Talking Evolution
Plön, Germany. Sept 26-28, 2018

The extended synthesis: a human evolution perspective

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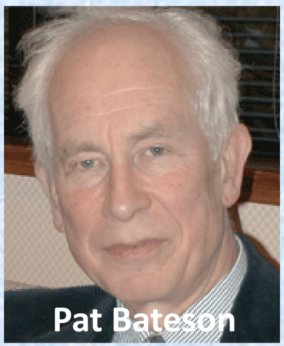
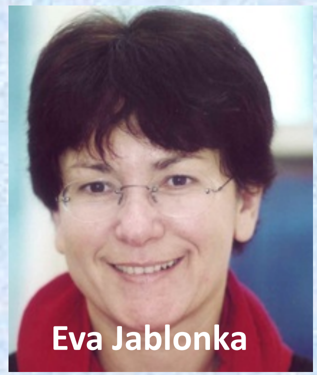
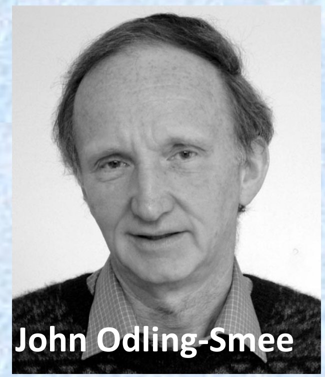
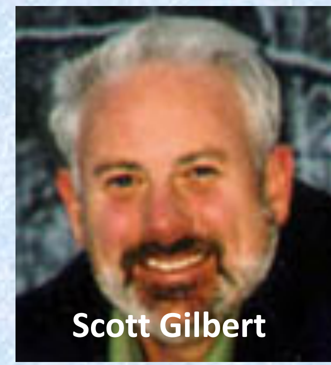
Collaborators









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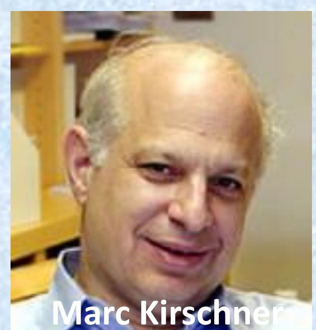

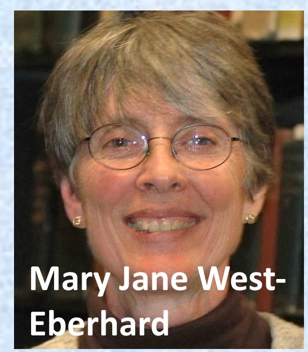

COMMENT

HEALTH Lasting legacy of wartime battle against malaria **p.166**

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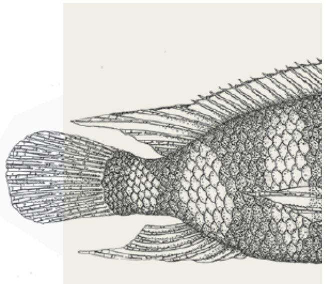

Cichlids from Lake Tanganyika (left) and from Lake Malawi (right) evolved similar body shapes.

Do
theor

Researchers are divic

POINT
Yes, urgently

Without an extended evolutionary fran key processes, say Kevin Laland and c

Charles Darwin conceived of ev without knowing that genes ex tionary theory has come to focus inheritance and processes that change g

Yet new data pouring out of adjacen mine this narrow stance. An alternative ning to crystallize, in which the proces and develop are recognized as causes of

Some of us first met to discuss these time since, as members of an interdisci intensively to develop a broader framew lutionary synthesis[1] (EES), and to flesh and predictions. In essence, this synthe drivers of evolution, ones that cannot woven into the very fabric of evolution

We believe that the EES will shed n

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Darwin review

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Cite this article: Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J. 2015 The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc. R. Soc. B* **282**: 20151019. http://dx.doi.org/10.1098/rspb.2015.1019

Received: 3 May 2015
Accepted: 9 July 2015

Subject Areas:
evolution

Keywords:
extended evolutionary synthesis, evolutionary developmental biology, developmental plasticity, inclusive inheritance, niche construction, reciprocal causation

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The extended evolutionary synthesis: its structure, assumptions and predictions

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Scientific activities take place within the structured sets of ideas and assumptions that define a field and its practices. The conceptual framework of evolutionary biology emerged with the Modern Synthesis in the early twentieth century and has since expanded into a highly successful research program to explore the processes of diversification and adaptation. Nonetheless, the ability of that framework satisfactorily to accommodate the rapid advances in developmental biology, genomics and ecology has been questioned. We review some of these arguments, focusing on literatures (evo-devo, developmental plasticity, inclusive inheritance and niche construction) whose implications for evolution can be interpreted in two ways—one that preserves the internal structure of contemporary evolutionary theory and one that points towards an alternative conceptual framework. The latter, which we label the 'extended evolutionary synthesis' (EES), retains the fundaments of evolutionary theory, but differs in its emphasis on the role of constructive processes in development and evolution, and reciprocal portrayals of causation. In the EES, developmental processes, operating through developmental bias, inclusive inheritance and niche construction, share responsibility for the direction and rate of evolution, the origin of character variation and organism–environment complementarity. We spell out the structure, core assumptions and novel predictions of the EES, and show how it can be deployed to stimulate and advance research in those fields that study or use evolutionary biology.

1. Introduction

To make progress, scientists must specify phenomena that require explanation, identify causes and decide on what methods, data and analyses are explanatorily sufficient. In doing so, they may inadvertently create a 'conceptual framework'—a way of thinking for their field, with associated assumptions, concepts, rules and practice, that allows them to get on with their work [1–3]. Conceptual frameworks are necessary in science, but they, and their associated practices, inevitably encourage some lines of research more readily than others. Hence, it is vital that the conceptual frameworks themselves evolve in response to new data, theories and methodologies. This is not always straightforward, as habits of thought and practice are often deeply entrenched. In this regard, alternative conceptual frameworks can be valuable because they draw attention to constructive

Why these four topics?

Focus on:

i. Developmental bias
ii. Developmental plasticity
iii. Extra-genetic inheritance
iv. Niche construction

not because “more important” or “neglected” but because

a) they divide opinion, with ‘established’ and ‘alternative’ interpretations of literatures,
b) the ‘alternative’ readings show collective coherence, implying a different causal structure for evolution.

Common themes

In all four literatures some, but not all, researchers are emphasizing that:

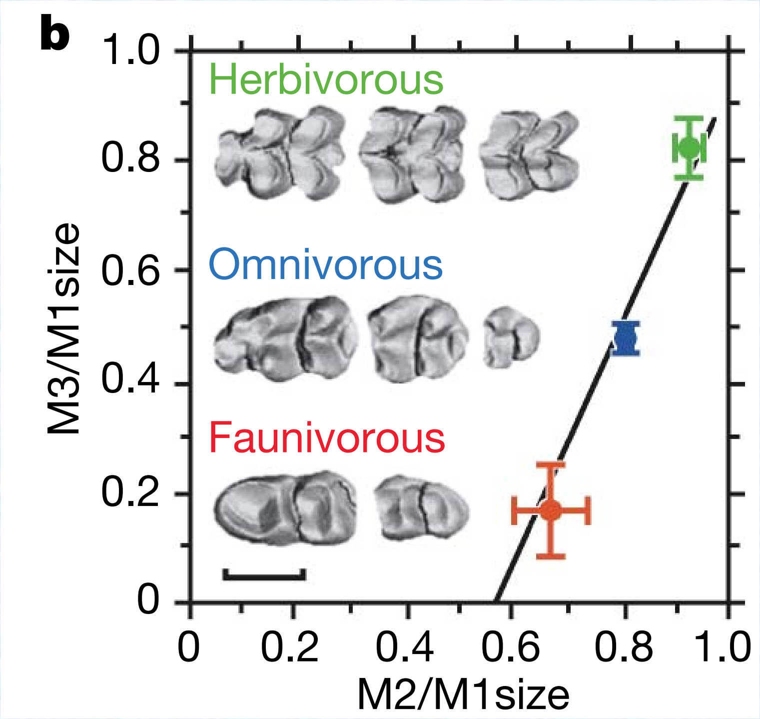
(i) Developmental processes play evolutionary roles

(ii) Development is constructive

(iii) Biological causation is reciprocal

Developmental Bias

Traits can be channeled by the processes of development to produce some variants more readily than others.



Natural selection may shift species along highly specific pathways created by the mechanisms of development.

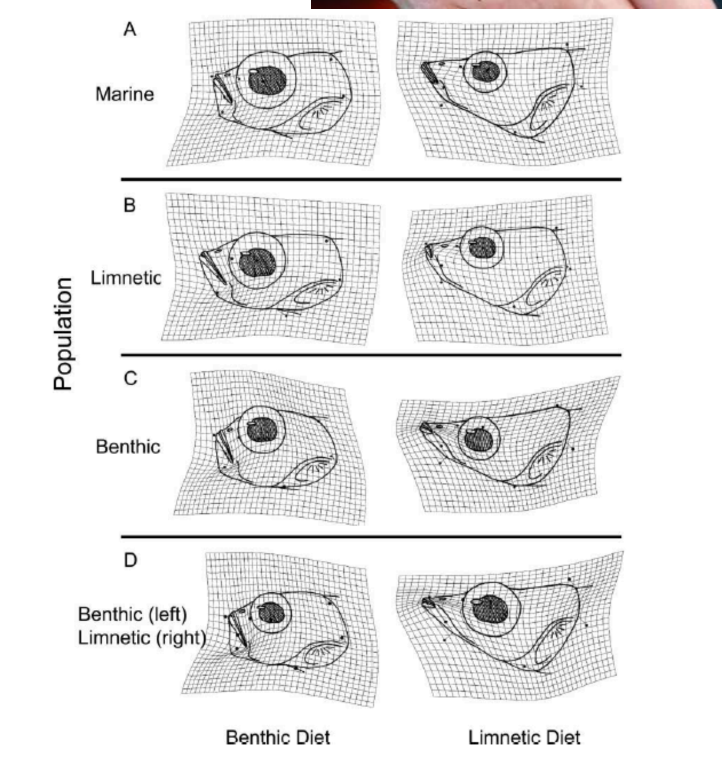
Kavanagh et al (2007) Science

Developmental plasticity

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.



