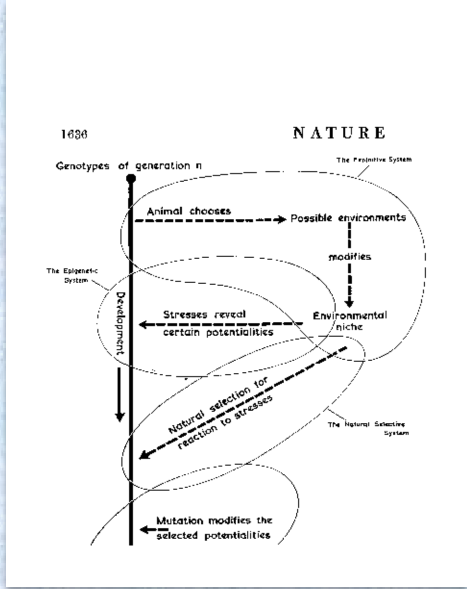
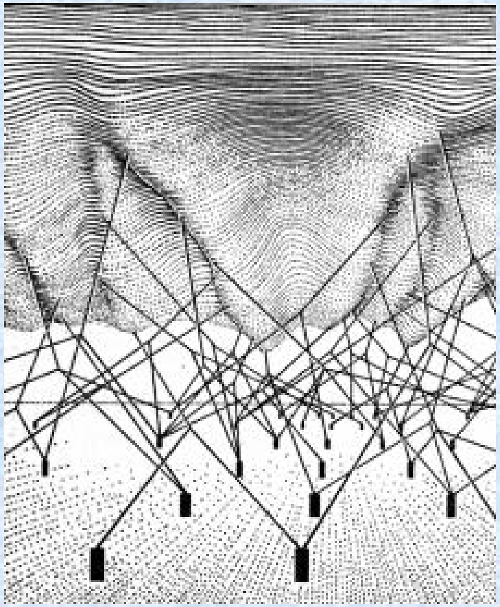
A celebration of the life and thinking of Conrad Waddington

15th-17th April 2016. Abbazia di Spineto, Sarteano, Tuscany, Italy

Waddington's influence on some recent developments in the evolutionary sciences





Kevin N. Laland

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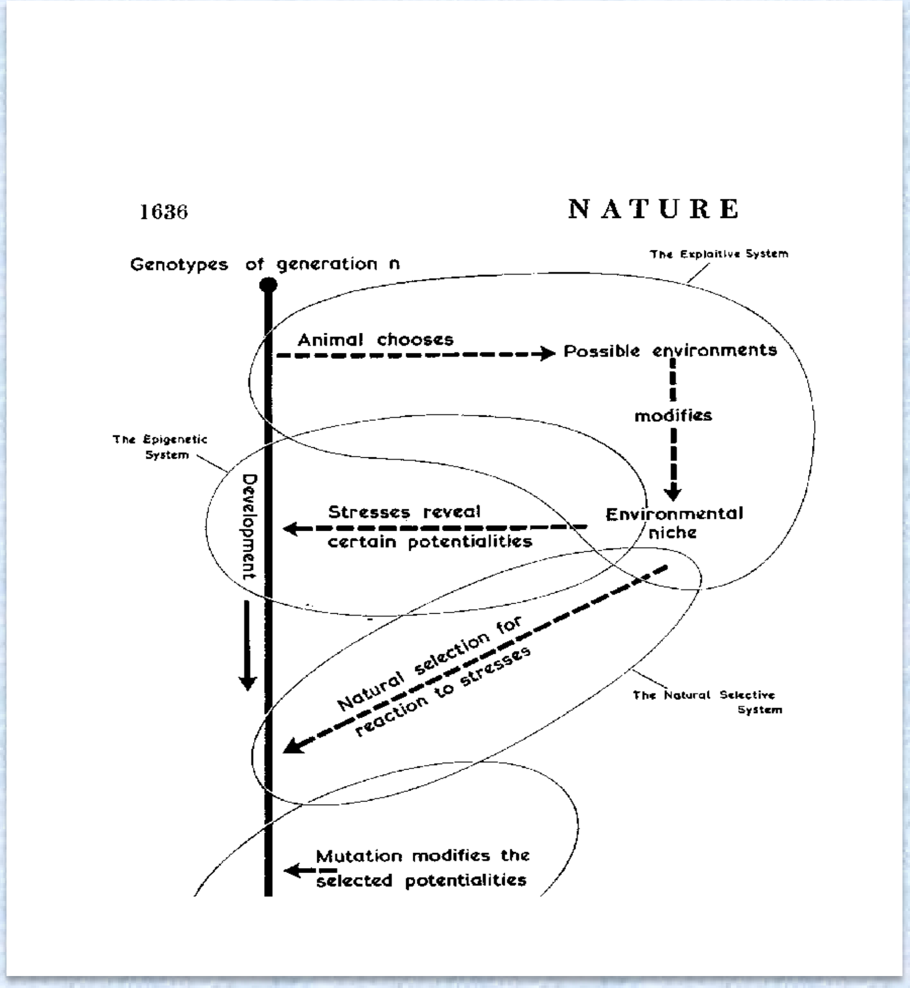
http://lalandlab.st-andrews.ac.uk/

The exploitive system

Animals … are usually surrounded by a much wider range of environmental conditions than they are willing to inhabit. They live in a highly heterogeneous 'ambience', from which they themselves select the particular habitat in which their life will be passed. Thus **the animal by its behaviour contributes in a most important way to determining the nature and intensity of the selective pressures which will be exerted on it**.

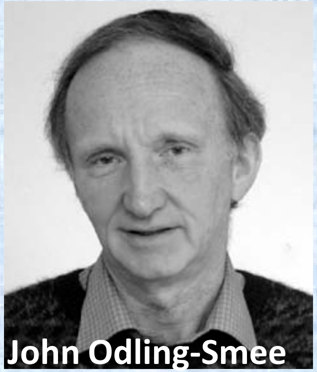
Waddington, 1959, Evolutionary Systems – Animal and Human. Nature

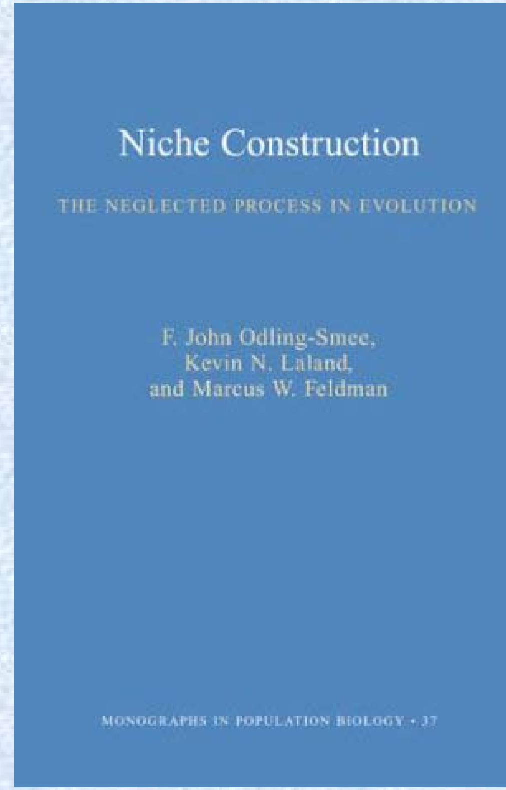
The exploitive system



Biological evolution…is carried out by a mechanism which involves four major factors: a genetic system, an epigenetic system, an exploitive system, and a system of natural selection pressures.

Waddington, 1959, Evolutionary Systems – Animal and Human. Nature





Niche Construction: The process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches.

