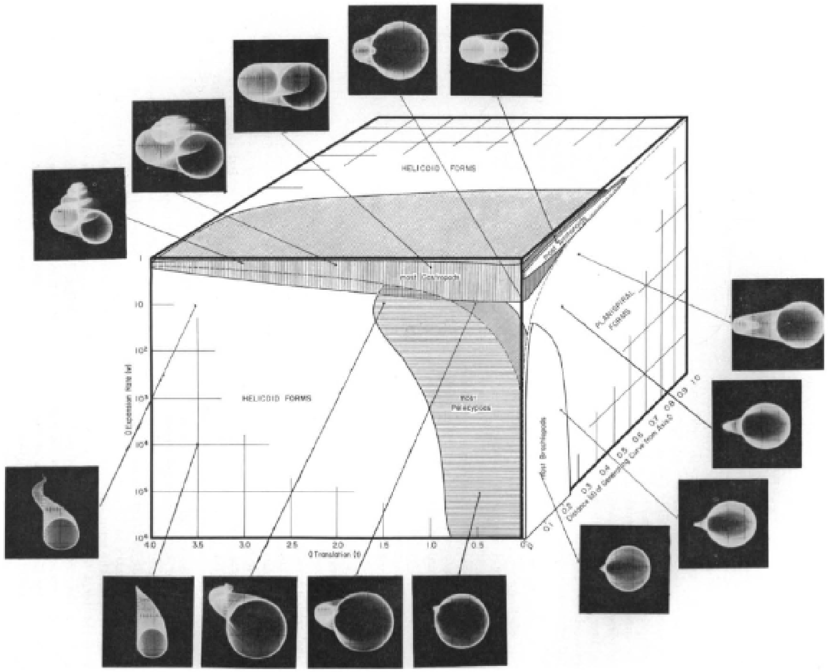
Inclusive inheritance

Niche construction

Developmental bias — Focal Topic



Mutation is random



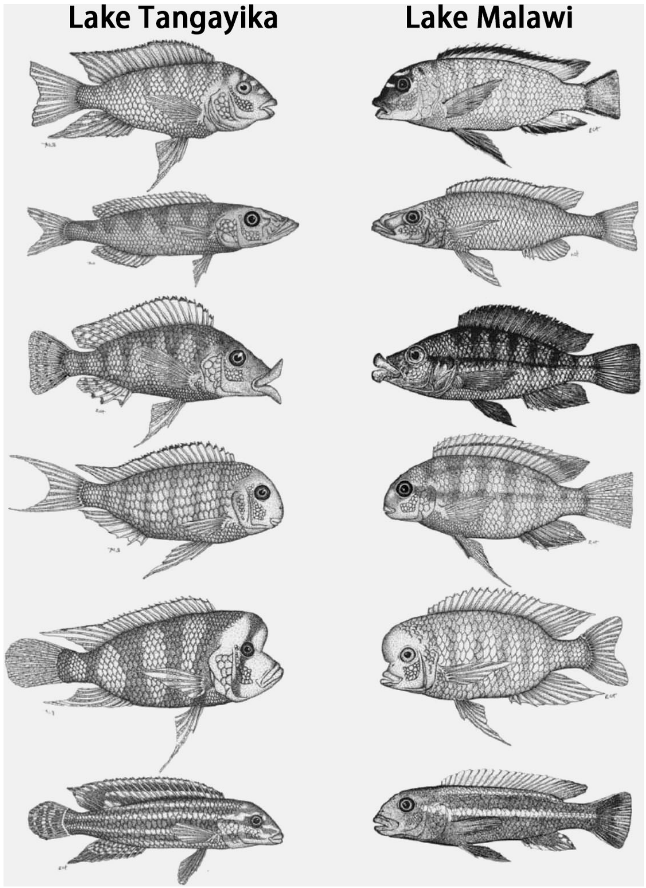
Phenotypic variation is NOT random

Possible cause:

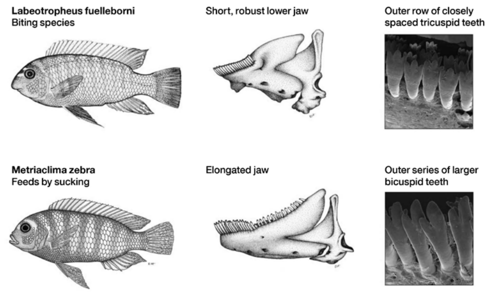
I Natural selection

II Unequal odds

Developmental bias — Example I



Two independent lines of diversification showed parallel evolution



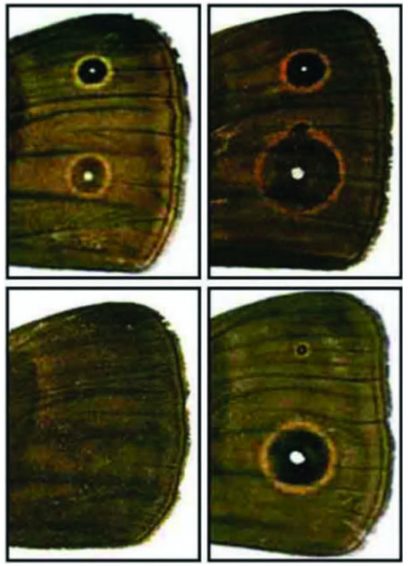
- Some traits are more plastic
- Inherent characteristics of development channeled the parallel evolution