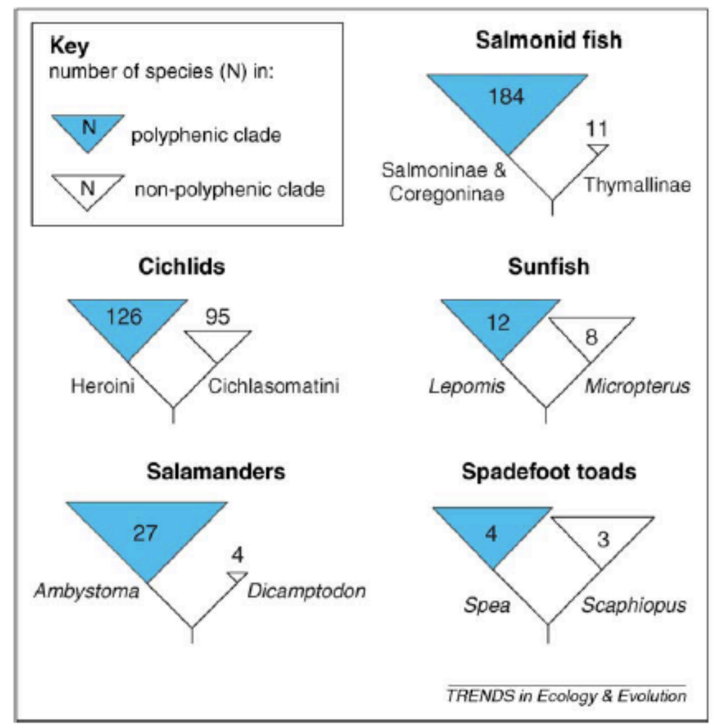
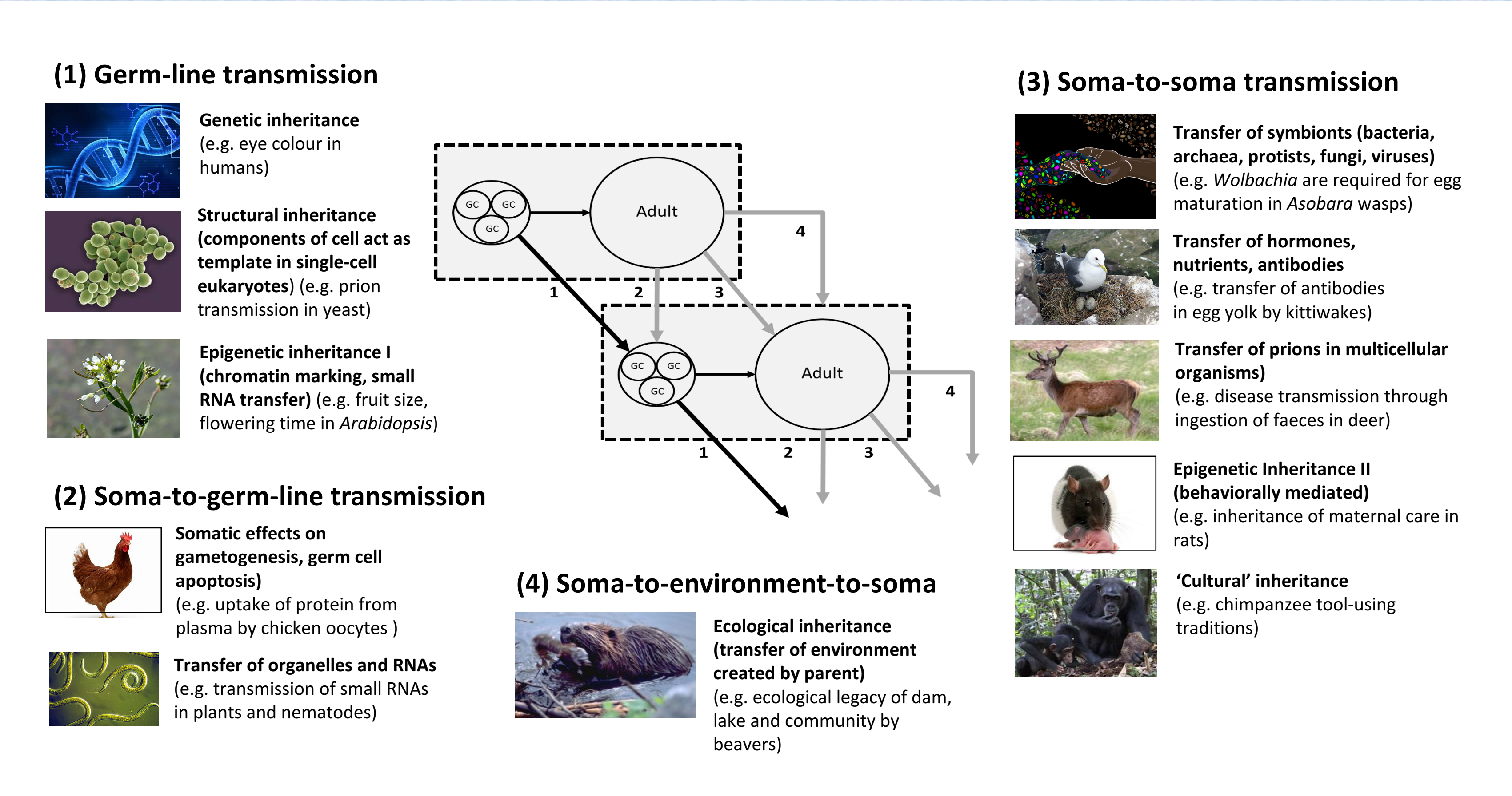


Figure 3. Evidence that resource polyphenism is associated with greater species richness in various clades of fish and amphibians. From [18].

Wund et al. (2008) Am Nat

Pfennig et al. (2010) TREE

Extra-genetic Inheritance



A bewildering array of developmental processes are now known to contribute to inheritance.

Figure based on Badyaev & Uller (2009), Jablonka & Raz (2009), Bonduriansky & Day 2018

Niche construction

The exploitive system

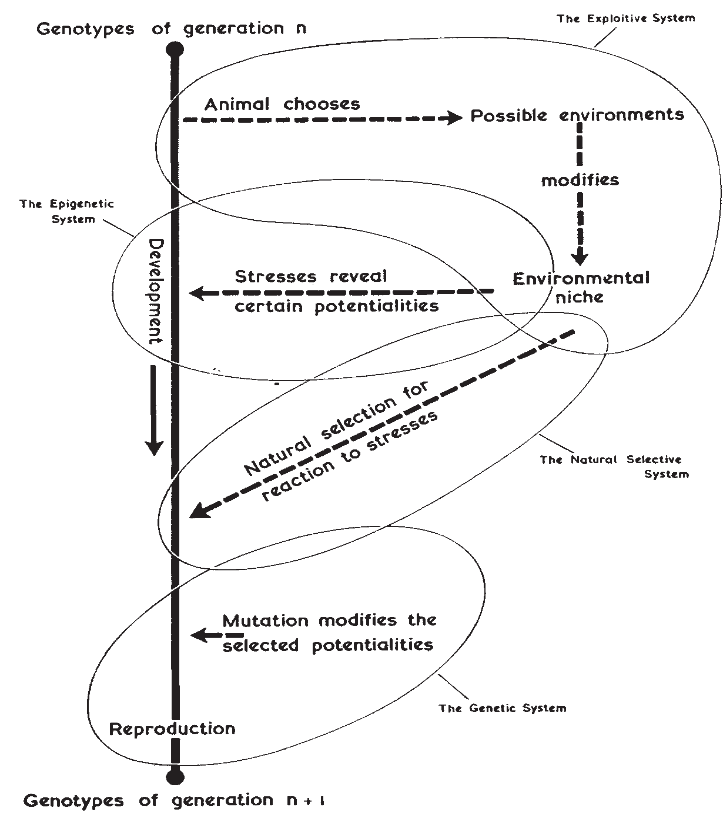


Fig. 1. The logical structure of the biological evolutionary system

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

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**.

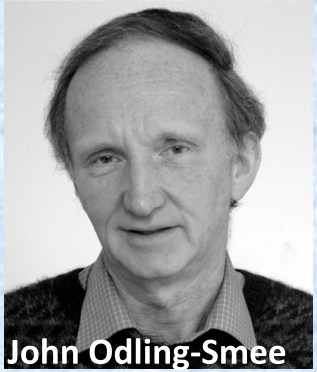
Waddington, 1959, Evolutionary Systems – Animal and Human. Nature

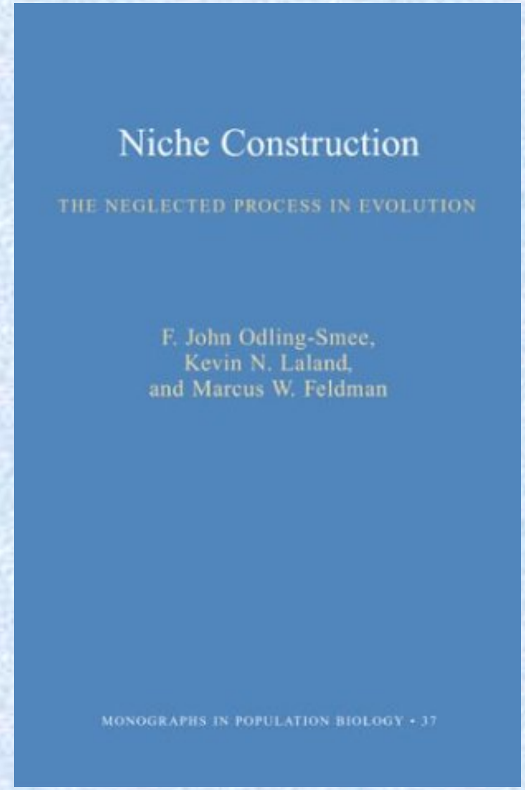
“The organism influences its own evolution, by being both the object of natural selection and the creator of the conditions of that selection.”

Richard Lewontin (Levins & Lewontin 1985)

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

George Williams (1992)





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)

We propose the following criteria to test for the presence of niche construction (Criteria 1 and 2) and determine when niche construction affects evolution (Criterion 3):

1) An organism (i.e., a candidate niche constructor) must significantly modify environmental conditions.

2) The organism-mediated environmental modifications must influence selection pressures on a recipient of niche construction.

3) There must be a detectable evolutionary response in a recipient of niche construction that is caused by the environmental modification of the niche constructor.

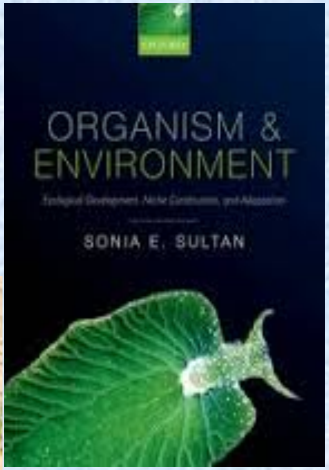
Matthews et al. 2014 *Ecological Monographs*







Constructing a mini oasis



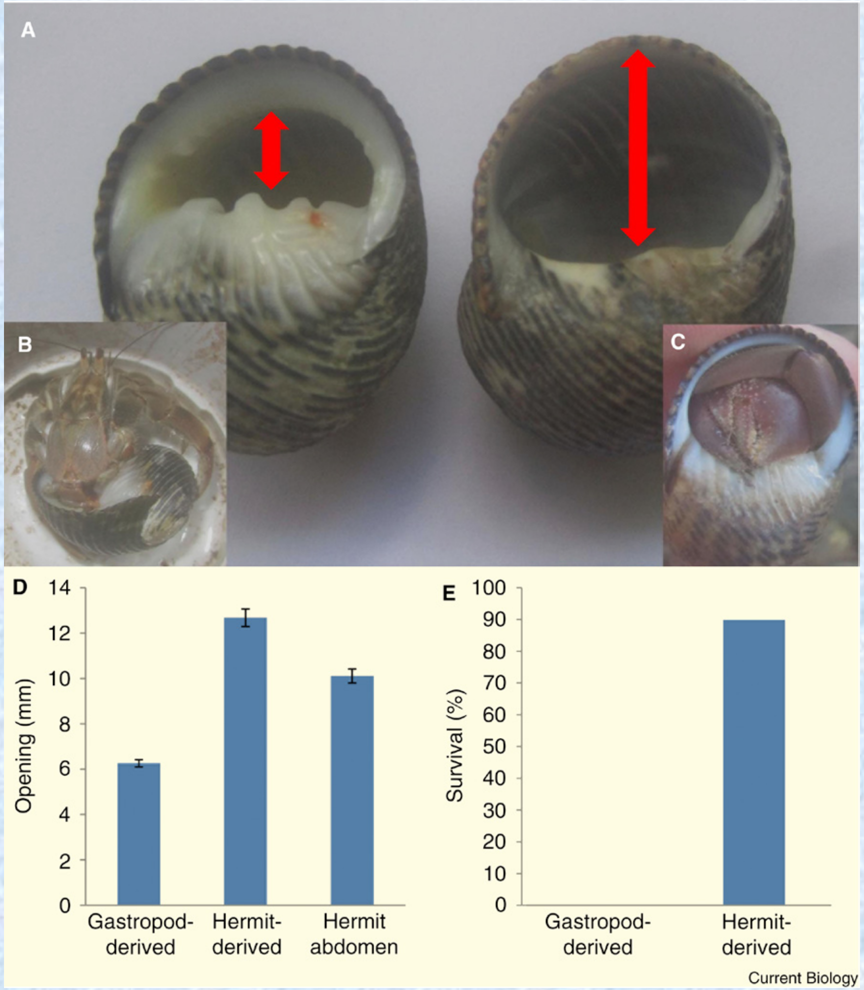
Self-irrigating plants, like the desert rhubarb (*Rheum palaestinum*) modify their environment to remove desiccation stress (Lev-Yadun et al., 2009).

Ecological inheritance

Beaver “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).