Odling-Smee *et al.* (2003)

Contemporary treatments of niche construction:

(*i*) Ecological and demographic models (e.g. resource depletion)
(*ii*) Frequency- and density-dependent selection
(*iii*) Habitat selection
(*iv*) Co-evolution
(*v*) Maternal inheritance and maternal effects
(*vi*) Epistasis and indirect genetic effects
(*vii*) Gene-culture co-evolution
(*viii*) Adaptive dynamics
(*ix*) Other approaches (e.g. the extended phenotype)

“Organisms do not adapt to their environments. They construct them out of the bits and pieces of their worlds.”

Richard Lewontin (1983)

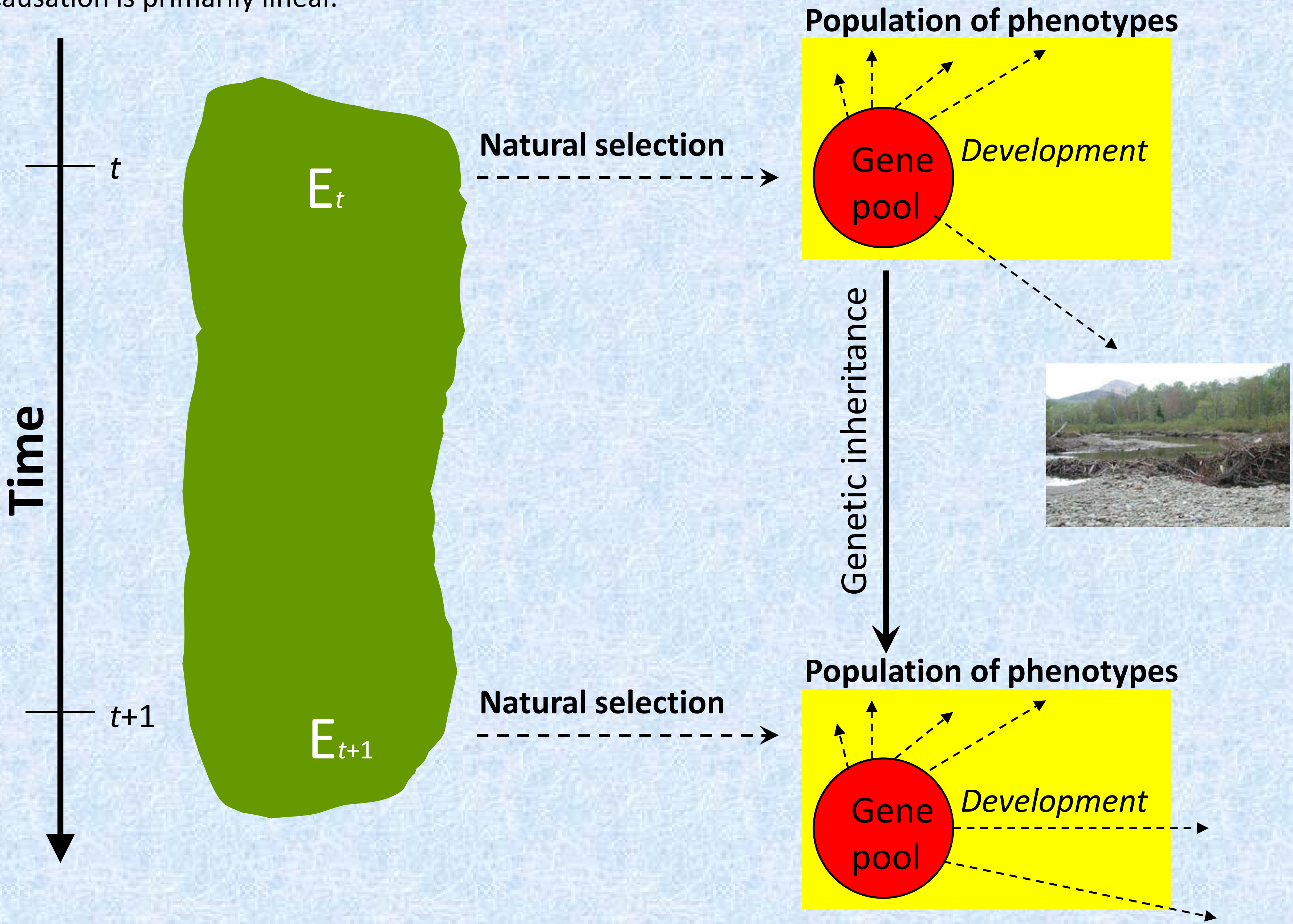
“Adaptation is always asymmetrical; organisms adapt to their environment, never vice versa”

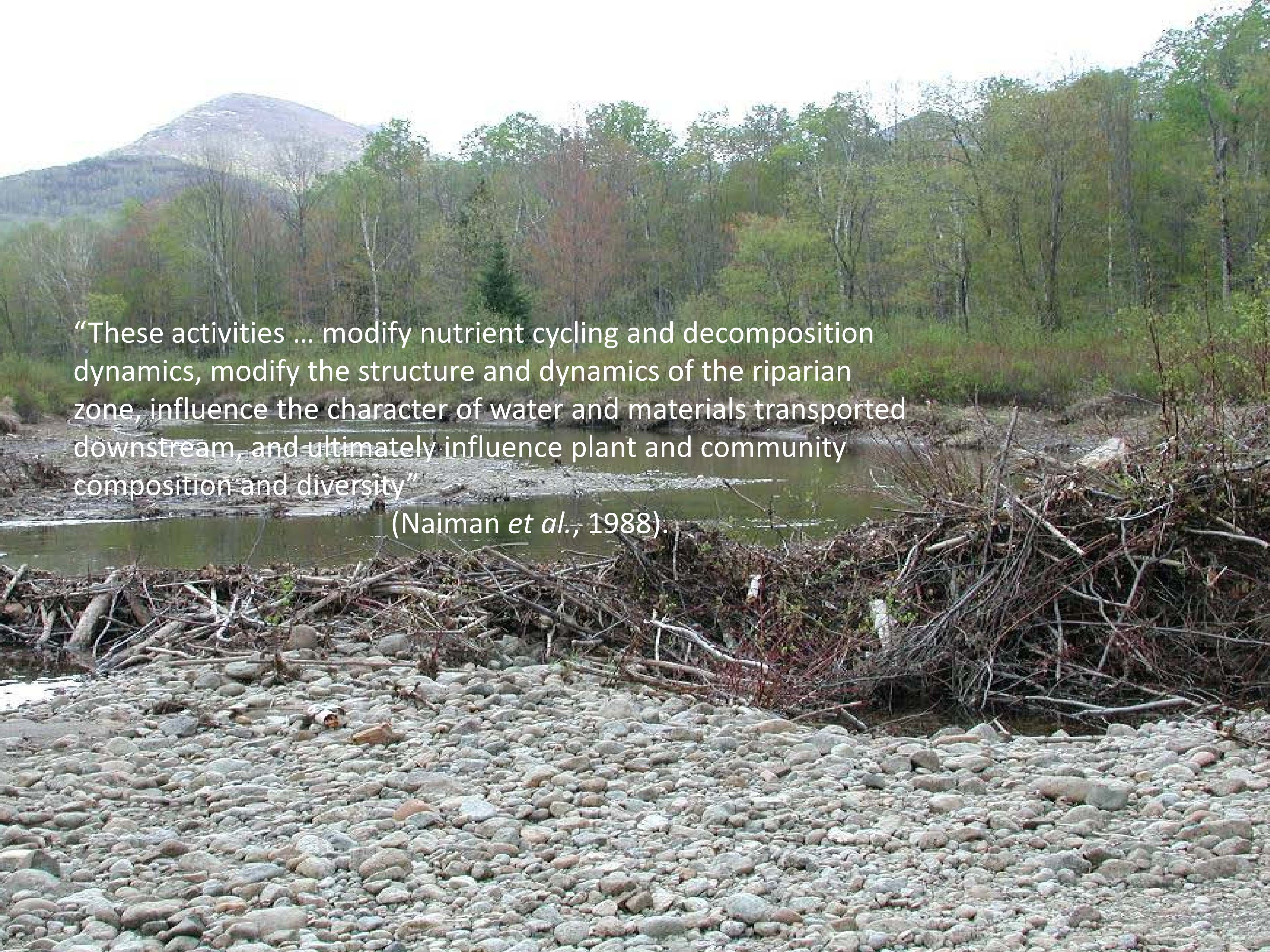
George Williams (1992)