- Cichlids may be particularly good at producing novel variants

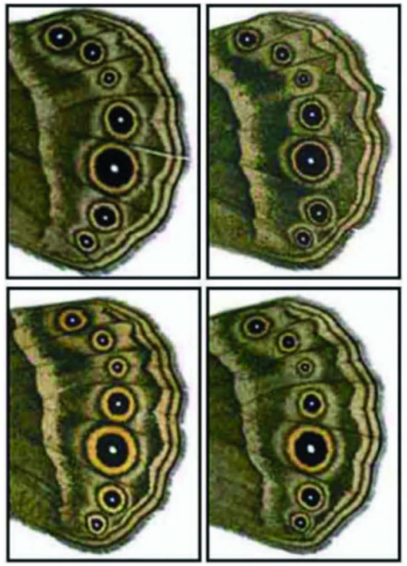
- Development bias can also constrain evolution
- Some phenotypes less able to be generatedare

Developmental bias — Example II

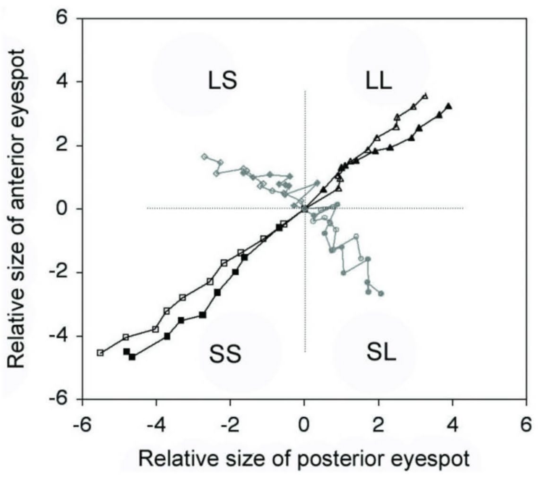
Eyespot sizes respond to both coordinated and antagonistic selection



Eyespot colour composition remains coordinated between eyespots even under antagonistic selection

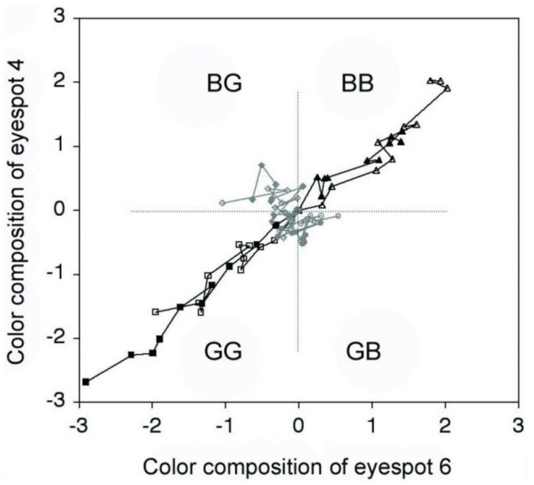


Eyespot size



L = Large
S = Small

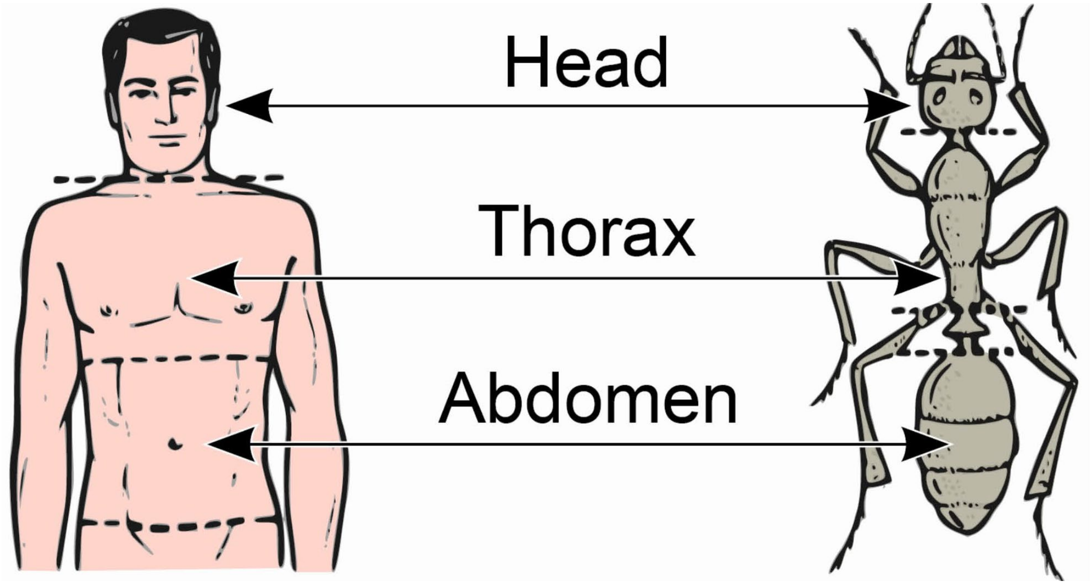
Eyespot colour composition



B = Black
G = Gold

Different responses to antagonistic selection of wing eye spots of Bicyclus butterflies
Selection for one LARGE and one SMALL eyespot introduces rapid responses, but it is far more difficult to select a GOLD and a BLACK eyespot.