Niche construction drives social dependence in hermit crabs

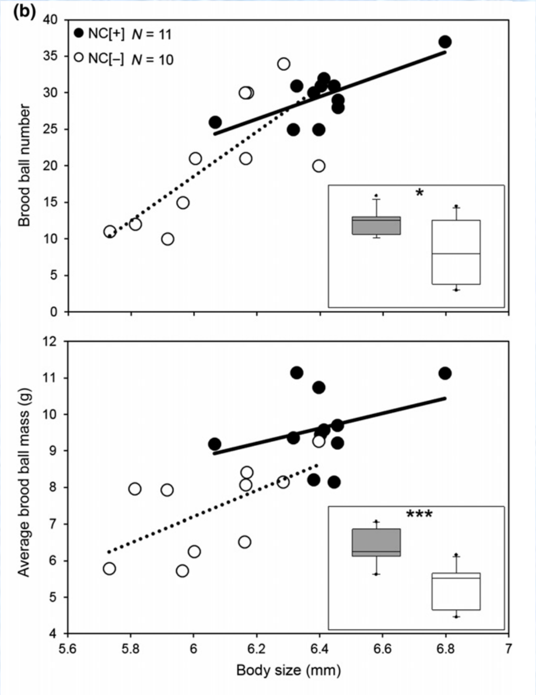


Coenobita compressus

Laidre ME 2012. Current Biology 22(20): 861-3

Developmental niche construction in dung beetles

Onthophagus spp.



Both maternal and larval niche construction strongly influence larval growth, fitness, sexual dimorphism and microbiome efficiency.

Schwab et al. 2016 *Am Nat*; Schwab et al., 2017 *Ecology Letters*

Contemporary theory that captures aspects 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*) Sexual selection
(*x*) Other approaches (e.g. the extended phenotype)

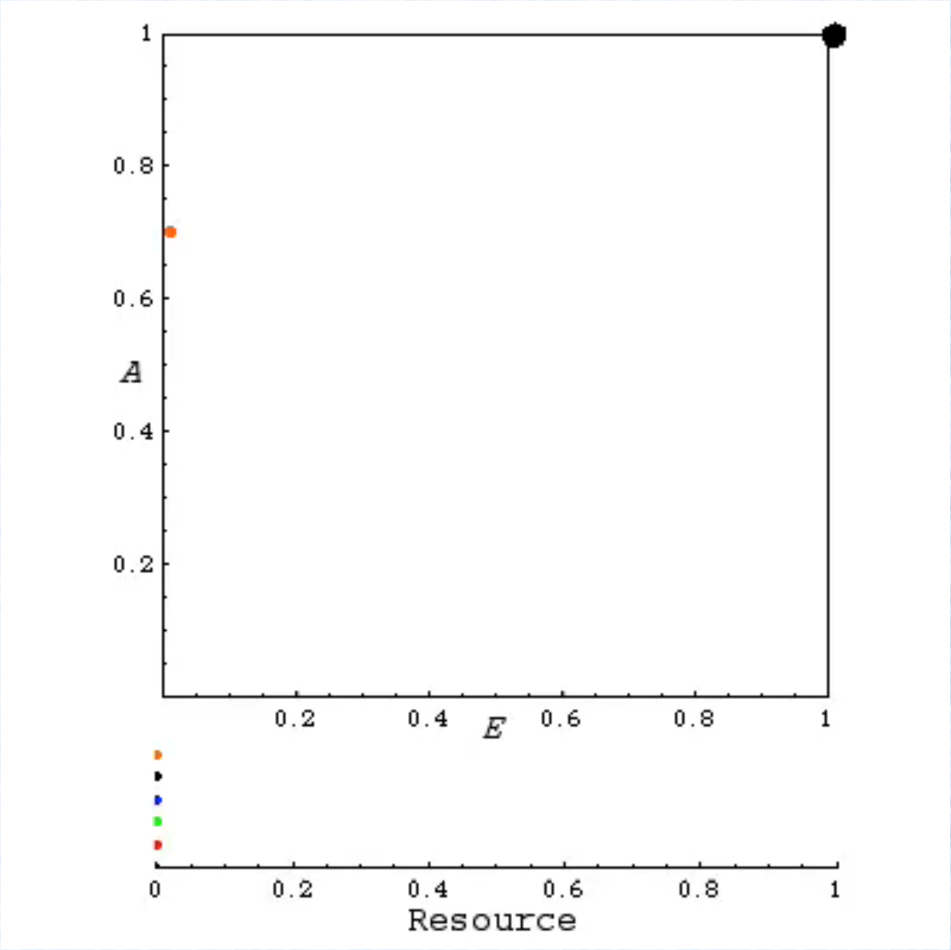
Reviewed in Odling-Smee, Laland & Feldman (2003)

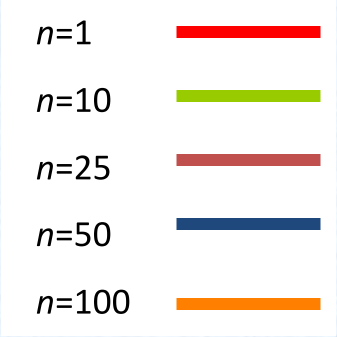
"Where NCT diverges from other frameworks … is in its explicit emphasis on environment-modifying abilities as sources of individual phenotypic variation, as an alternative route to adaptation and as an avenue for non-genetic inheritance in cases in which modified environments are passed on to subsequent generations"

Schwab, Casasa & Moczek (2017)

Modeling Niche Construction

Timelags in response to selection resulting from ecological inheritance





Laland KN *et al.* (1999) Proc. Natl. Acad. Sci. USA 96(18): 10242-7

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*

Opinion

Cell PRESS

Rethinking heredity, again

R. Bondurianksy

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Wales, Sydney, NSW, Australia

**The refutation of 'soft' inheritance and establishmen
Mendelian genetics as the exclusive model of heredi
widely portrayed as an iconic success story of scien
progress. Yet, we are witnessing a re-emergence
debate on the role of soft inheritance in heredity
evolution. I argue that this reversal reflects not only
weight of new evidence but also an important con
tual change. I show that the concept of soft inherita
rejected by 20th-century genetics differs fundament
from the current concept of 'nongenetic inheritar
Moreover, whereas it has long been assumed that
redity is mediated by a single, universal mechanism
pluralistic model of heredity is now emerging, based
a recognition of m
tance.**

A scientific revolu

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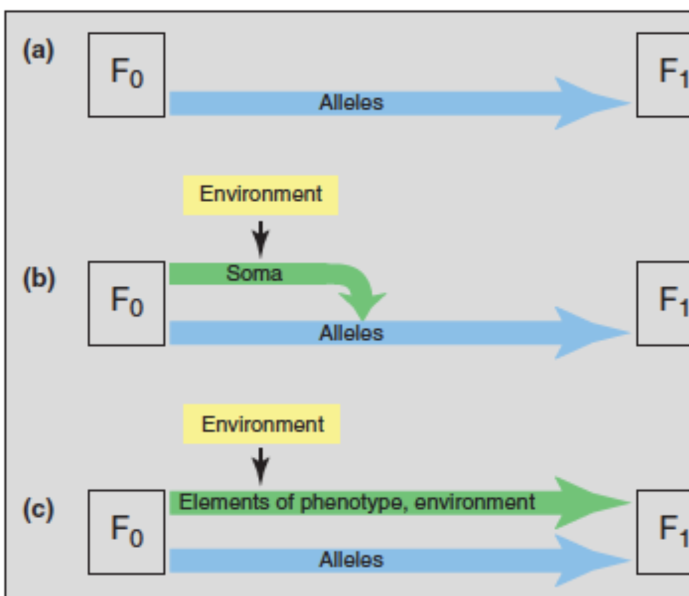
Beyond DNA: integrating inclusive inheritance into an extended theory of evolution

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

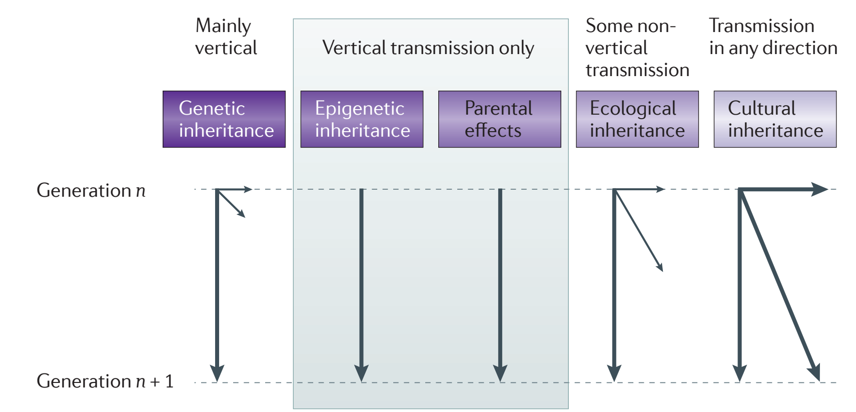
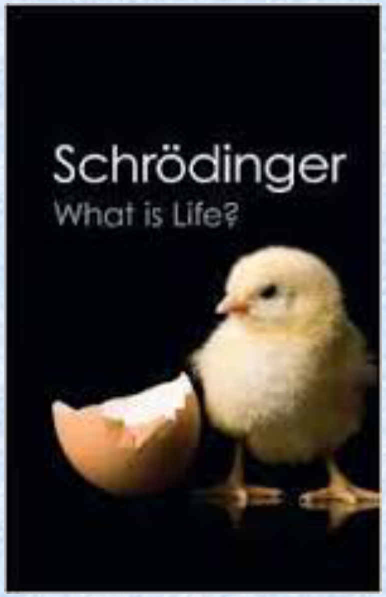


Figure 2 | **Main vectors of transmission for the various forms of information inheritance.** Vertical arrows represent lineages, and horizontal and oblique arrows

The niche construction literature

Why do we think niche construction is an evolutionary process?



Niche construction must be orderly and directed, since random niche construction would not support life (Schrodinger, 1944).

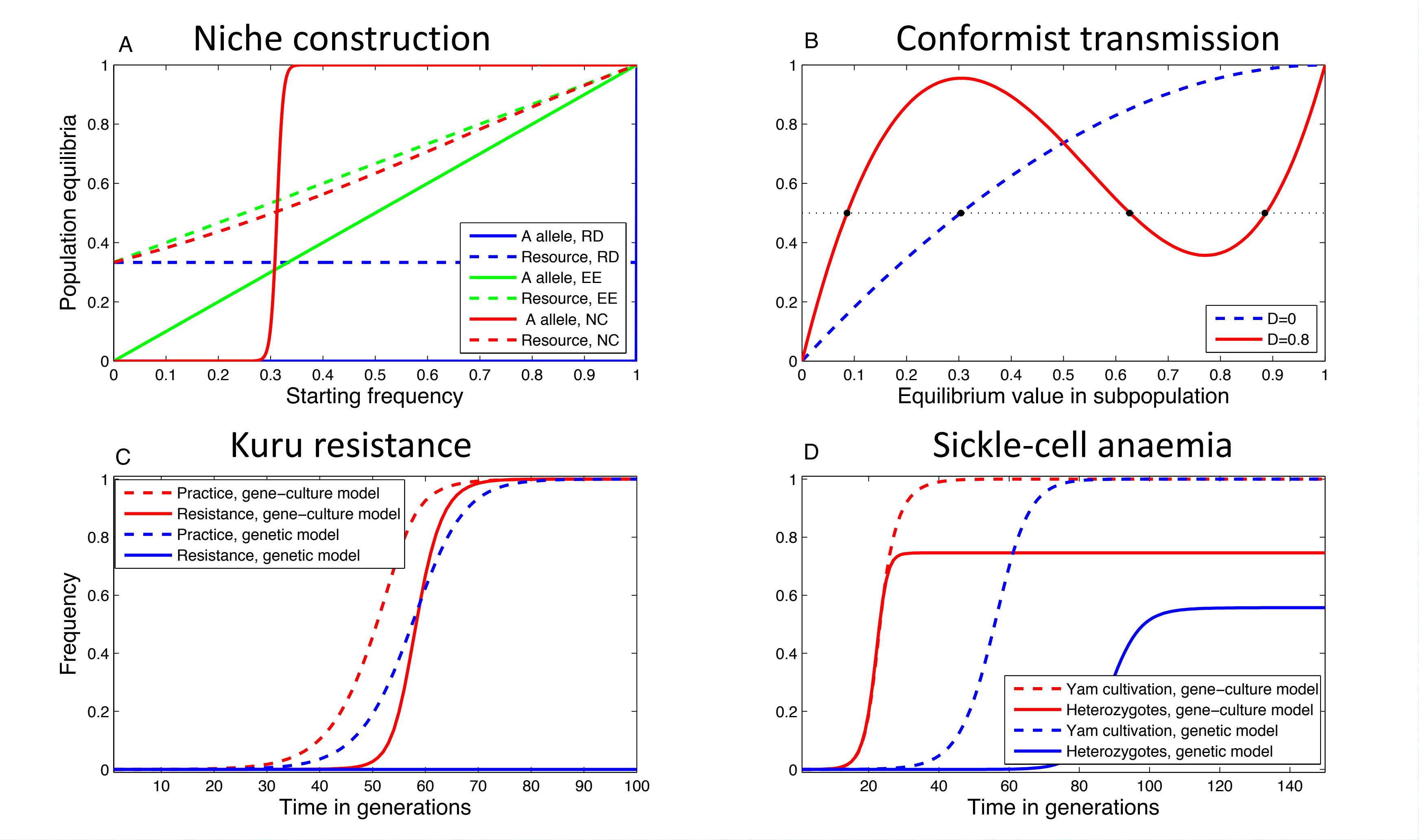
Niche construction generates environmental states that are coherent and integrated with the organism’s phenotype and its needs, and adaptive for the constructor, or its descendants.