The beaver’s dam

The extended phenotype perspective

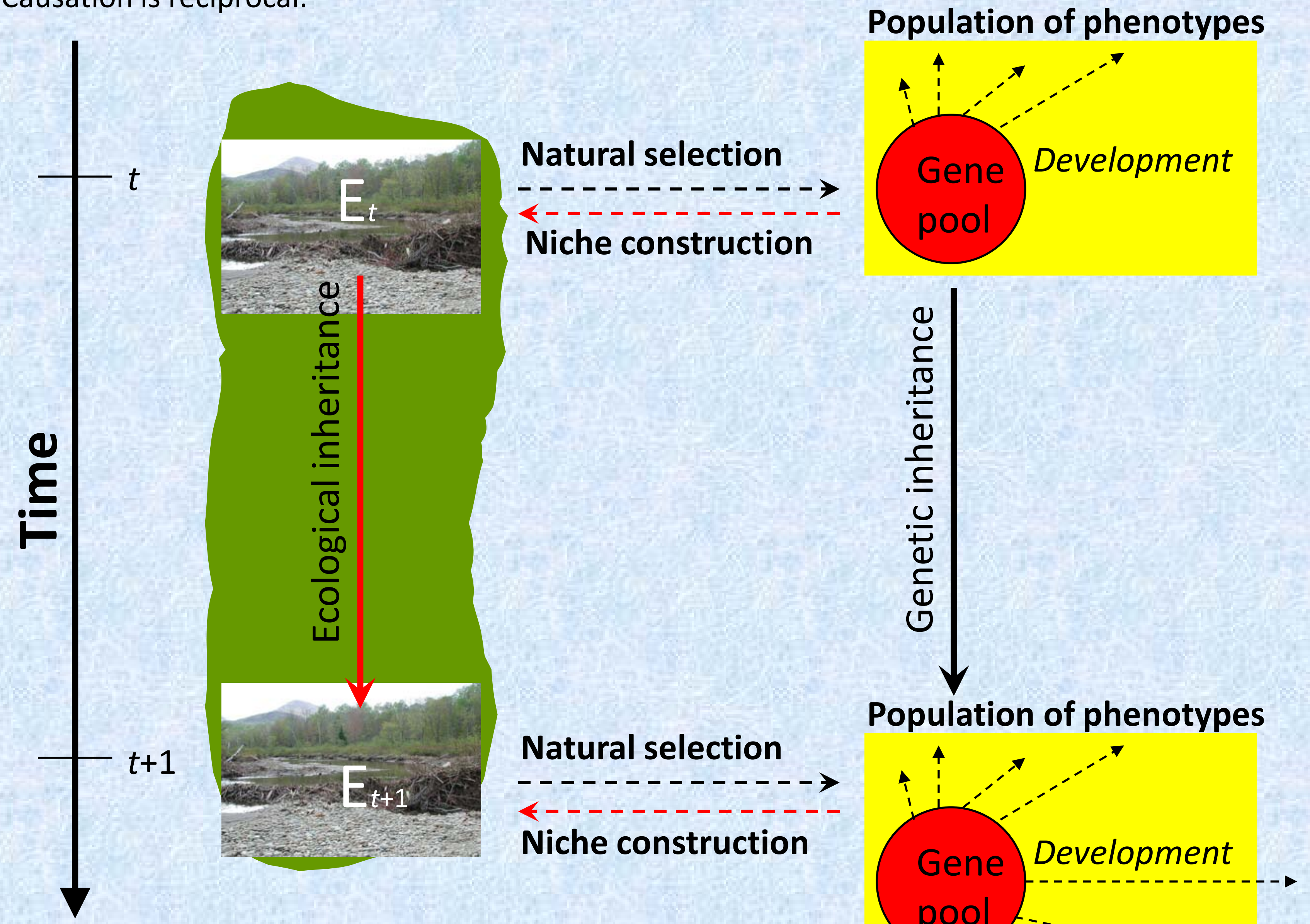
Causation is primarily linear.




"These activities … modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and community composition and diversity"
(Naiman *et al.*, 1988).

The niche-construction perspective

Causation is reciprocal.

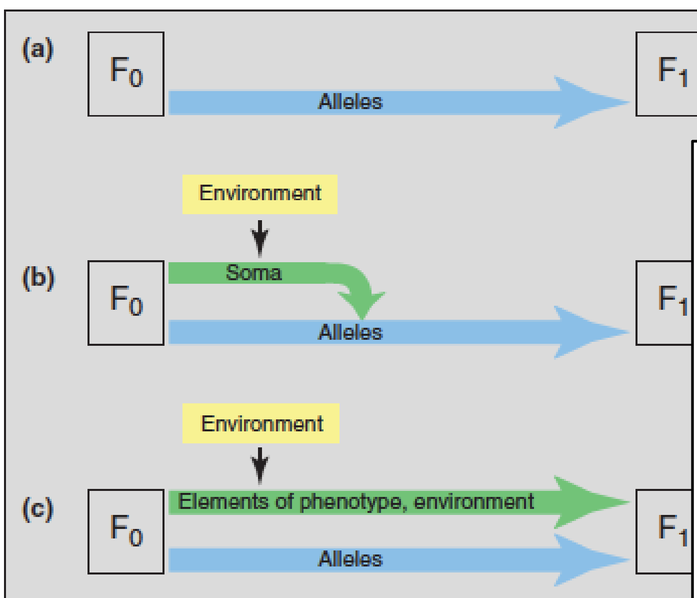


Cell PRESS

Beyond DNA: integrating inclusive inheritance into an extended theory of evolution

Étienne Danchin*‡, Anne Charmantier§, Frances A. Champagne||, Alex Mesoudi¶, Benoit Pujol*‡ and Simon Blanchet*#

Abstract | Many biologists are calling for an 'extended evolutionary synthesis' that would
rn synthesis' of evolution. Biological information is typically
ransmitted across generations by the DNA sequence alone, but
ce indicates that both genetic and non-genetic inheritance, and the
them, have important effects on evolutionary outcomes. We review
effects of epigenetic, ecological and cultural inheritance and



TRENDS in Ecology & Evo

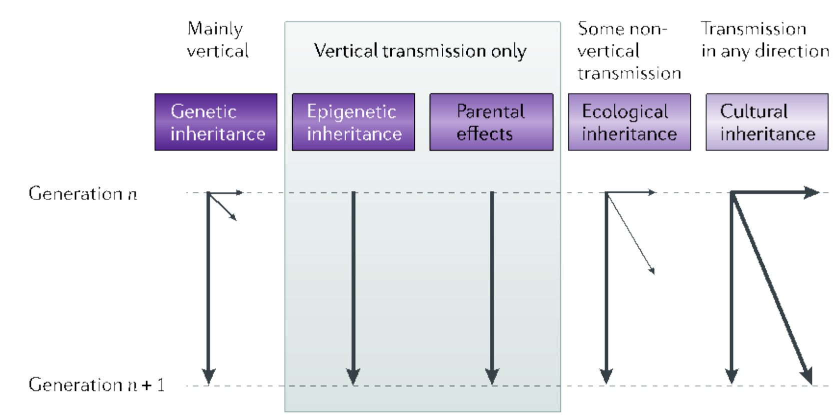


Figure 2 | **Main vectors of transmission for the various forms of information inheritance.** Vertical arrows represent lineages, and horizontal and oblique arrows