Developmental bias — Example III & IV



Non-random numbers of limbs, digits, and segments across many groups

Mammalian teeth development shows significant bias in number, size and shape of teeth

Focal Topics

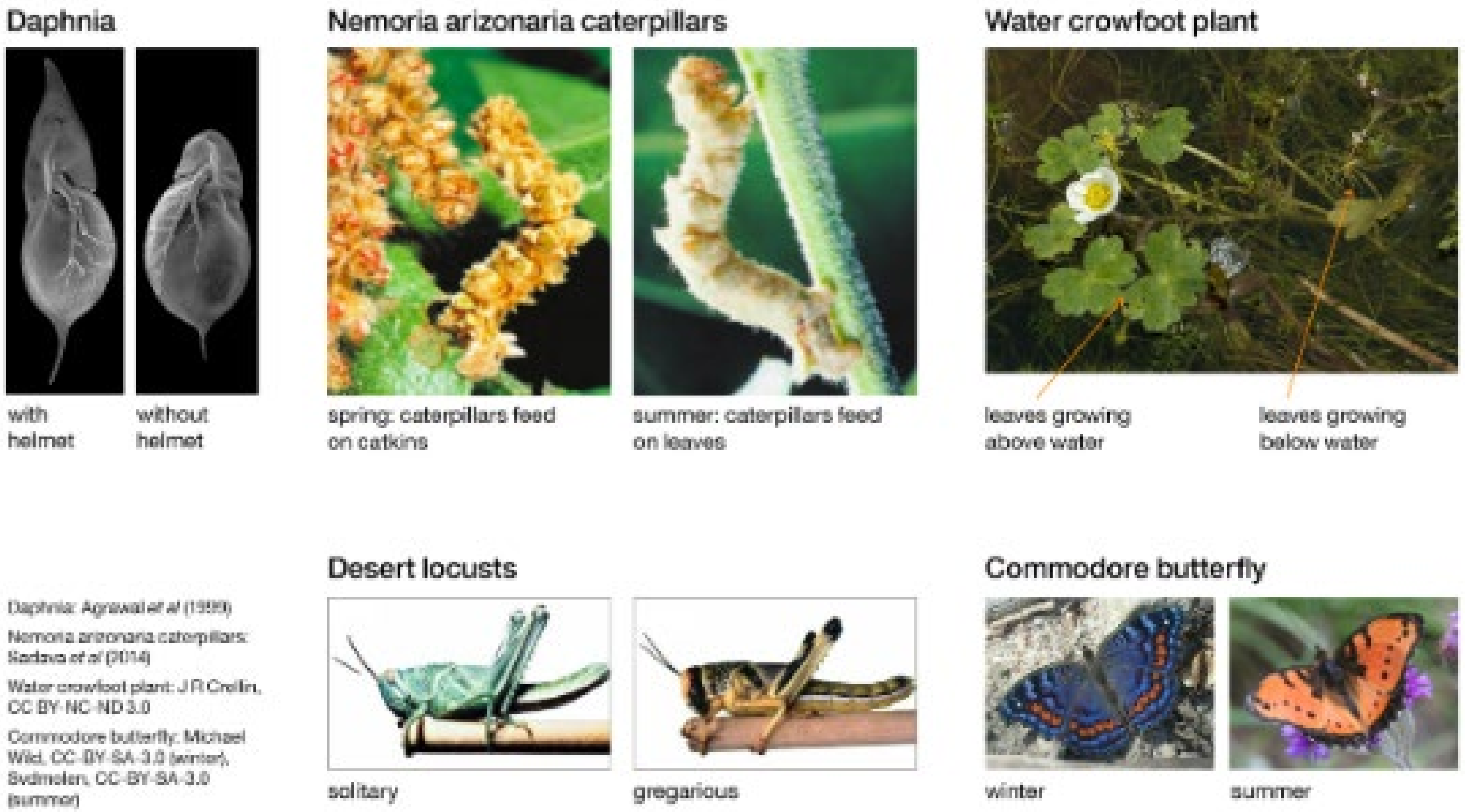
Developmental bias

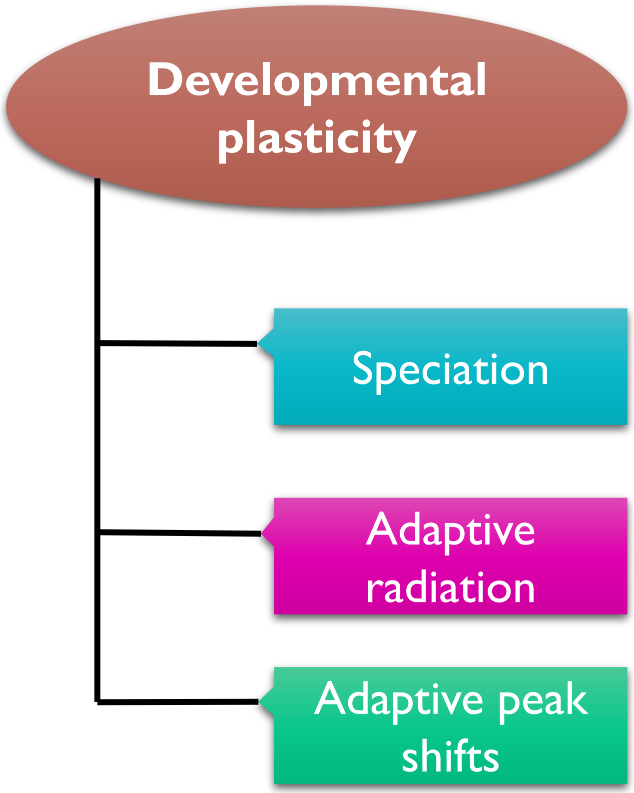
Developmental plasticity

Inclusive inheritance

Niche construction

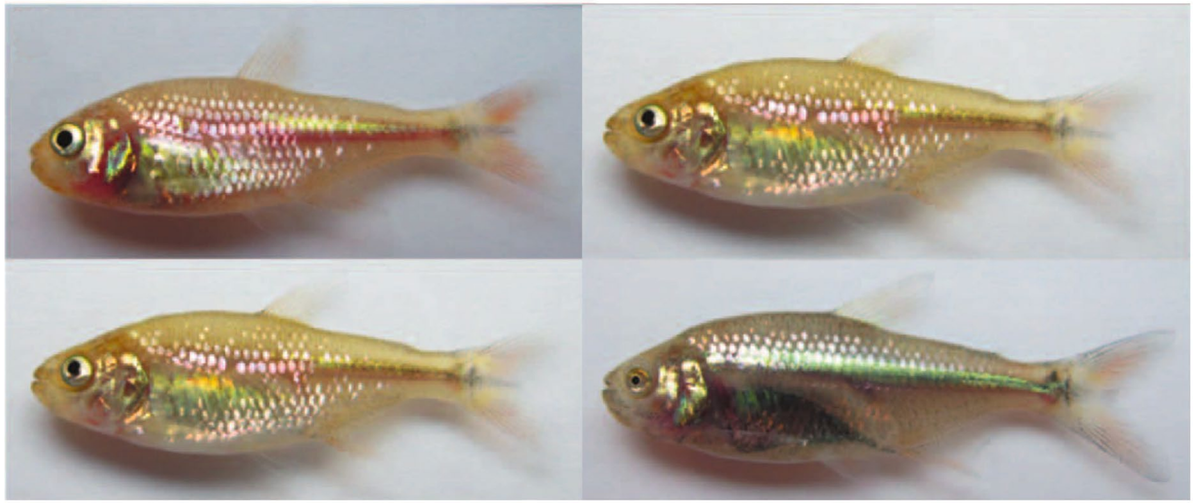
Developmental plasticity — Focal Topic