Niche construction *is* an externally expressed developmental bias.

Do developmental bias, plasticity, extra-genetic inheritance and niche construction matter to human evolution?

Extra-genetic inheritance

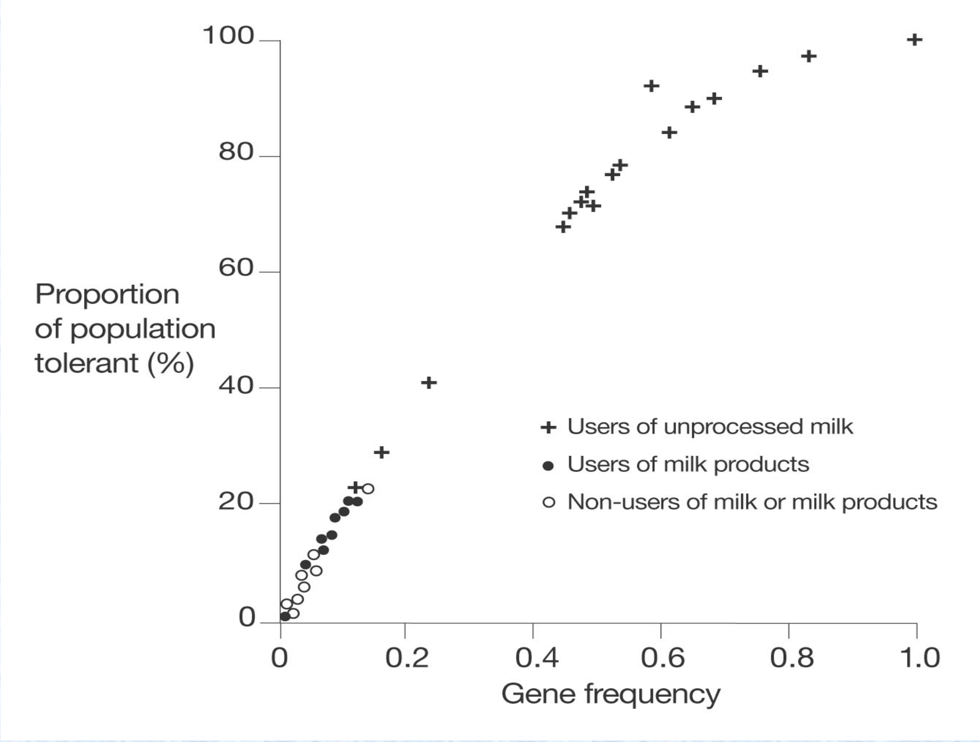
Culture frequently takes populations to new equilibria, affects dynamics, and influences how fitness is conceived and measured.



A. Laland et al. (1999); B. Boyd & Richerson (1985); C. Mead et al. (2009); D. Fogarty (2012)

Plasticity first evolution

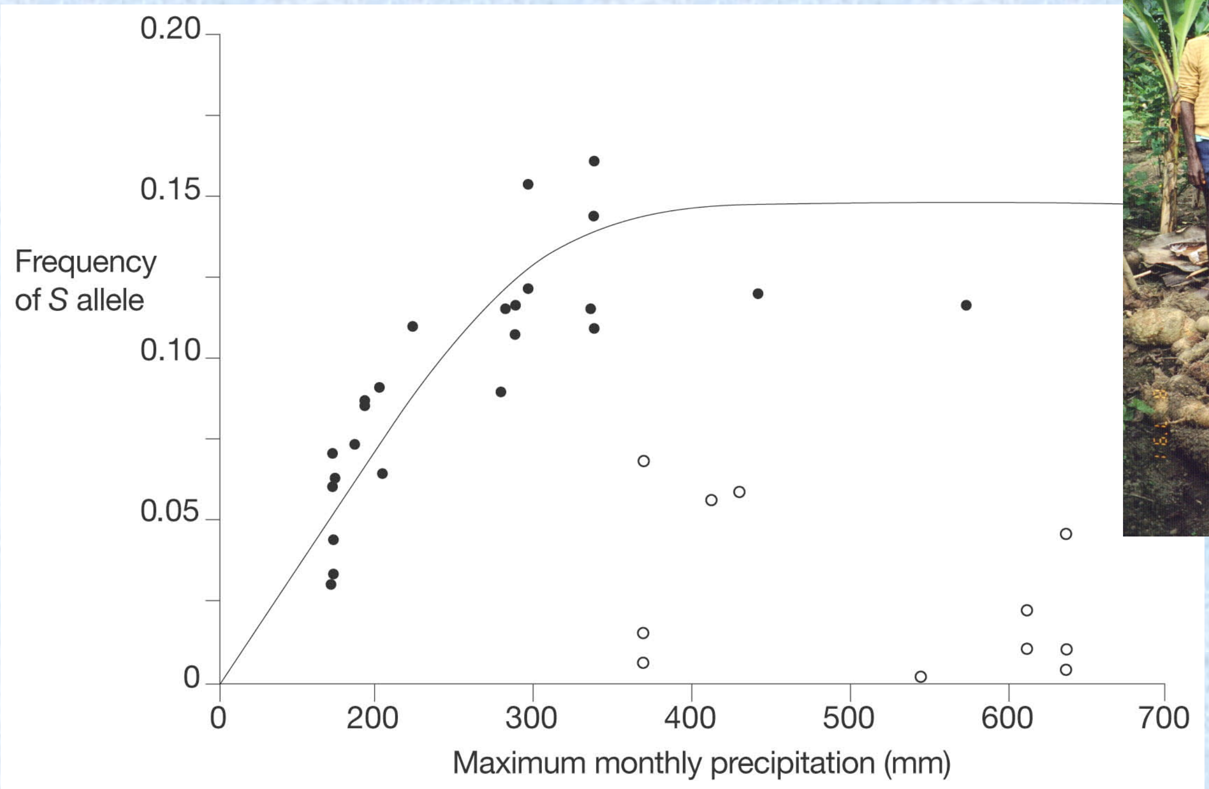
Comparative phylogenetic studies, ancient DNA, genotyping and archaeological data leave no doubt that dairy farming came first, and subsequently generated selection favoring adult lactose absorption.



The co-evolution of dairyfarming and lactose absorption in humans

(Ulijaszek & Strickland, 1993; Holden & Mace, 1997; Burger et al., 2007; Gerbault et al 2011)

Niche construction



The cultural niche-constructing practice of yam cultivation created an agricultural niche rife with malaria, which drove the selection of the sickle-cell allele in West African populations.

(Durham 1990; O'Brien & Laland, 2012)

Developmental Bias

Much of the variation in mammalian brain component size can be understood as aligned along a single dimension predicted by brain size, channeled by conserved features of neurogenesis.

In primates, variation in diverse measures of behavioral flexibility and cognitive performance are aligned along a single dimension (i.e. general intelligence) predicted by brain size.

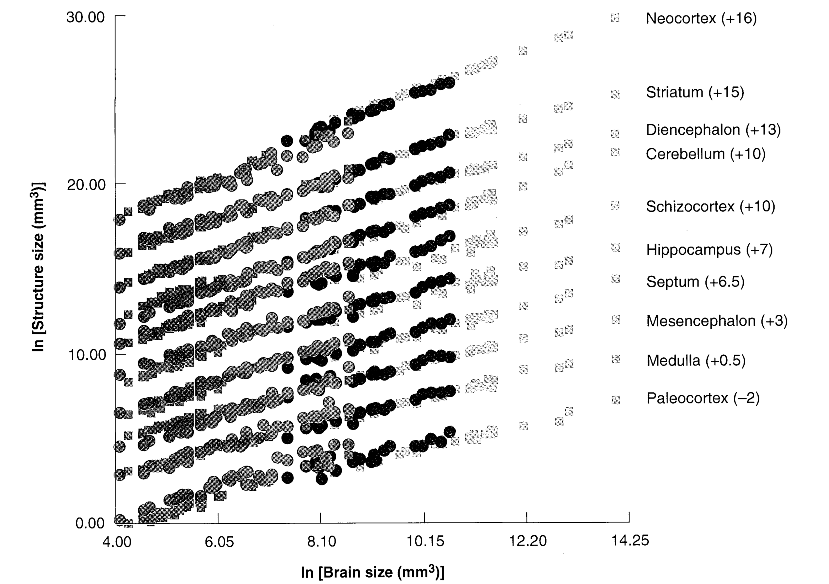
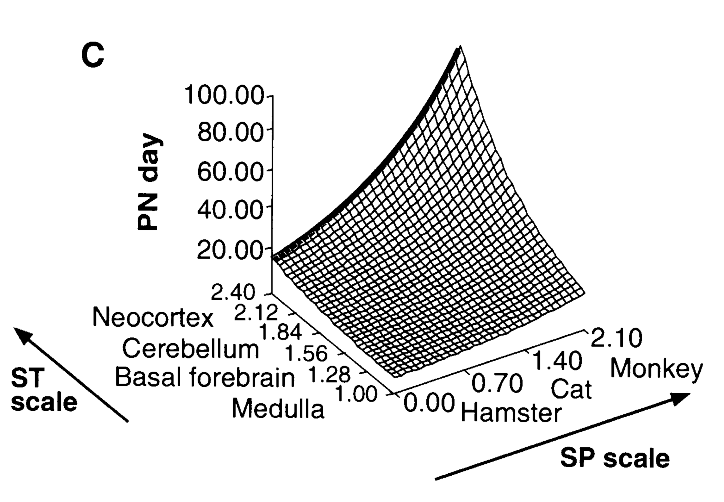


Fig. 1. Sizes of 10 measured brain subdivisions from 131 species plotted as a function of total brain size



(Finlay & Darlington, 1995; Reader & Laland, 2002; Reader et al 2011; Street et al 2017)

Do these processes operate outside of humans?

Culture is driving speciation and coevolution

Orca clans with different socially learned feeding habits have evolved morphological specializations

Reed warblers learn to recognize cuckoo parasites through attending to neighbours' mobbing, which selects for a cuckoo plumage polymorphisms that thwart host detection.

Even short-lived traditions can affect evolutionary dynamics

Mate choice copying in insects, birds and fishes influences sexual selection

Whitehead & Rendell 2015; Thorogood & Davies 2012; Gibson et al 1991; Kirkpatrick & Dugatkin 1994.