TABLE 1

Twelve insights from niche construction theory

Finding	References
Niche construction can:	
1. Fix genes or phenotypes that would, under standard evolutionary theory, be deleterious; support stable polymorphisms where none are expected and eliminate polymorphisms that without niche construction would be stable.	Laland et al. 1996, 1999, 2001; Kerr et al. 1999; Creanza et al. 2012
2. Affect evolutionary rates, both speeding up and slowing down responses to selection under different conditions.	Laland et al. 1996, 1999, 2001; Silver and Di Paolo 2006
3. Cause evolutionary time lags, generate momentum, inertia, and autocatalytic effects. Interactions with evolving environments can produce catastrophic responses to selection, as well as cyclical dynamics.	Laland et al. 1996, 1999, 2001; Kerr et al. 1999
4. Drive niche-constructing traits to fixation by creating statistical associations with recipient traits.	Silver and Di Paolo 2006; Rendell et al. 2011
5. Influence the dynamics, competition, and diversity of meta-populations.	Hui et al. 2004; Borenstein et al. 2006
6. Be favored, even when currently costly, because of the benefits that will accrue to distant descendants.	Lehmann 2007, 2008
7. Allow the persistence of organisms in currently inhospitable environmental conditions that would otherwise lead to their extinction; facilitate range expansion.	Kylafis and Loreau 2008
8. Regulate environmental states, keeping essential parameters within tolerable ranges.	Laland et al. 1996, 1999; Kylafis and Loreau 2008
9. Facilitate the evolution of cooperative behavior.	Lehmann 2007, 2008; Van Dyken and Wade 2012
10. Drive coevolutionary events, both exacerbate and ameliorate competition, and affect the likelihood of coexistence.	Krakauer et al. 2009; Kylafis and Loreau 2011
11. Affect carrying capacities, species diversity and robustness, and macroevolutionary trends.	Krakauer et al. 2009
12. Affect long-term fitness (not just the number of offspring or grand-offspring) by contributing to the long-term legacy of alleles, genotypes, or phenotypes within a population.	McNamara and Houston 2006; Lehmann 2007; Palmer and Feldman 2012

Odling-Smee et al (2013) *Quarterly Review Biology*

A traditional interpretation

Aspects of niche construction studied under different labels (e.g. extended phenotype).

Niche construction typically reduced to genetically controlled aspects of phenotypes, or adaptations.

Niche construction treated as a product of evolution, but not an evolutionary process.

An alternative interpretation

Views evolutionary causation as reciprocal (e.g. organism-environment co-evolution).

Niche construction may also result from acquired characters, byproducts, and output of multiple species.

Niche construction treated as a process that directs evolution through **nonrandom modification of environments**.

Waddington's position may be closer to the latter.

Niche construction books and papers

Table S1. Textbook treatments of evolutionary processes

Textbook	Explicitly recognized processes	Constructive development (# pages)	Developmental bias (# pages)	Developmental plasticity (# pages)	Inclusive inheritance (# pages)	Niche construction (# pages)
Herron & Freeman 2014. Evolutionary analysis 5th Ed. Benjamin Cummings (864 pp) [154]	S,D,M,G,L,T,P,N	0	7[a]	9[b]	2	0
Losos. 2014. The Princeton Guide to Evolution. (853 pp) [155]	S,D,M,G,R,N	0	8	7	2	0
Zimmer & Emlen 2013. Evolution. Making Sense of Life. Roberts. (680pp) [156]	S,D,M,G,N	0	0[c]	10[b]	0	0
Futuyma 2013. Evolution Sinauer. (656 pp) [95]	S,D,M,G,L,T,P,N	0	5[a]	9[d]	3	1
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Arthur 2011. Evolution: a developmental approach (404 pp) [26]	S,D,M,G,B	0	26	20	0	0
Barton et al 2007 Evolution Cold Spring Harbor (833 pp) [96]	S,D,M,G,L,T,Sy	2[g]	0[h]	0	1[i]	0
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Ridley 2004. Evolution, 3rd Ed. Blackwell (472 pp) [97]	S,D,M,G	0	0[i]	0	0	0
Futuyma 1998. Evolutionary Biology, 3rd Ed. (875 pp) [6]	S,D,M,G,L,T,P	0	1[j]	1	1[k]	0

Legend. Explicitly recognized evolutionary processes, and treatments of constructive development, developmental bias, developmental plasticity, inclusive inheritance and niche construction, in 10 contemporary evolutionary biology textbooks. Key: S=Selection, D=Drift, M=Mutation, G=gene flow/migration, R=Recombination, N=Nonrandom mating, L=Lateral gene transfer, T=Transposons, B=Developmental bias, Sy=Symbiosis, P=Polyploidy. Notes: a. Constraints given space in several places. b. No mention of plasticity first argument. c. Brief discussion of constraint. d. 1 page on plasticity first argument e. Codon usage bias mentioned. Physical constraints given 6 pages. f. Brief mention of cultural evolution and gene-culture coevolution. g. Exploratory processes discussed (2 pages). h. Constraints afforded 1 paragraph. i. Brief mention of cultural inheritance in human evolution chapter. i. 12 page discussion of genetic, developmental and historical constraints. j. Seven pages on developmental constraints. k. One sentence on human culture.

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Science and Conceptual Frameworks

"The history of science refutes both Popper and Kuhn: on close inspection both Popperian crucial experiments and Kuhnian revolutions turn out to be myths."

(Lakatos, 1978, p6)

We know of many cases in which the environment of a particular locality…will produce in individuals from some other region non-hereditary modifications which are strikingly similar to aberrant forms which in the local population have become genetically determined. Are we to suppose that such parallelism is completely beside the point, and that evolution of a local genetically fixed ecotype has been based on mutations which have occurred at random and are thus quite unconnected with the direct developmental effects of the environment?

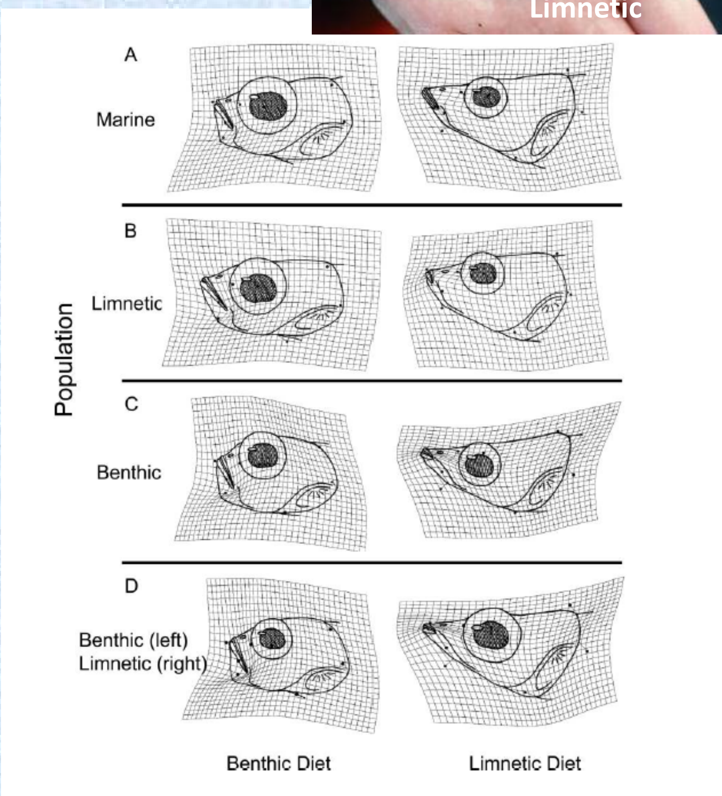
Waddington, 1957, The Strategy of the Genes

Developmental plasticity and speciation

Table 1. Representative examples in which populations that differ in the expression of alternative, environmentally influenced, resource-use morphs appear to be evolving reproductive isolation.