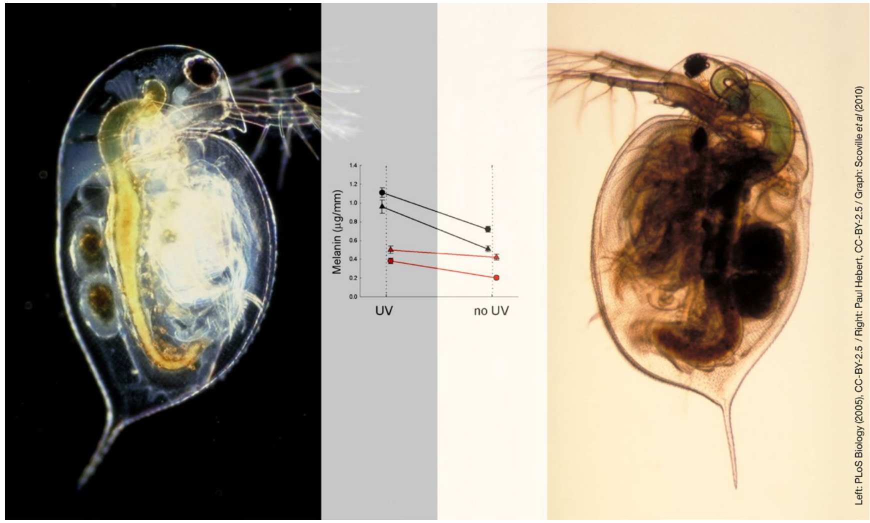


Developmental plasticity is ubiquitous across all levels of biological organization
It enables developmental robustness in the face of environmental fluctuations

Developmental plasticity — Focal Topic



Developmental process may act as capacitors for cryptic genetic variation that becomes expressed in novel or stressful conditions
Example: cryptic genetic variation played a role in the evolution of eye loss in cavefish