Novel adaptive variation

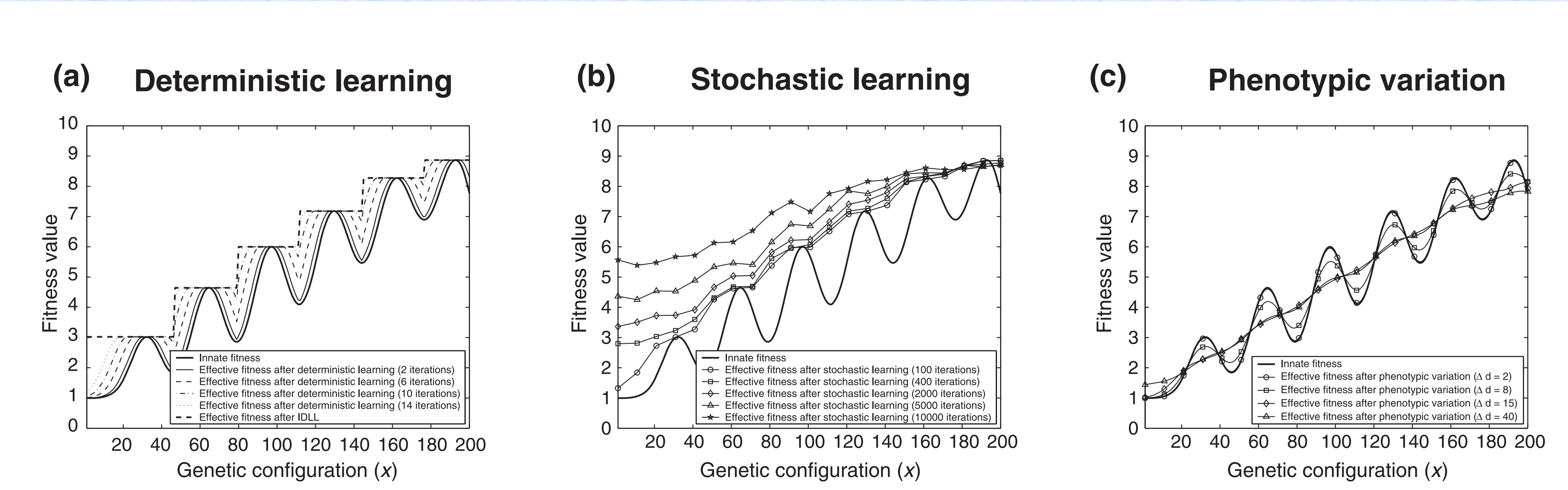
Unlike random mutations, learned innovations are typically functional and adaptive…

Copying is directed and strategic

…whilst adaptive learned information is far more likely to spread than maladaptive information. For instance, redwing blackbirds produce disgust displays on consuming toxins which leads to reduced copying.

Reader & Laland (2003) *Animal Innovation*. OUP; Mason, 1988; Galef 1996; Laland 2004;
Hoppitt & Laland (2013) *Social Learning. An introduction to Mechanism, Methods & Models.*

Learning (and other forms of plasticity)



In multi-peaked fitness landscapes, learning increases fitness, accelerates evolutionary rates, reduces time to reach global optima.

Stochastic learning performs better than deterministic learning, and even random phenotypic variation is beneficial.

Implication for plasticity-first evolution.

Borenstein et al. 2006 *J. Evol. Biol.*

Why do we disagree?

Researchers differ in how significant they regard developmental bias, developmental plasticity, extra-genetic inheritance and niche construction to be to evolution because…

1. … of how we conceptualise development
2. ...of how we think about causality

Laland et al. 2015; Uller & Helantera 2017

The Explanatory Gap

Ancestral selection → Determinate gene effects →| Explanatory Gap |→ Realized impacts of organisms on environments

From the outset (Lewontin 1982, 1983, 2000), the niche construction perspective has always emphasized a view of developmental processes as open and constructive, and … rejected the idea that organisms and their activities are fully specified by genetic programs.

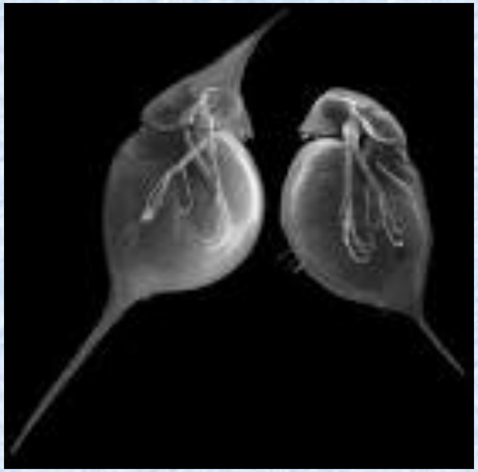
The Explanatory Gap

Ancestral selection → Determinate gene effects → [Developmental processes] → Realized impacts of organisms on environments

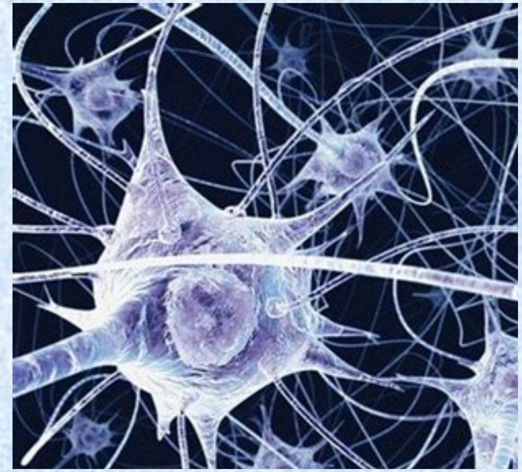
From the outset (Lewontin 1982, 1983, 2000), the niche construction perspective has always emphasized a view of developmental processes as open and constructive, and … rejected the idea that organisms and their activities are fully specified by genetic programs.

Niche construction theory seeks to plug the explanatory gap by treating niche construction as an evolutionary process.

Programmed development



Constructive development



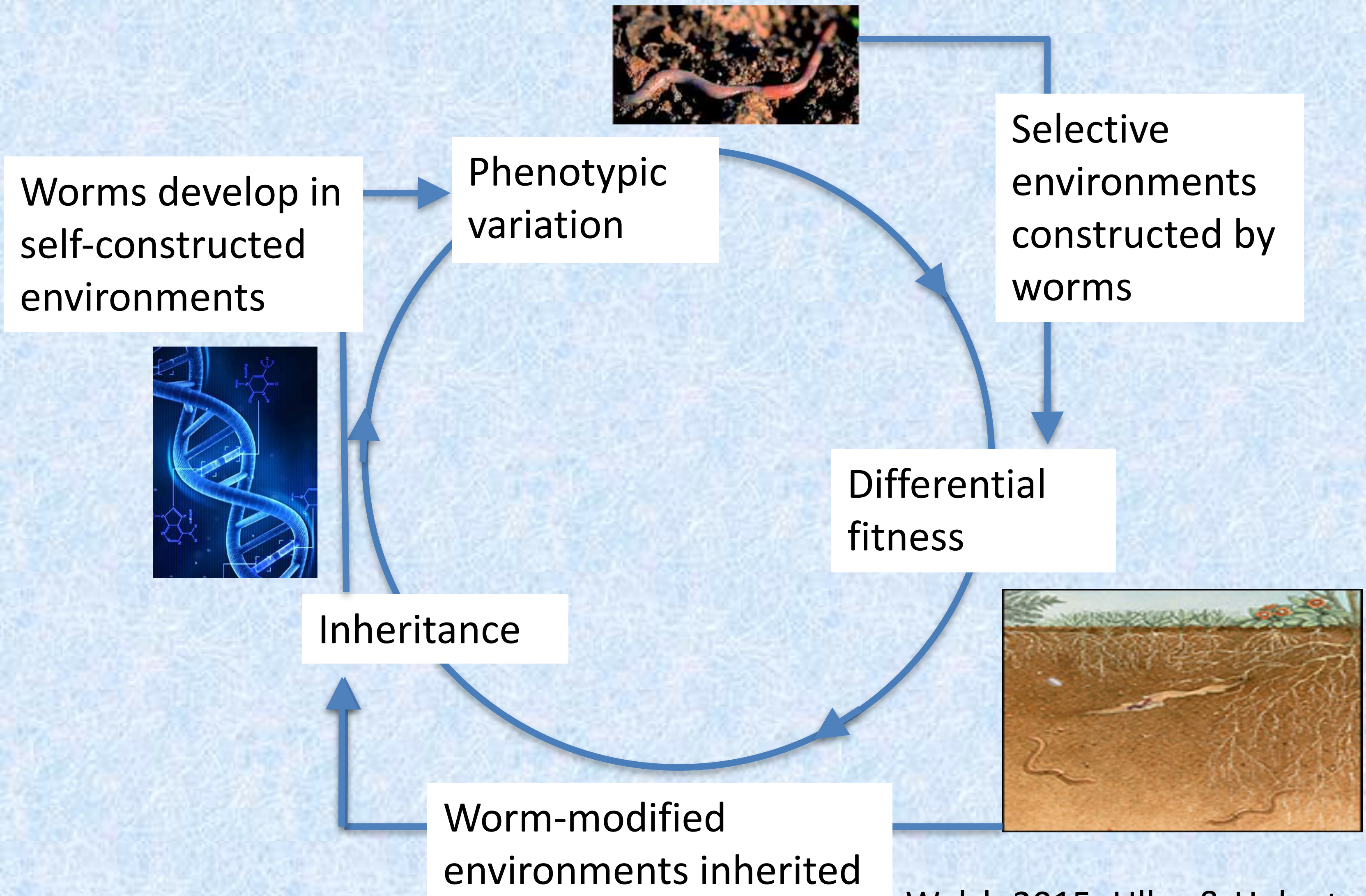
Exploratory processes:

Animal central-place foraging
Microtubule assembly
Vertebrate immune system
Animal learning
The nervous system
The vascular system
The tracheal system

Randomness of exploration

Gerhart & Kirschner, 1997 *Cells, Embryos and Evolution*

Are Evolutionary Processes are Causality Independent or Causally Intertwined?



Walsh 2015; Uller & Helantera 2017

Conclusions

1. Research over the last three decades has established that niche construction is ubiquitous in nature, and that it has important ecological and evolutionary consequences. Controversy nonetheless remains regarding whether niche construction should be recognized as an evolutionary process.

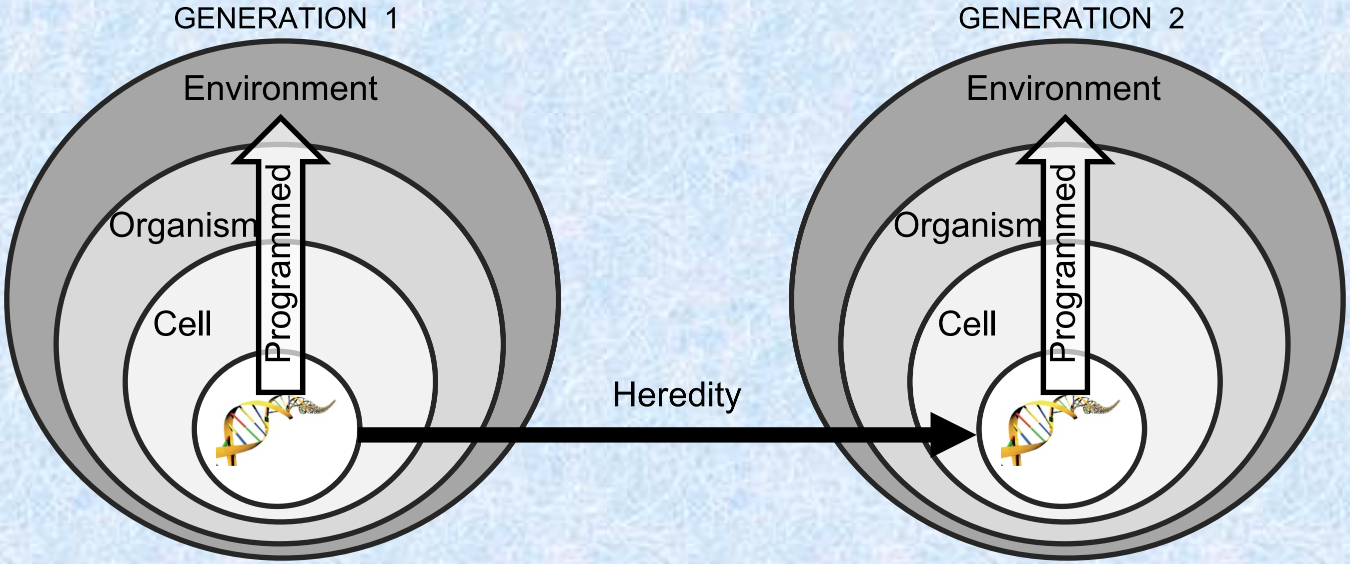
2. Recent research into human evolution suggests that extra-genetic inheritance, developmental bias, plasticity and niche construction may have been of central importance. Similar processes operate in other taxa.

3. Disagreements over the evolutionary significance of extra-genetic inheritance, developmental bias, plasticity and niche construction may in part reflect differing views of development and causation.