Species	Type of divergence	Citation for evidence of reproductive isolation	Citation for evidence of environmental influence on morph determination
Numerous species of phytophagous insects	Different host plants	[78]	[85][a]
Sticklebacks (*Gasterosteus aculeatus*)	Benthic and limnetic niches	[86]	[16]
Midas cichlids (*Amphilophus* sp.)	Benthic and limnetic niches	[87]	[68]
Spadefoot toads (*Spea multiplicata*)	Omnivore and carnivore niches	[66]	[64]
Crossbills (*Loxia curvirostra*)	Different food types	[88]	[89][a]
Darwin's finches (*Geospiza fortis*)	Different food types	[90]	[89][a]

[a]An individual's resource-use phenotype might be influenced by learning, a type of plasticity.



Wund et al. (2008) Am Nat

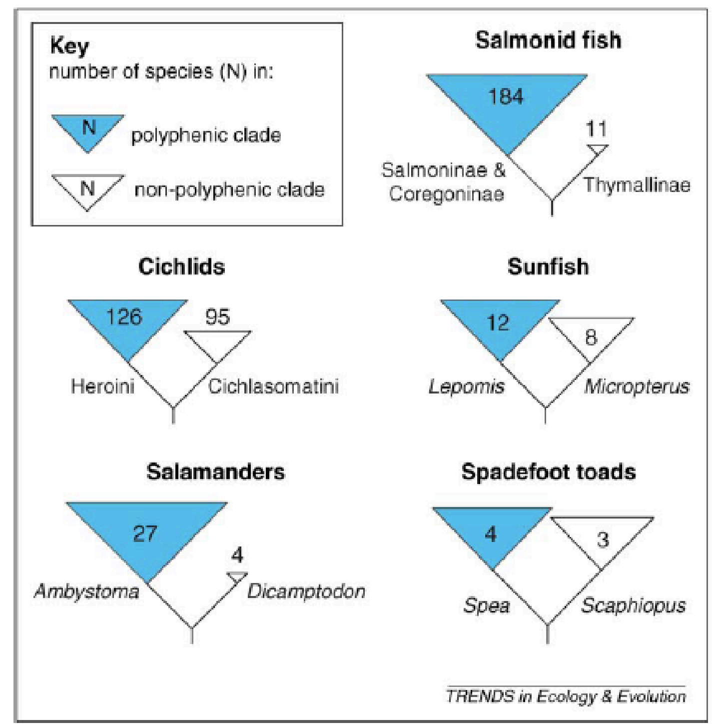


Figure 3. Evidence that resource polyphenism is associated with greater species richness in various clades of fish and amphibians. From [18].

Pfennig et al. (2010) TREE

A traditional interpretation

Developmental plasticity conceptualized as a genetically specified feature of individuals (e.g. a reaction norm).

Primary role for plasticity is to adjust phenotypes to environment.

Plastic responses regarded as pre-filtered by past selection.

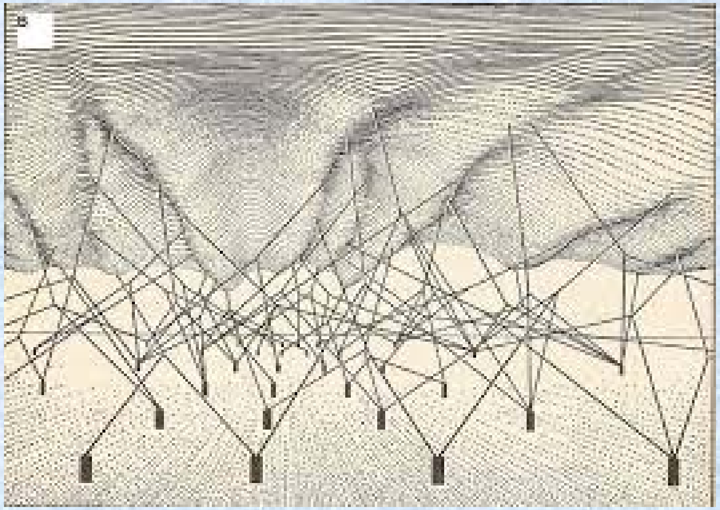
An alternative interpretation

Many plastic responses viewed as reliant on open-ended (e.g. exploratory) developmental processes.

Plasticity initiates evolutionary responses, and enhances evolvability.

Plastic responses capable of introducing phenotypic novelty, which can then be stabilized by selection.

Waddington’s position may be closer to the latter.



The effect of a gene mutation on the phenotype is determined by the interaction of the mutant gene with all the other genes and with the environment during epigenesis. Thus, if the epigenetic system has certain stabilities and instabilities built into it – as is obviously the case – the effect of random changes in genes will not be random by the time they are worked out into phenotypes.

Waddington, 1969, Towards a Theoretical Biology, 2. Sketches

Developmental bias and adaptive radiation

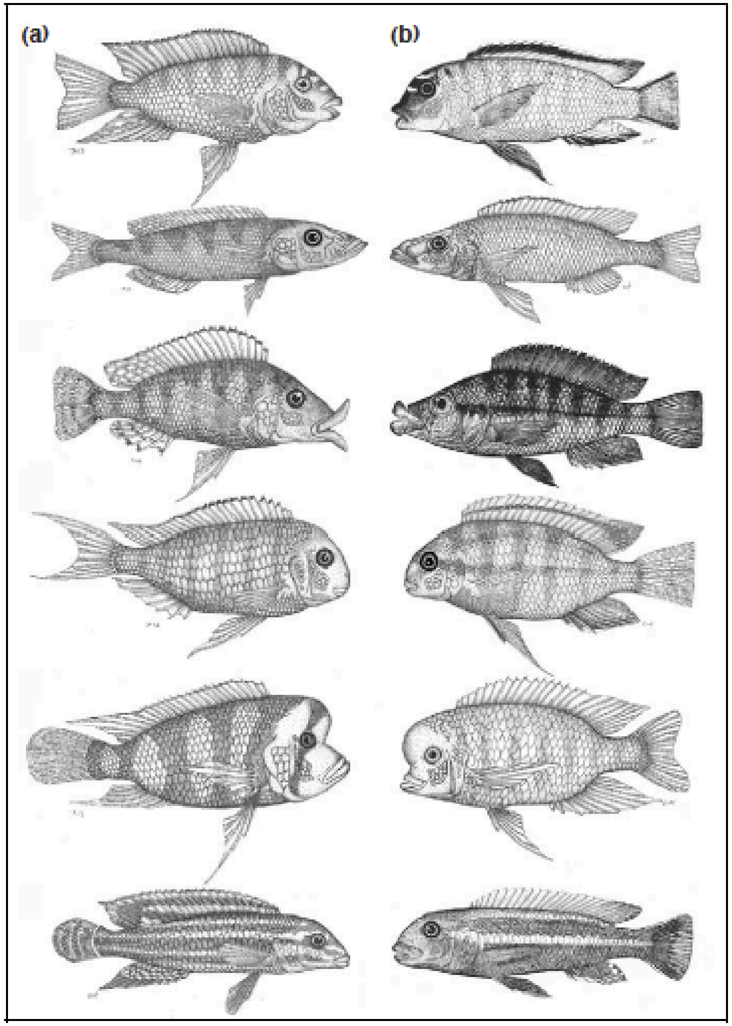


Figure 1. Parallel evolution of trophic morphologies (ecomorphs) in the species flocks of cichlid fishes from two African lakes: **(a)** Lake Tanganyika and **(b)** Lake Malawi. The species in each lake are more closely related to one another than to any species in another lake. Reproduced with permission from [47].

Brakefield (2006) TREE, based on Albertson & Kocher (2006).

A traditional interpretation

Bias in the generation of phenotypic variation treated as phylogenetic or developmental constraints.