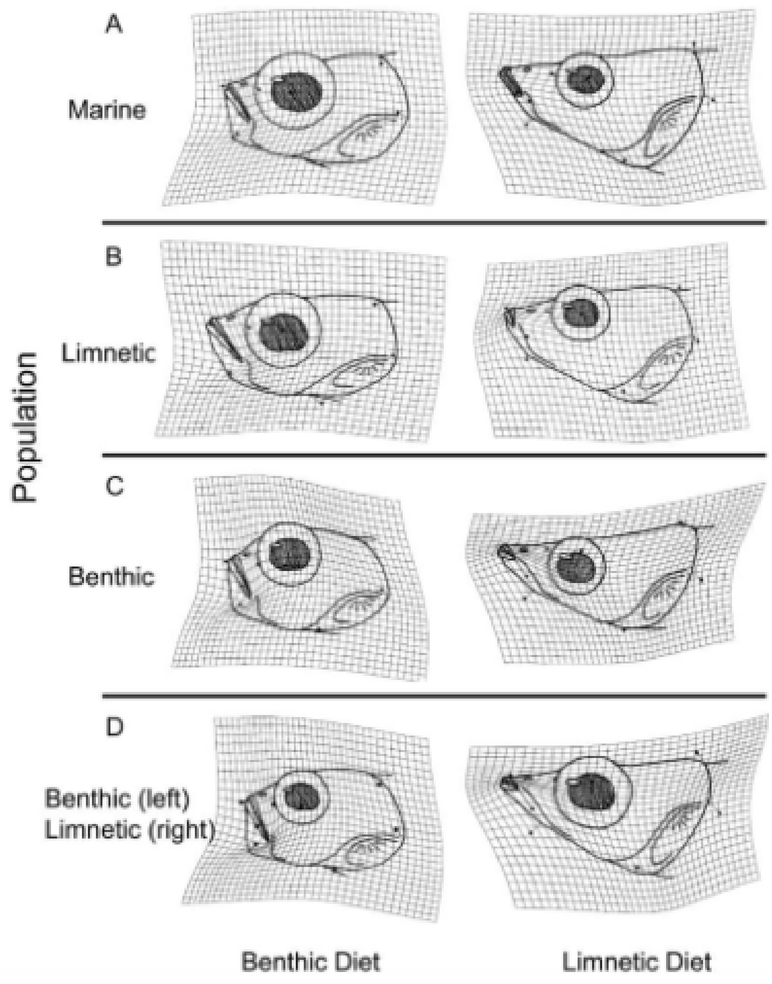


Environmentally-induced phenotypes can be stabilized across generations by selection
Example: loss of color in water fleas when exposed to predators

Developmental plasticity — Focal Topic

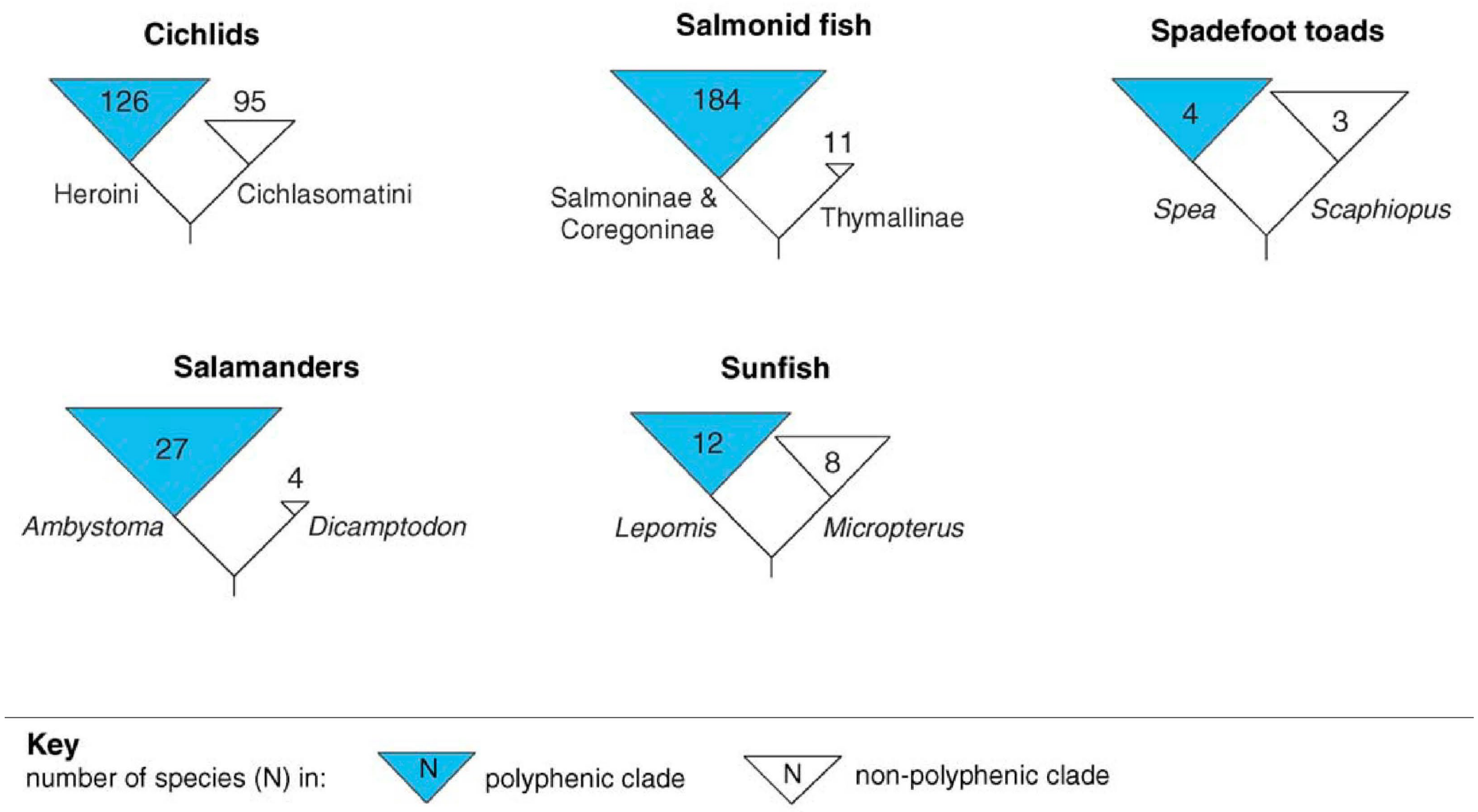
Flexible stem hypothesis: an ancestral plastic species can be at the origin of sister lineages

An ancestral population with high developmental plasticity may be the cause of trait diversity in Galapagos finches