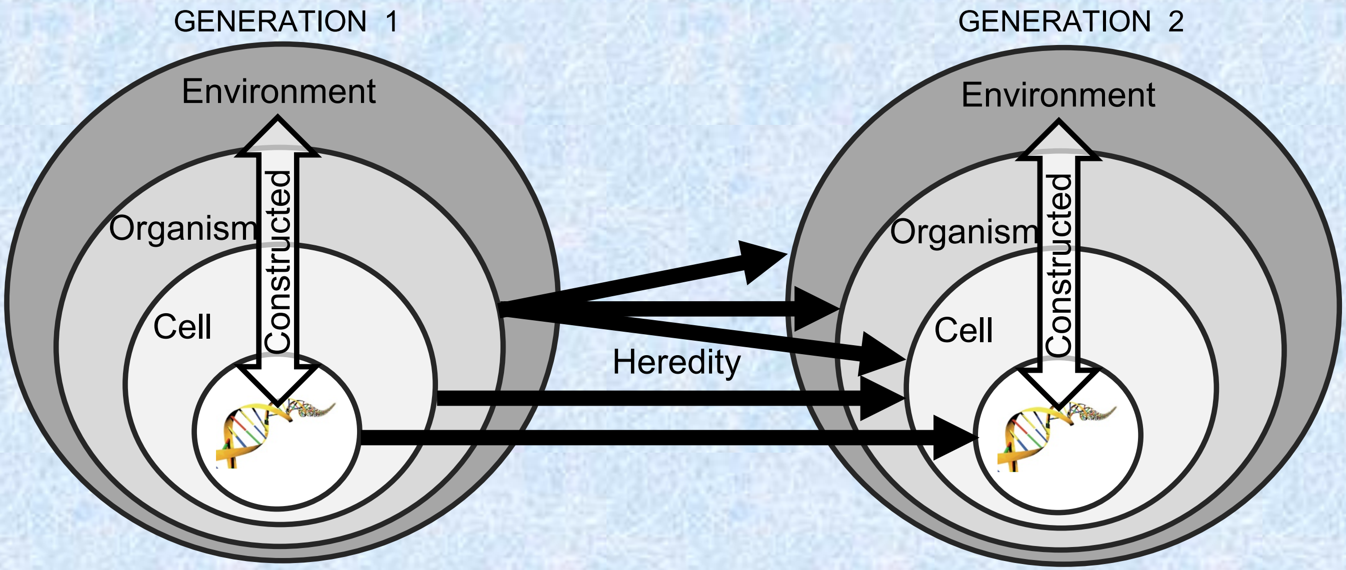
Why do we disagree?

Two views of development

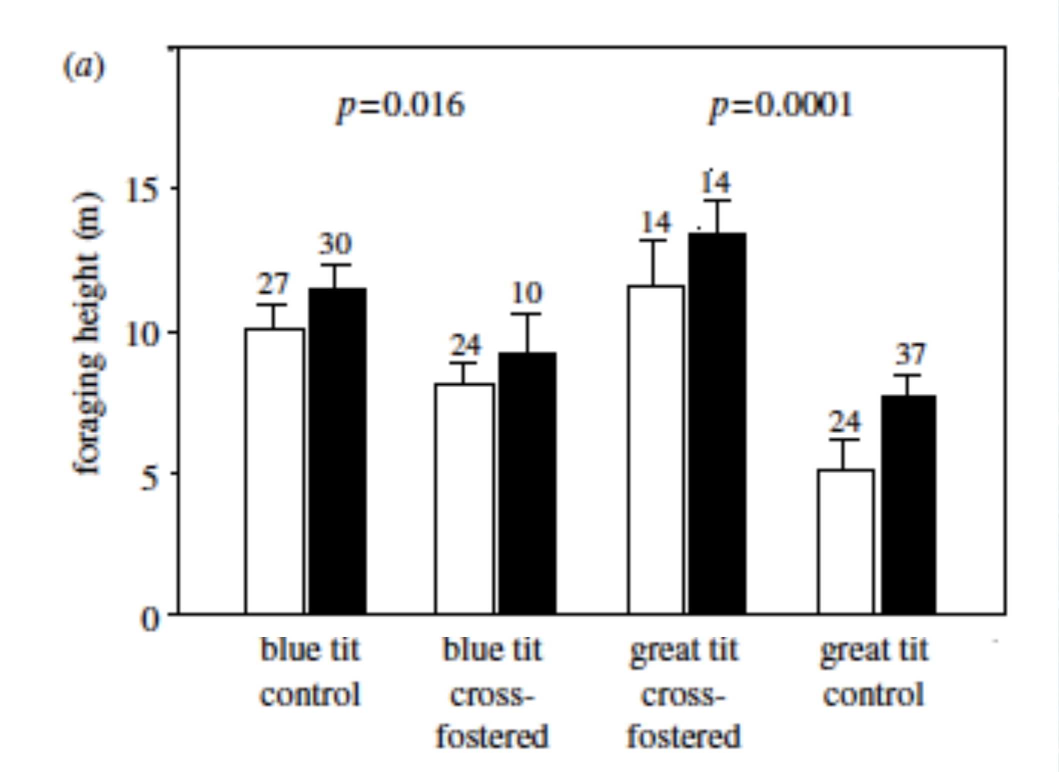
a. Programmed development



b. Constructive development



Learning the ecological niche



Slagsvold & Weibe (2007, 2011)

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 and accounts for patterns of taxonomic diversity.

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, hence not a source of phenotypic novelty.

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. Plasticity is a major source of developmental bias.

A traditional interpretation

Transmission genetics considered explanatorily sufficient for the evolution of adaptations.

Extra-genetic inheritance treated as a special case (e.g. cultural inheritance), unstable or under genetic control (e.g. epigenetic inheritance).

An alternative interpretation

Heredity defined to include all causal mechanisms by which offspring come to resemble their parents.

Phenotypes are not (solely) inherited, they are part reconstructed in development.

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.

Socially learned migration routes in birds

Among migrating whooping cranes more experienced birds transmit route knowledge to less experienced individuals.

Mueller et al., 2013 *Science*

Socially learned fears

Rhesus monkeys can be conditioned to acquire a fear of real and toy snakes (but not flowers) through observing fearful conspecifics. But…

Stephenson 1967; Cook et al., 1987; Mineka et al., 1988

Socially learned fears

Rhesus monkeys can be conditioned to acquire a fear of real and toy snakes (but not flowers) through observing fearful conspecifics. But they can be socially conditioned to fear kitchen utensils.

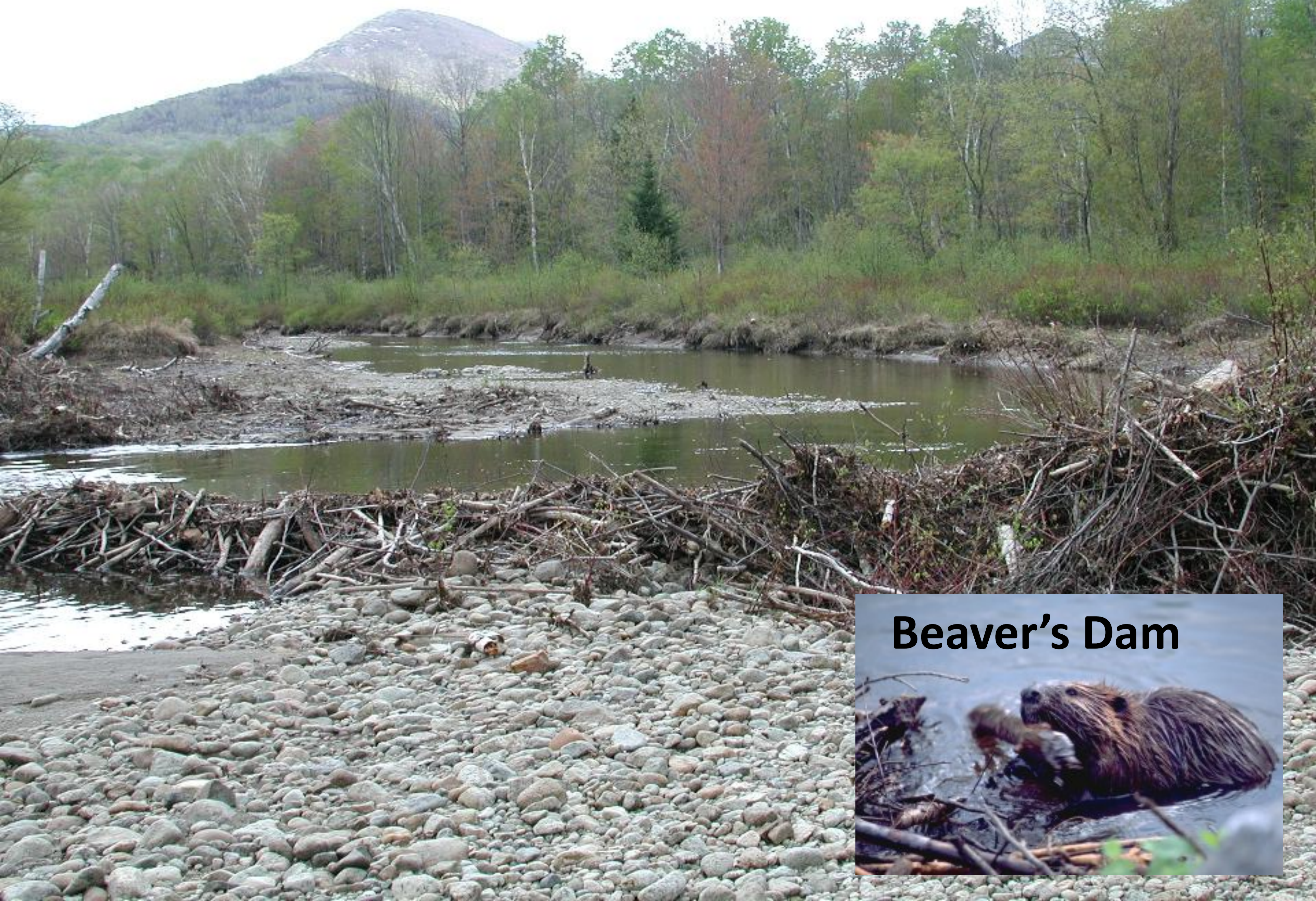
Stephenson 1967; Cook et al., 1987; Mineka et al., 1988

Socially learned fears

Blackbirds learn to recognize predators through social transmission (mobbing behaviour) but can also be conditioned to acquire a fear of arbitrary objects, such as plastic bottles.