Recognized in evolutionary analyses e.g. components of optimality models, G matrix in quantitative genetics.

Explains absence of evolution or of adaptation.

An alternative interpretation

Bias in the generation of phenotypic variation considered an evolutionary cause or process.

Recognized as a major source of evolvability, crucial to understanding evolutionary diversification.

Explains existence of evolution and of adaptation.

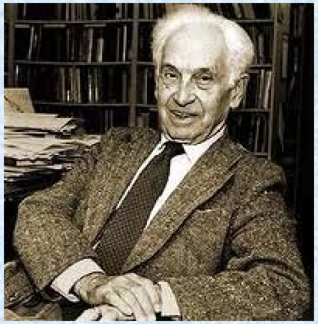
Waddington's position is clearly closer to the latter.

	A Traditional Interpretation	Extended Evolutionary Synthesis
Developmental bias	Bias in phenotypic variation treated as constraint. Explains the absence of evolution or adaptation.	Bias in phenotypic variation considered an evolutionary cause or process. Explains the existence of evolution and adaptation.
Developmental Plasticity	Plasticity conceptualized as a genetically specified feature of individuals (i.e., a reaction norm). Its primary evolutionary role is to adjust phenotypes to environments. Plastic responses regarded as pre-filtered by past selection.	Many plastic responses viewed as reliant on open-ended (e.g. exploratory) developmental processes, and hence capable of introducing phenotypic novelty. Plasticity initiates evolutionary responses and enhances evolvability.
Niche Construction	Aspects of niche construction studied under different labels (e.g. extended phenotypes). Niche construction reduced to genetically specified aspects of phenotypes, or adaptations. Treated as a product of evolution but not an evolutionary process.	Views evolutionary causation as reciprocal (e.g. organism-environment co-evolution). Niche construction may also result from acquired characters, byproducts and outputs of multiple species. Treated as a process that directs evolution by non-random modification of environments.

Laland et al, 2015

Two views of development.

a. Programmed development



"All of the directions, controls and constraints of the developmental machinery are laid down in the *blueprint* of the DNA genotype as instructions or potentialities" (Mayr, 1984, p.126, my italics).

b. Constructive development

"The genome is sometimes described as a program that directs the creation and behaviour of all other biological processes in an organism. But this is not a fact. It is a metaphor. It is also an unrealistic and unhelpful one" (Noble, 2006, p51).

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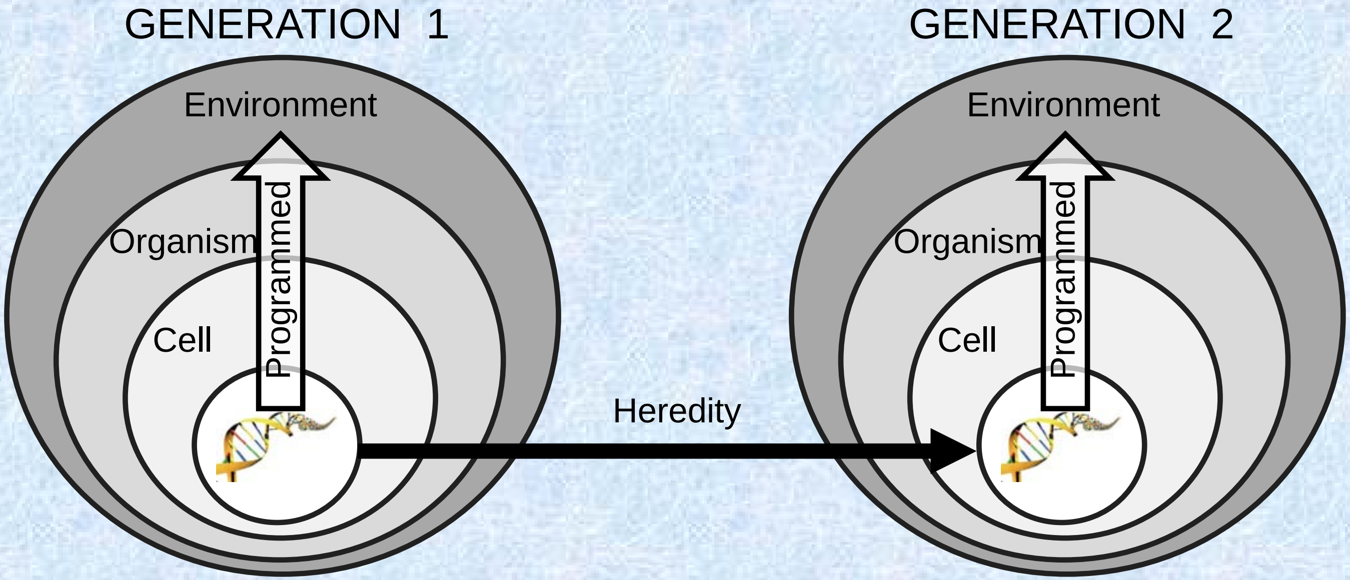
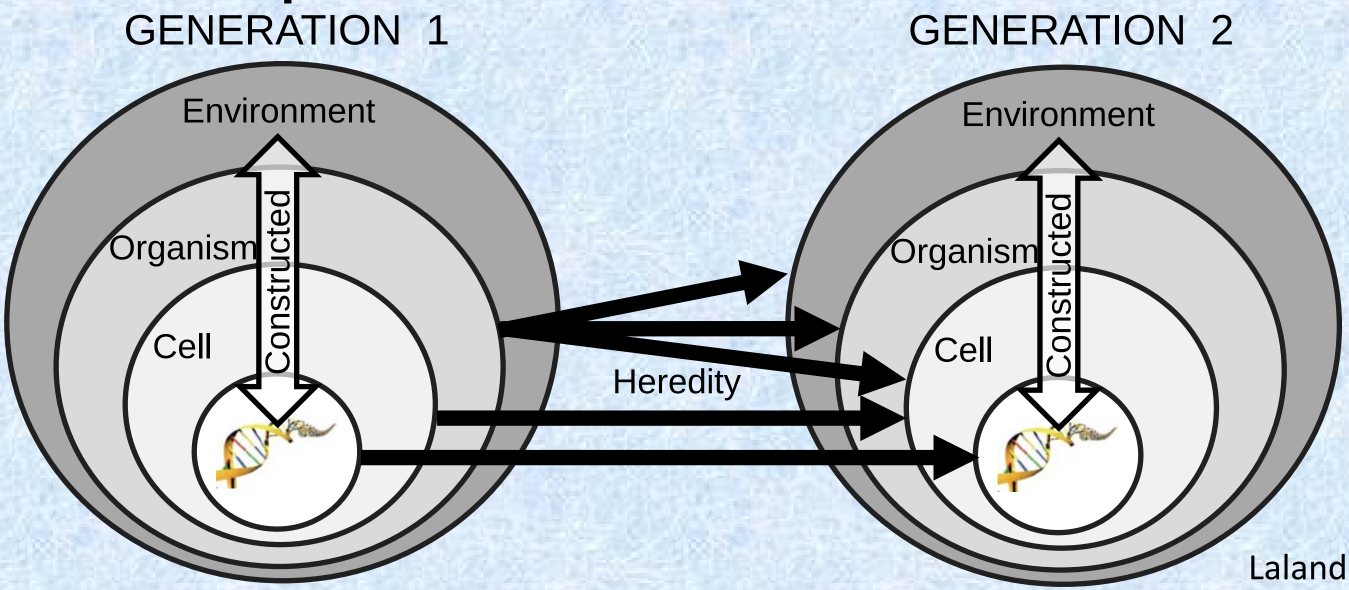
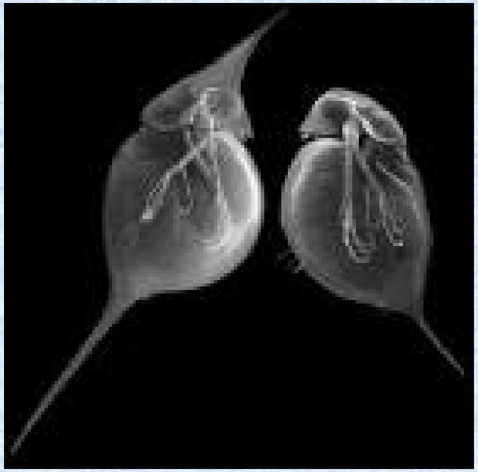