Benthic and limnetic diets induced similar mouth morphs in different populations

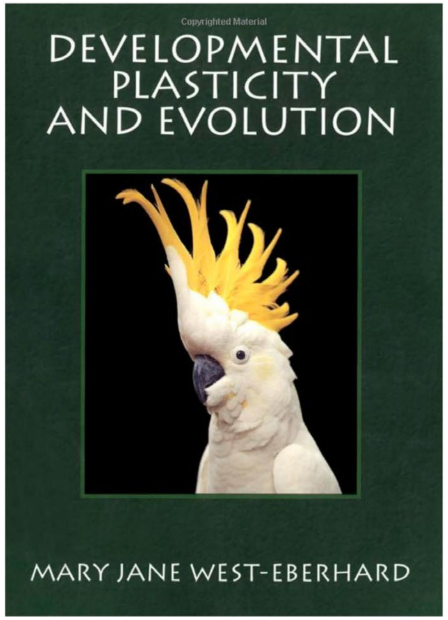
Developmental plasticity — Focal Topic



Studies in fishes proved that developmental plasticity influences biodiversity
Clades with developmental plasticity have higher number of descendant species

Developmental plasticity — Focal Topic

Smithsonian



"Genes may often be followers rather than leaders in phenotypic evolution"

Mary Jane West-Eberhard, 2003

New environmental conditions + **Random mutations** → **Natural selection** → **Adaptation**

New environmental conditions → **Development plastic responses** → **Novel phenotypes** → **Adaptation**

Focal Topics

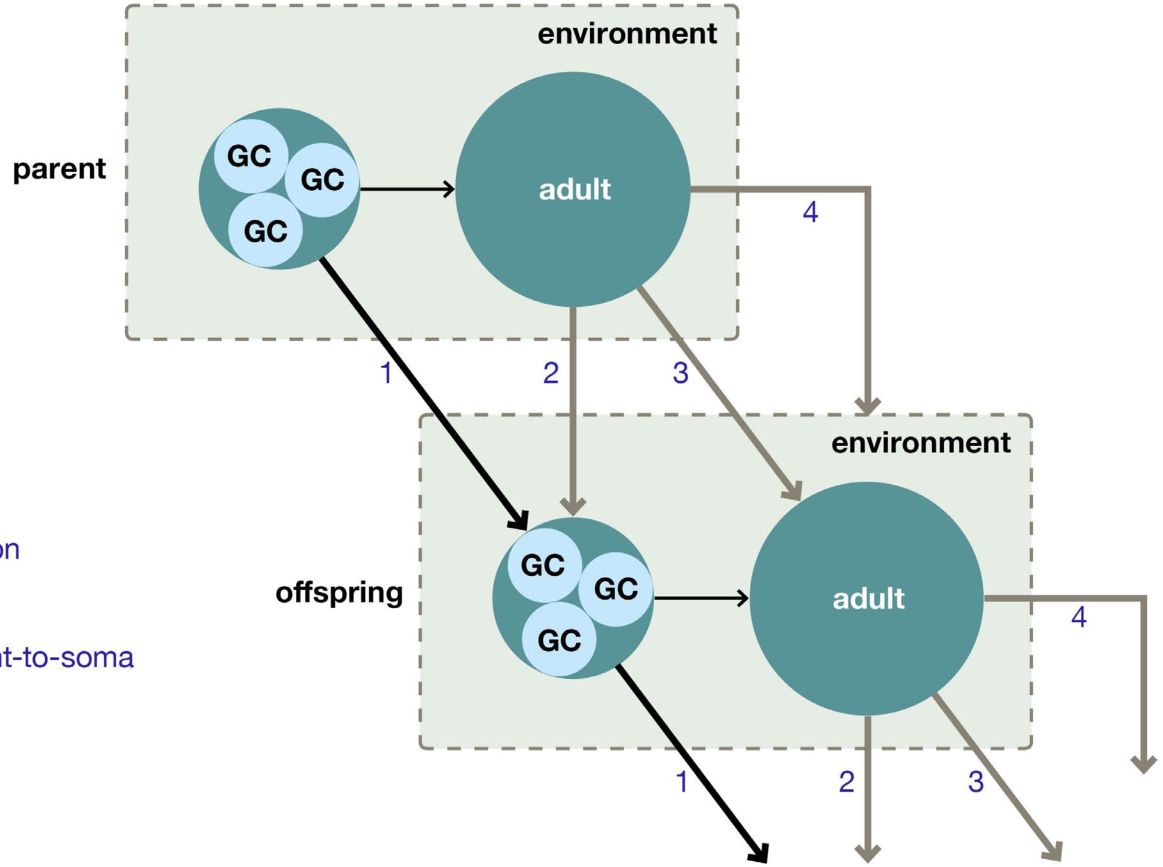
Developmental bias

Developmental plasticity

Inclusive inheritance

Niche construction

Inclusive inheritance — Focal Topic



Modes of inheritance
1. germ line transmission
2. soma-to-germ line
3. soma-to-soma
4. soma-to-environment-to-soma

GC = germ cell

Adapted from Badyaev & Uller (2009)

Transmitted factors across generations which are:
beyond genes extended to developmental process beyond germ line cells
can also contribute to heredity

Inclusive inheritance — Focal Topic

Contents of fertilized egg, such as organelles, enzymes, hormones, antibodies, and transcription factors are sometimes passed on to the developing embryo

Attached chemicals on genes sometimes can be passed on to the next generation.
Epigenetic marks attached to a single gene has led to one wild population flowering later

Inclusive inheritance — Focal Topic

Maternal microbiota are passed on to offspring actively or passively and influence offspring development, morphology and resistance to pathogens

Cultural inheritance occurs in many animals from crickets to humans. Cultural inheritance refers to the storage and transmission of learned information by communication, imitation, teaching and learning.