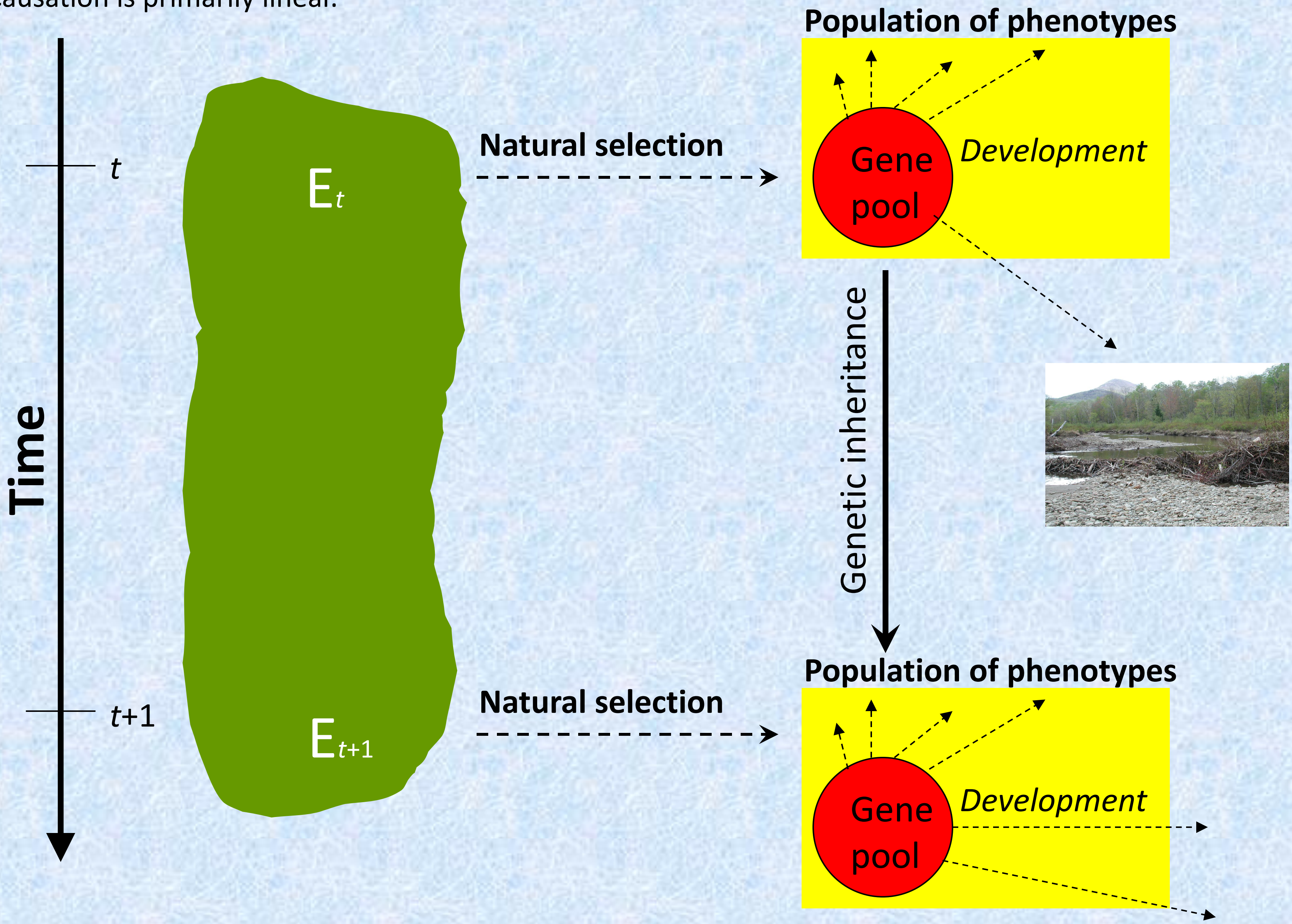
Vieth et al., 1980; Curio, 1988

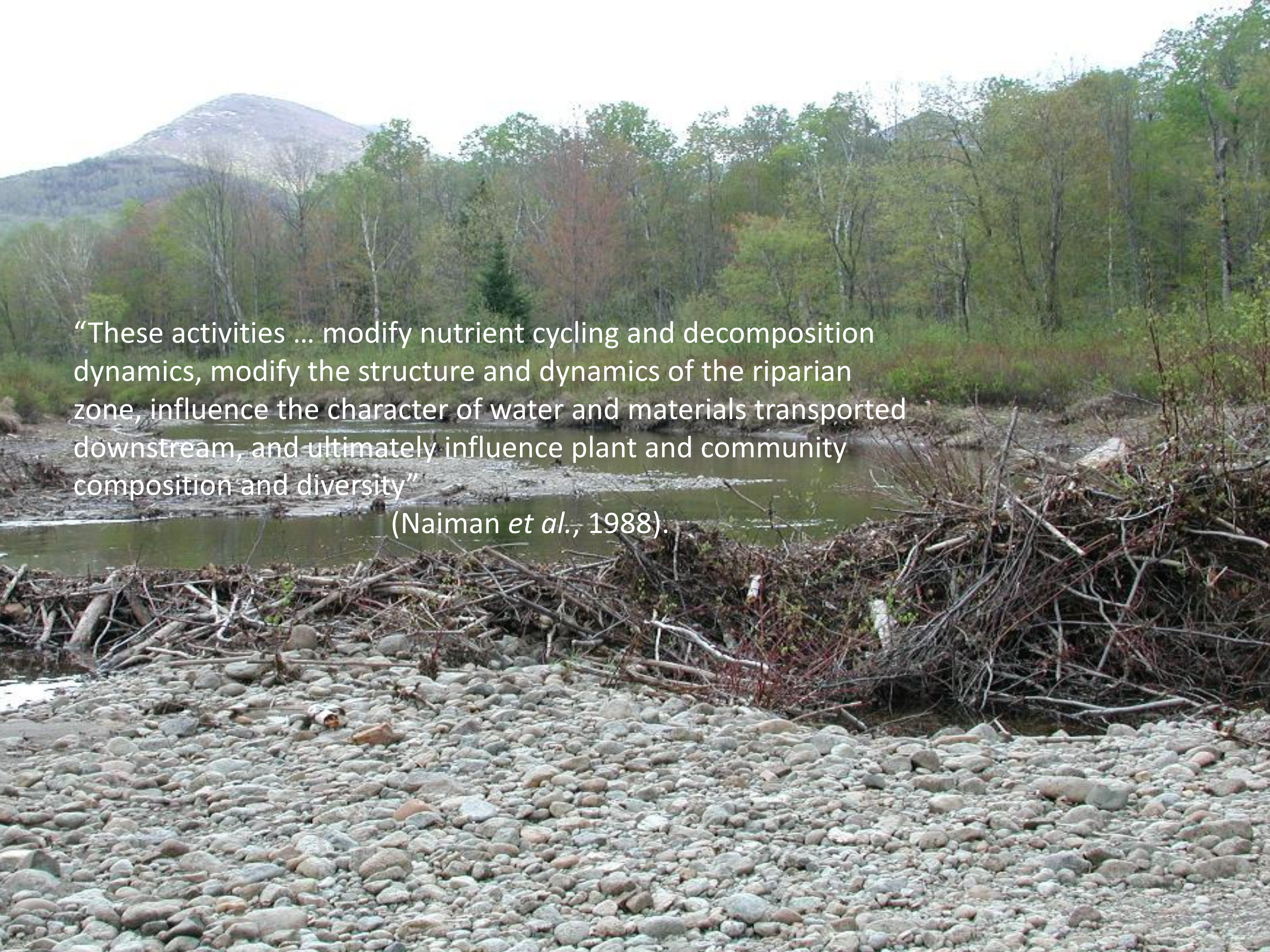
Niche Construction



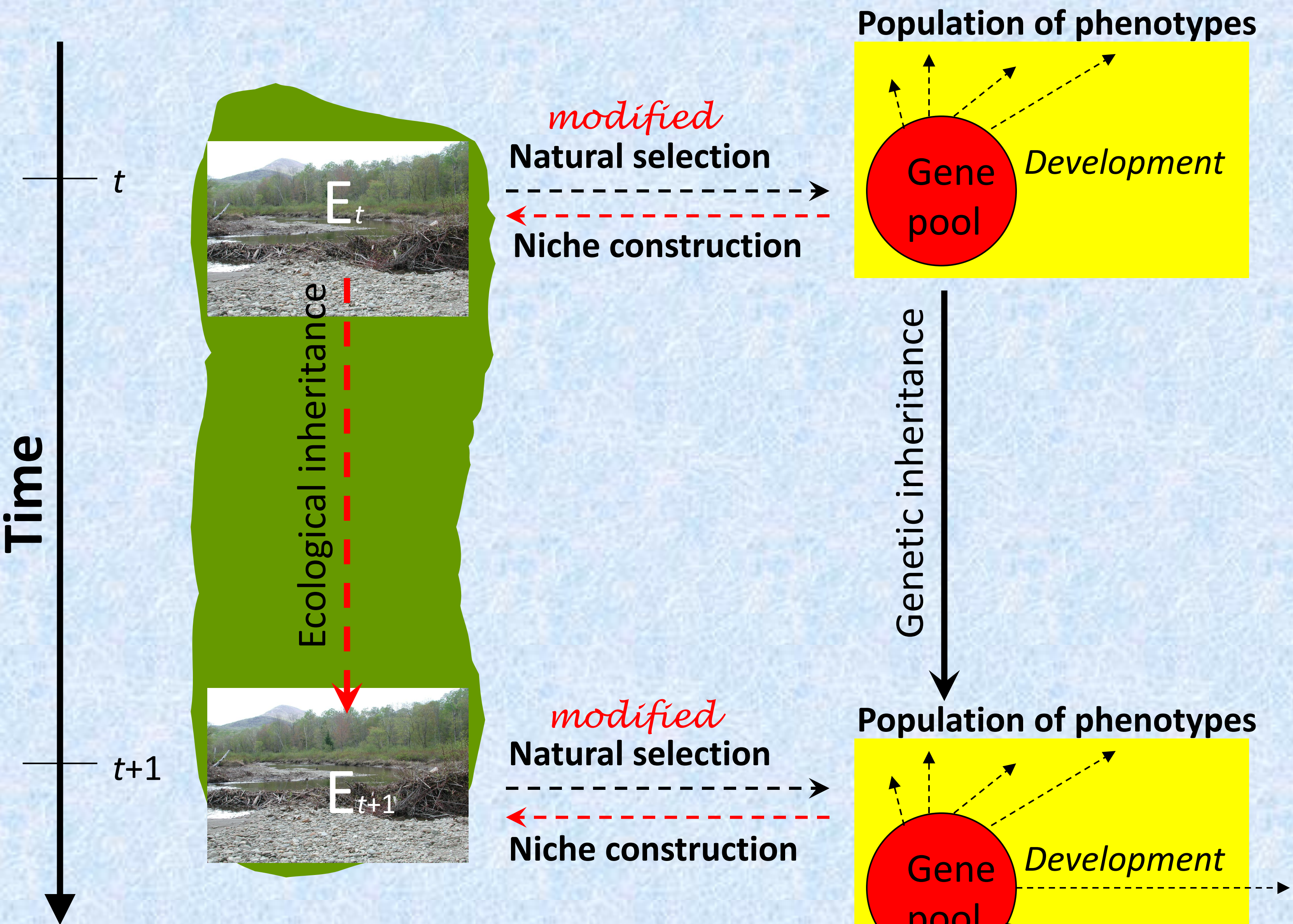
The extended phenotype perspective

Causation is primarily linear.



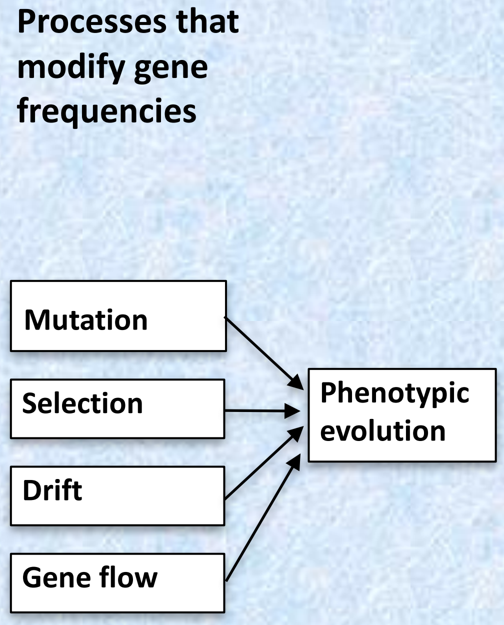

"These activities … modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and community composition and diversity"
(Naiman *et al.*, 1988).

The niche-construction perspective



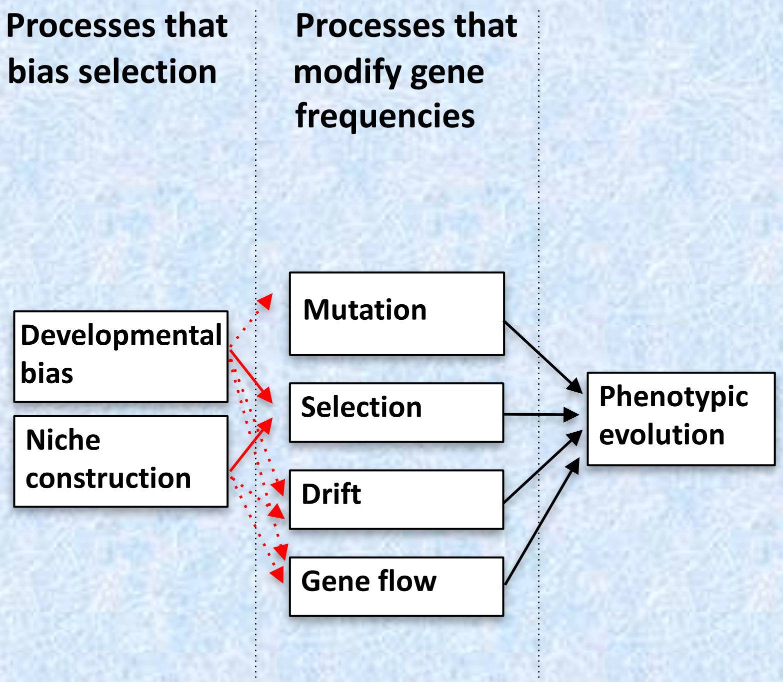
	A Traditional Interpretation	Extended Evolutionary Synthesis
Developmental bias	Bias in phenotypic variation treated as constraint. Explains the absence of evolution or adaptation.	Bias in phenotypic variation considered an evolutionary cause or process. Explains the existence of evolution and adaptation.
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.
Inclusive Inheritance	Transmission genetics considered explanatorily sufficient for the evolution of adaptations. Extra-genetic inheritance treated as a special case (e.g. cultural inheritance), or unstable / under genetic control (e.g. epigenetic inheritance).	Heredity defined to include all causal mechanisms by which offspring come to resemble their parents. Phenotypes are not solely inherited, but are partly reconstructed in development.
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.