b. Constructive development



Laland et al, 2015

Programmed development



Constructive development

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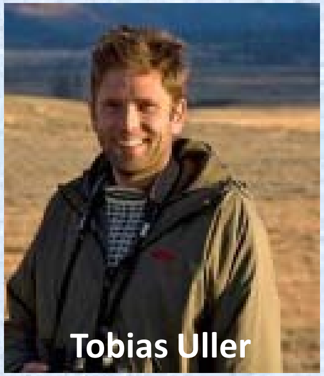
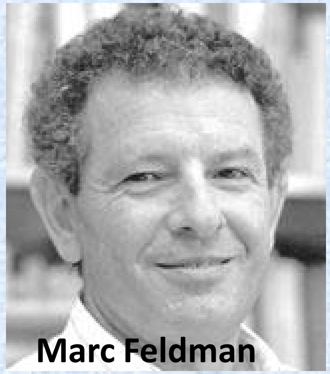
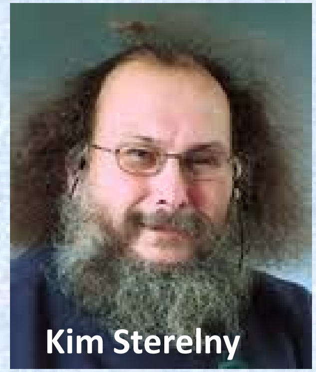
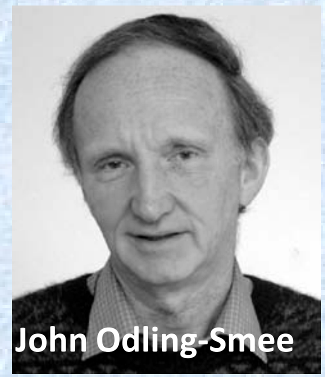
The Extended Evolutionary Synthesis Project









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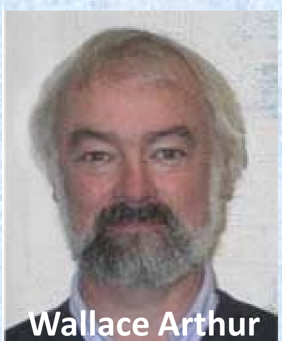
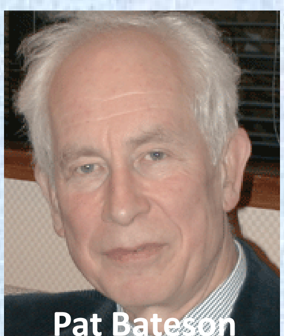
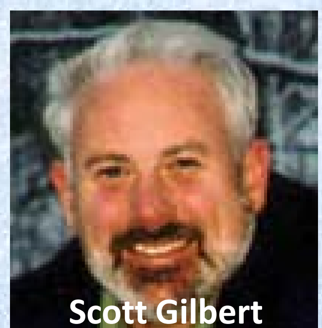




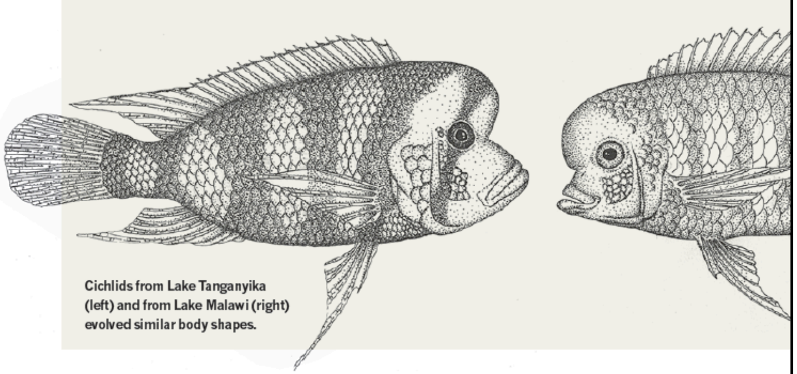


COMMENT

HEALTH Lasting legacy of wartime battle against malaria p.166

AGEING Atul Gawande's call to action on end-of-life medical care p.167

ENERGY Don't assume that renewable energies are problem-free p.168



Cichlids from Lake Tanganyika (left) and from Lake Malawi (right) evolved similar body shapes.

Does evolutionar
theory need a rethi

Researchers are divided over what processes should be conside

POINT
Yes, urgently

Without an extended evolutionary framework, the theory neglects key processes, say Kevin Laland *and colleagues.*

Charles Darwin conceived of evolution by natural selection without knowing that genes exist. Now mainstream evolutionary theory has come to focus almost exclusively on genetic inheritance and processes that change gene frequencies.

Yet new data pouring out of adjacent fields are starting to undermine this narrow stance. An alternative vision of evolution is beginning to crystallize, in which the processes by which organisms grow and develop are recognized as causes of evolution.

Some of us first met to discuss these advances six years ago. In the time since, as members of an interdisciplinary team, we have worked intensively to develop a broader framework, termed the extended evolutionary synthesis[1] (EES), and to flesh out its structure, assumptions and predictions. In essence, this synthesis maintains that important drivers of evolution, ones that cannot be reduced to genes, must be woven into the very fabric of evolutionary theory.

We believe that the EES will shed new light on how PAGE 162 ▶

COUNTERPOINT
No, all is well

Theory accommodates evidence th
Gregory A. Wray, Hopi E. Hoeks

In October 1881, just six month
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Through the Actions of Worms
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Darwin's lead in its emphasis on ev
mation from other fields.
A profound shift in evolution

PROCEEDINGS B

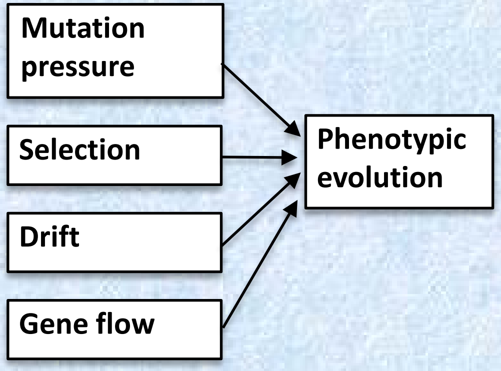
EES assumptions

Classical MS core assumptions	EES core assumptions
(i) The major directing or creative influence in evolution is natural selection, which alone explains why the properties of organisms match the properties of their environments (adaptation).	(i) Developmental processes share with natural selection some responsibility for the direction and rate of evolution and contribute to organism-environment complementarity.
(ii) *Genetic inheritance*: Genes constitute the only general inheritance system. Acquired characters are not inherited.	(ii) Inheritance extends beyond genes to encompass epigenetic, physiological, ecological and cultural inheritance. Acquired characters play evolutionary roles.
(iii) *Random variation*: No relationship between the direction in which mutations occur - and hence the supply of phenotypic variants - and the direction that would lead to enhanced fitness.	(iii) *Non-random variation*: developmental systems sometimes facilitate well-integrated, functional phenotypic responses to mutation or environmental induction.
(iv) *Gene-centred perspective:* Evolution requires, and is often defined as, *change in gene frequencies*. Populations evolve through changes in gene frequencies brought about through natural selection, drift, mutation and gene flow.	(iv) *Organism-centred perspective*. Evolution redefined as a *transgenerational change in the distribution of heritable traits of a population*. There is a broadened notion of evolutionary process and inheritance.
(v) Macro-evolutionary patterns explained by micro-evolutionary processes of selection, drift, mutation and gene flow.	(v) Additional evolutionary processes (e.g. ecological inheritance, developmental bias) help explain macro-evolutionary patterns, and contribute to evolvability.
(vi) etc	(vi) etc