Ecological inheritance is also a kind of inclusive inheritance. Parental generations modified and pass on environmental conditions to offspring

Focal Topics

Developmental bias

Developmental plasticity

Inclusive inheritance

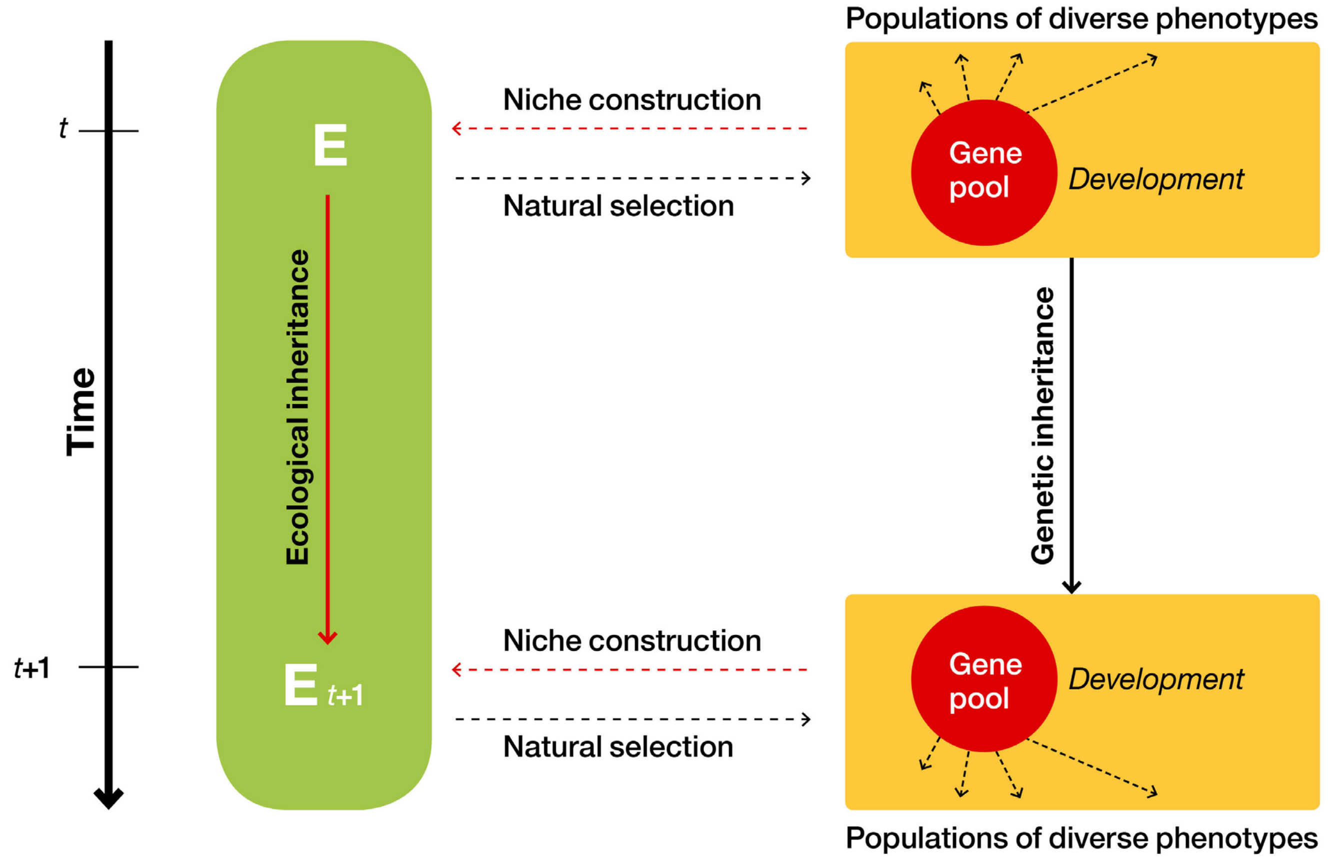
Niche construction

Niche construction — Focal Topic

All organisms actively determine the characteristics of their niche by selecting and modifying habitat and environmental resources. These activities are known as niche construction

Beaver dams **Self-irrigating plants** **Corals** **Cyanobacteria**

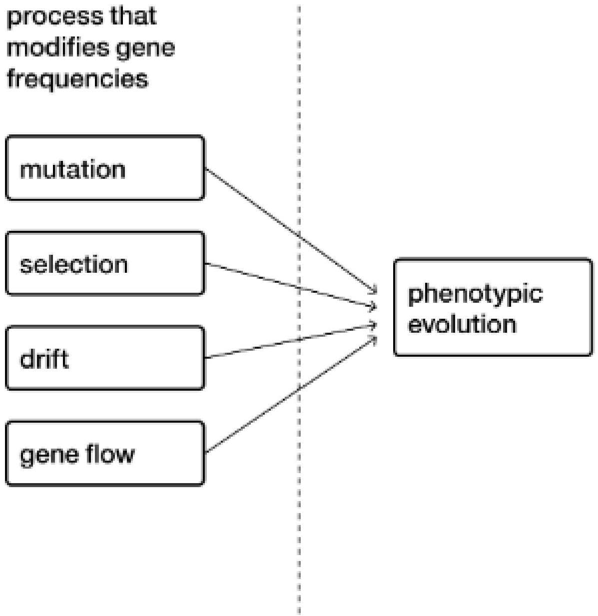
Niche construction — Focal Topic



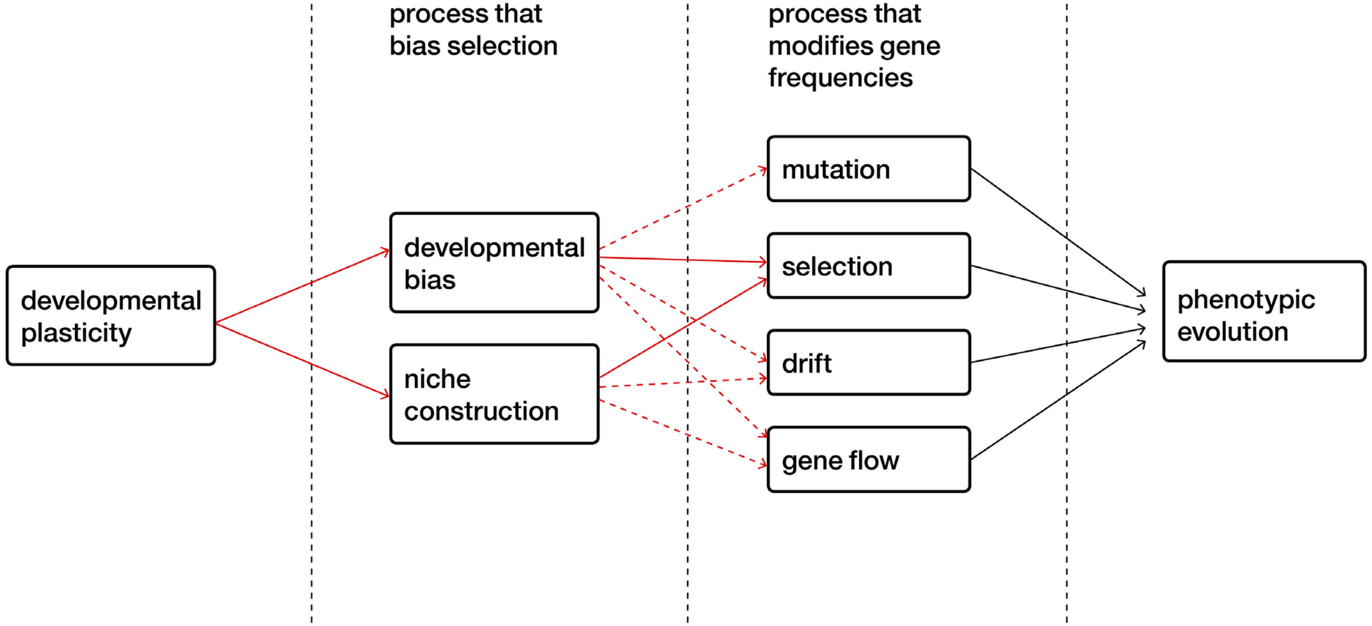
Niche construction bring about environmental changes which lead to changes in selective pressures exerted on organisms. There is a feedback relationship between niche construction and natural selection —— Adaptation is a BIDIRECTIONAL process.

Niche construction — Focal Topic

SET



EES



Compared to SET, EES has a broader view of evolutionary causation. Niche construction systematically modifying selection and biases the direction of evolution.

How the EES differs from MS/SET?

How the EES differs from MS/SET?

	Traditional predictions	EES predictions
i	genetic change causes, and logically precedes, phenotypic change, in adaptive evolution	phenotypic accommodation can precede, rather than follow, genetic change, in adaptive evolution
ii	genetic mutations, and hence novel phenotypes, will be random in direction and typically neutral or slightly disadvantageous	novel phenotypic variants will frequently be directional and functional
iii	isolated mutations generating novel phenotypes will occur in a single individual	novel, evolutionarily consequential, phenotypic variants will frequently be environmentally induced in multiple individuals
iv	adaptive evolution typically proceeds through selection of mutations with small effects	strikingly different novel phenotypes can occur, either through mutation of a major regulatory control gene expressed in a tissue-specific manner, or through facilitated variation
v	repeated evolution in isolated populations is due to convergent selection	repeated evolution in isolated populations may be due to convergent selection and/or developmental bias
vi	adaptive variants are propagated through selection	in addition to selection, adaptive variants are propagated through repeated environmental induction, non-genetic inheritance, learning and cultural transmission

Marc Kirschner (2005)

How the EES differs from MS/SET?

vii	rapid phenotypic evolution requires strong selection on abundant genetic variation	rapid phenotypic evolution can be frequent and can result from the simultaneous induction and selection of functional variants
viii	taxonomic diversity is explained by diversity in the selective environments	taxonomic diversity will sometimes be better explained by features of developmental systems (evolvability, constraints) than features of environments
ix	heritable variation will be unbiased	heritable variation will be systematically biased towards variants that are adaptive and well-integrated with existing aspects of the phenotype
x	environmental states modified by organisms are not systematically different from environments that change through processes independent of organismal activity	niche construction will be systematically biased towards environmental changes that are well suited to the constructor's phenotype, or that of its descendants, and enhance the constructor's, or its descendant's, fitness
xi	parallel evolution explained by convergent environmental conditions	repeated evolution in isolated population may be due to niche construction
xii	ecosystem stability, productivity and dynamics explained by competition and trophic interactions	ecosystem stability, productivity and dynamics critically dependent on niche construction/ecological inheritance

Objectives of EES

- **Provide definitive evaluati [redacted] notly conSETted processes in evolution (e.g [redacted] genetic inheritance)**
- **Clarify the evolutionary i [redacted] sponses to the environment (plasticity)**
- **Devise new theoretical approaches for complex genotype-to-phenotype relations**
- **Establish to what extent developmental processes explain long-term trends, parallel evolution, biological diversity and evolvability**

Thank You

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