Laland et al, 2015

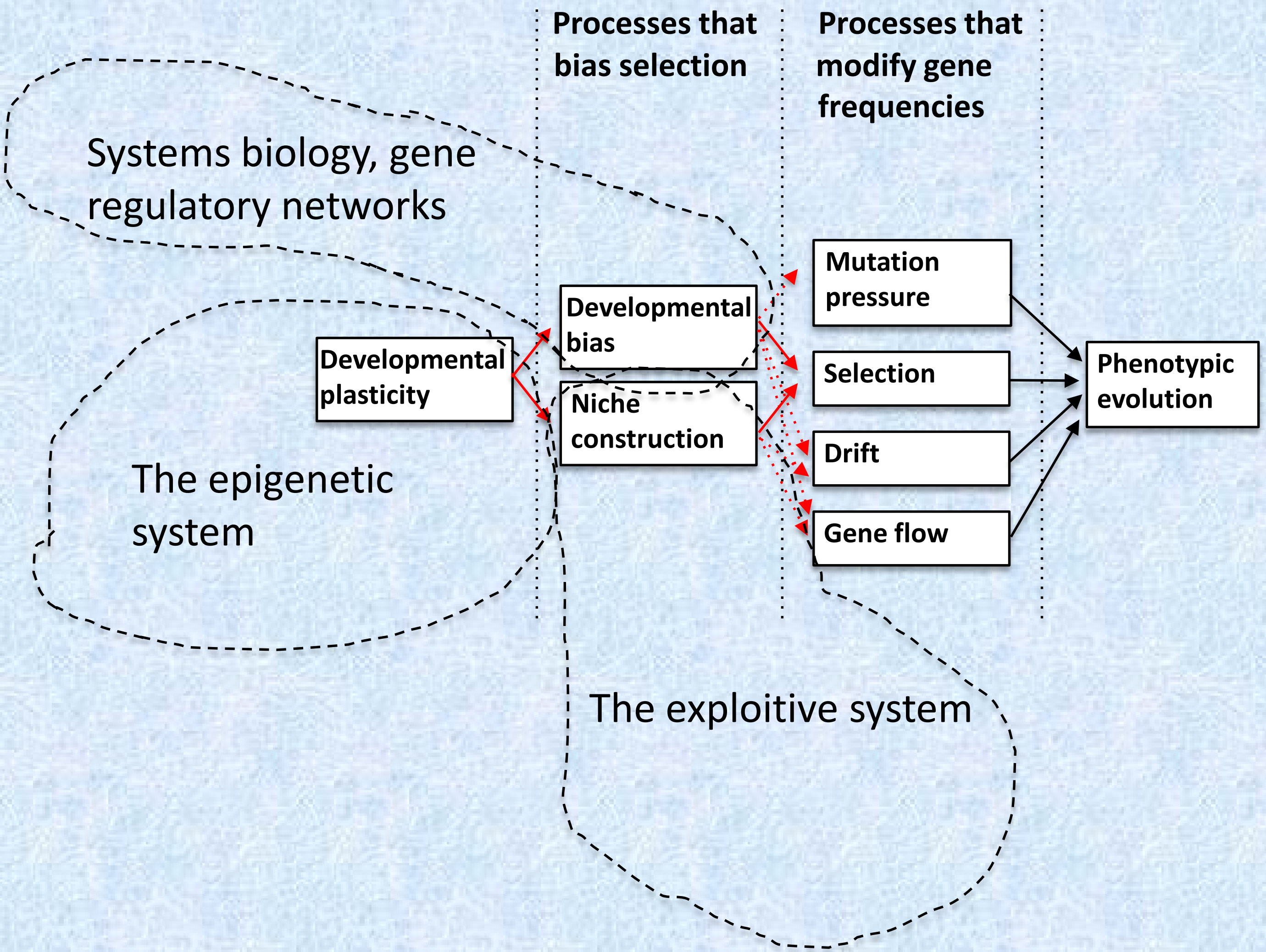
Orthodox evolutionary processes

Processes that modify gene frequencies



Laland et al, 2014

Processes that bias selection



Laland et al, 2014

EES Predictions

Traditional predictions	Proposed EES predictions
(i) Genetic change causes, and logically precedes, phenotypic change, in adaptive evolution.	(i) Phenotypic accommodation can precede, rather than follow, genetic change, in adaptive evolution.
(ii) Genetic mutations (and novel phenotypes) random in direction and typically neutral or disadvantageous.	(ii) Novel phenotypic variants will frequently be directional and functional.
(iii) Isolated mutations generating novel phenotypes will occur in a single individual.	(iii) Novel, evolutionarily consequential, phenotypic variants will frequently be environmentally induced in multiple individuals.
(iv) Repeated evolution in isolated populations is due to convergent selection.	(iv) Repeated evolution in isolated populations may be due to convergent selection and/or developmental bias.
(v) Adaptive variants propagated through selection.	(v) Adaptive variants propagated through selection, repeated induction, learning and non-genetic inheritance.
(vi) Rapid phenotypic evolution requires strong selection on abundant genetic variation.	(vi) 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.	(viii) Taxonomic diversity will sometimes be better explained by features of developmental systems (evolvability, constraints) than features of environments.
(ix) etc	(ix) etc

Laland et al, 2015

Putting the extended evolutionary synthesis to the test

The John Templeton Foundation has awarded a major grant (£5.7m) to an international team of leading researchers for a three-year research program comprising 22 interlinked projects to put the predictions of the extended evolutionary synthesis to the test.

The research program will involve 29 PIs, based at eight funded academic institutions, plus a further 20 'satellite' researchers.

(A) University of St Andrews: Kevin Laland, Andy Gardner, Graeme Ruxton, Maria Dornelas, David Paterson, Susan Healy, Mat Holden
(B) University of Lund: Tobias Uller, Charlie Cornwallis, Per Lundberg, Erik Svensson, Nathalie Feiner
(C) Stanford University: Marcus Feldman
(D) Cambridge University: Tim Lewens, Nick Hopwood, Marta Halina, Patrick Bateson, Paul Brakefield, Rufus Johnstone
(E) Santa Fe Institute: Jessica Flack, David Krakauer, Doug Erwin, Michael Lachmann
(F) Indiana University: Armin Moczek, Michael Wade
(G) Clark University: Susan Foster, John Baker, John Gibbons
(H) Southampton University: Richard Watson

Satellite researchers: Jonathan Birch (LSE), Ellen Clarke (Oxford), William Cresko (Oregon), John Endler (Deakin), Heikki Helanterä (Helsinki), Mia Hoogenboom (James Cook), Eva Jablonka (Tel Aviv), Hilton Japyassu (Bahia), Bram Kuijper (Exeter), Joshua Madin (Macquarie), Juha Merilä (Helsinki), Gerd Müller (Vienna), Denis Noble (Oxford), John Odling-Smee (Oxford), Emilie Snell-Rood (Minnesota), Kim Sterelny (ANU), Sally Street (Hull), Gunter Wagner (Yale), Stefan Williams (Sydney), Matt Wund (New Jersey).

Conclusions

1. Current interest in the role that niche construction (and plasticity) play in evolution can be traced back to Waddington’s seminal writings.

2. Waddington’s ideas have had a pervasive influence on the emerging Extended Evolutionary Synthesis.

3. Waddington’s ideas are recognized to be of considerable interest and importance within the wider evolutionary sciences, although their impact on evolutionary genetics is, as of yet, modest.

With thanks to...