Widely recognized evolutionary processes



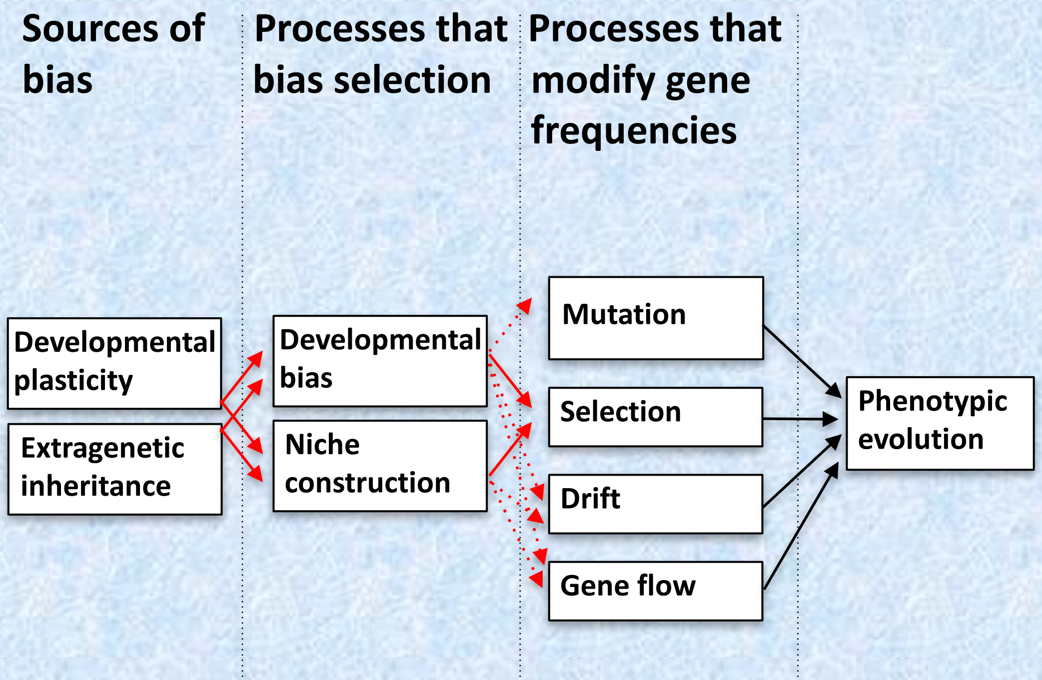
Laland KN et al., 2014. Nature; Laland et al., 2015 Proc. R. Soc. B

A broader conception of evolutionary causation



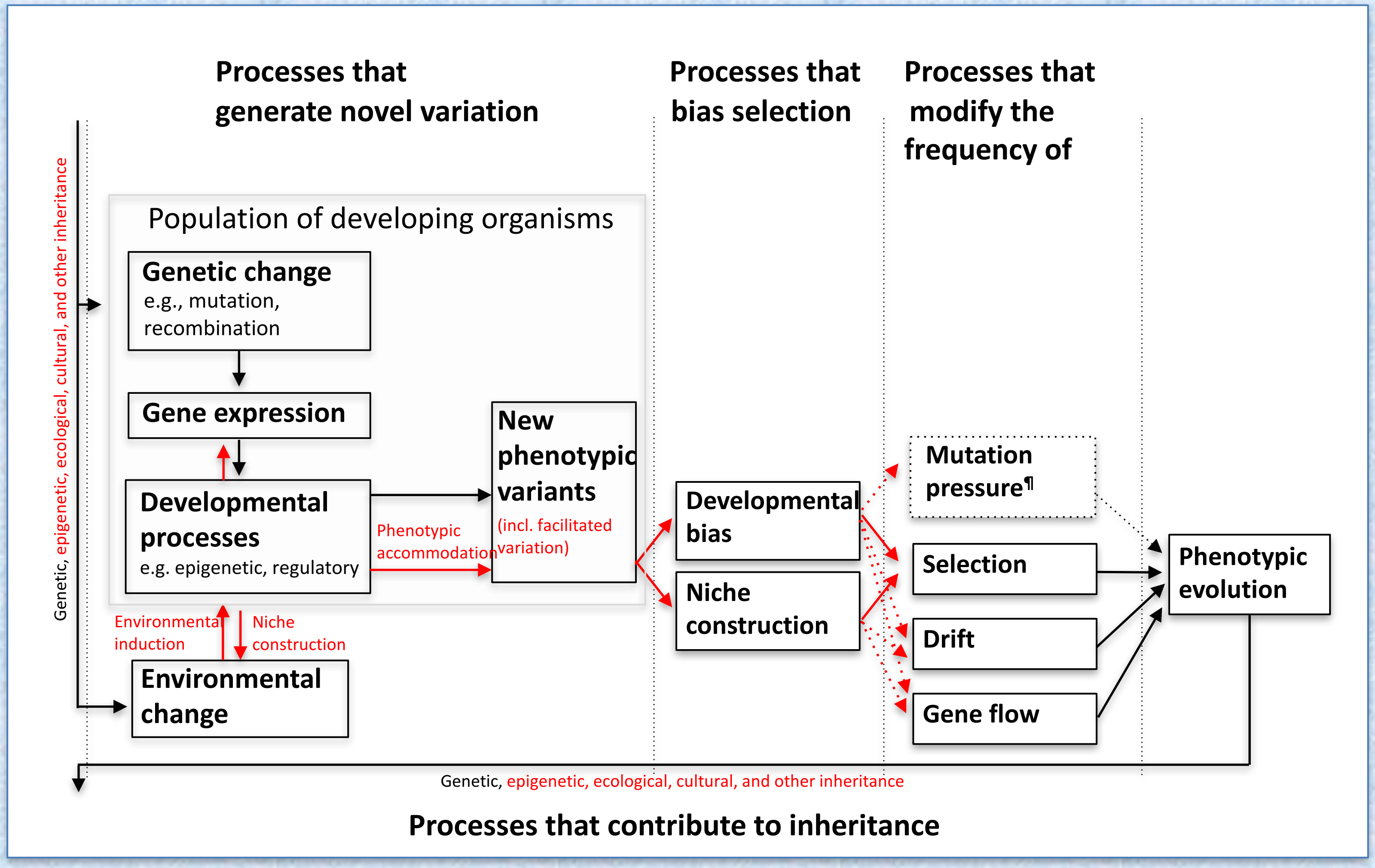
Laland KN et al., 2014. Nature; Laland et al., 2015 Proc. R. Soc. B

A broader conception of evolutionary causation

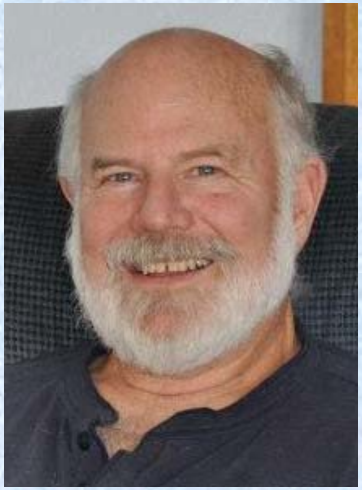


Laland KN et al., 2014. Nature; Laland et al., 2015 Proc. R. Soc. B

The structure of the EES



Laland KN et al., 2014. Nature; Laland et al., 2015 Proc. R. Soc. B



"To synthesize, we need diverse perspectives and bridges between them."

(Arnold, 2014)

The EES potentially opens up some novel lines of inquiry:

- *Documenting the extent of developmental bias and niche construction.*
- *Determining the role of plasticity in evolutionary innovation.*
- *Incorporating constructive development into formal evolutionary models.*
- *Documenting extent of constructive development.*

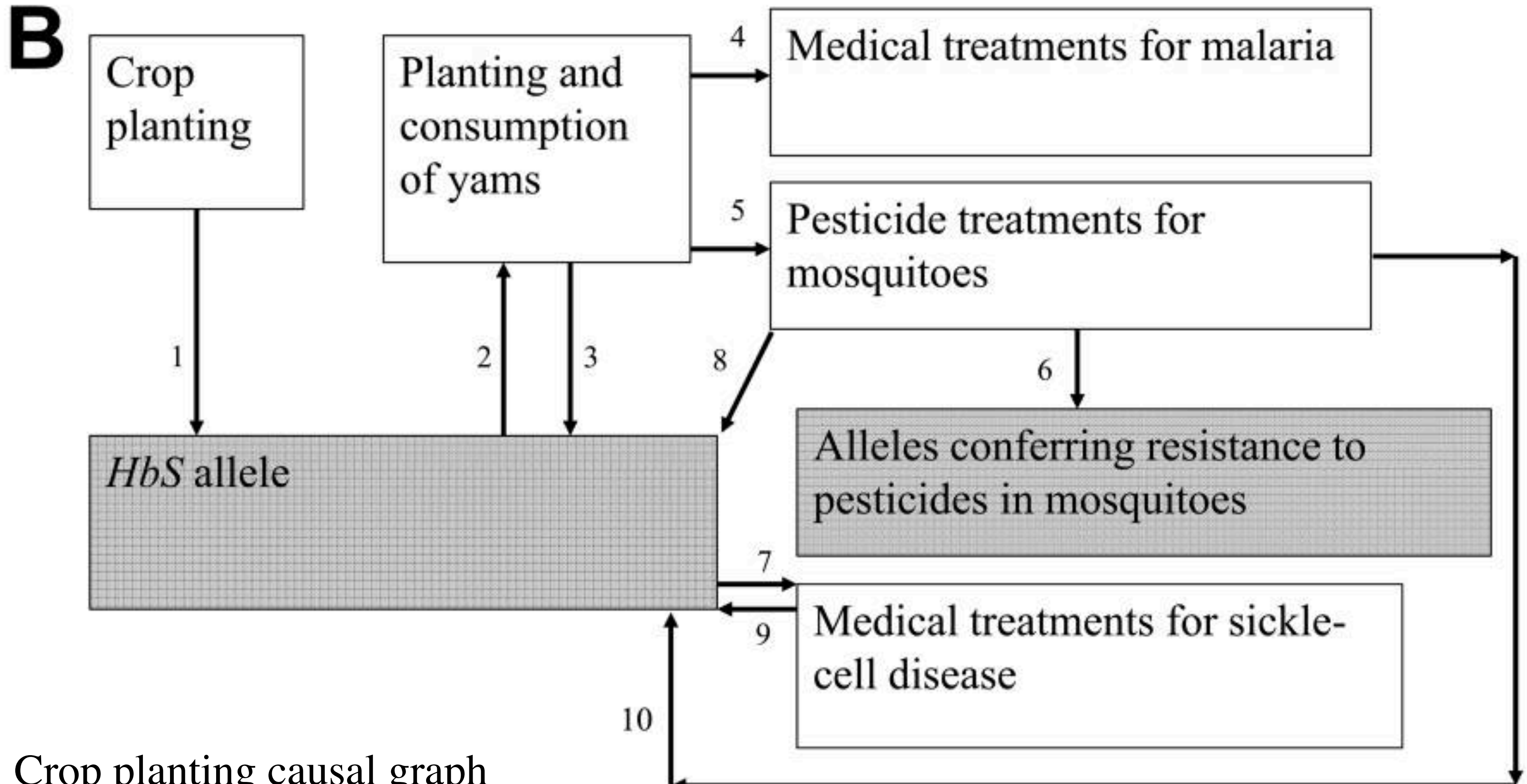
Other findings take on new significance in the EES, for instance:

- *Multi-level selection* - selection can operate on all forms of heritable variation

- *Genome evolution* - horizontal gene transfer is part of broader suite of such phenomena

  - genome change is an active cell-mediated physiological process fits with the EES's treatment of plasticity.

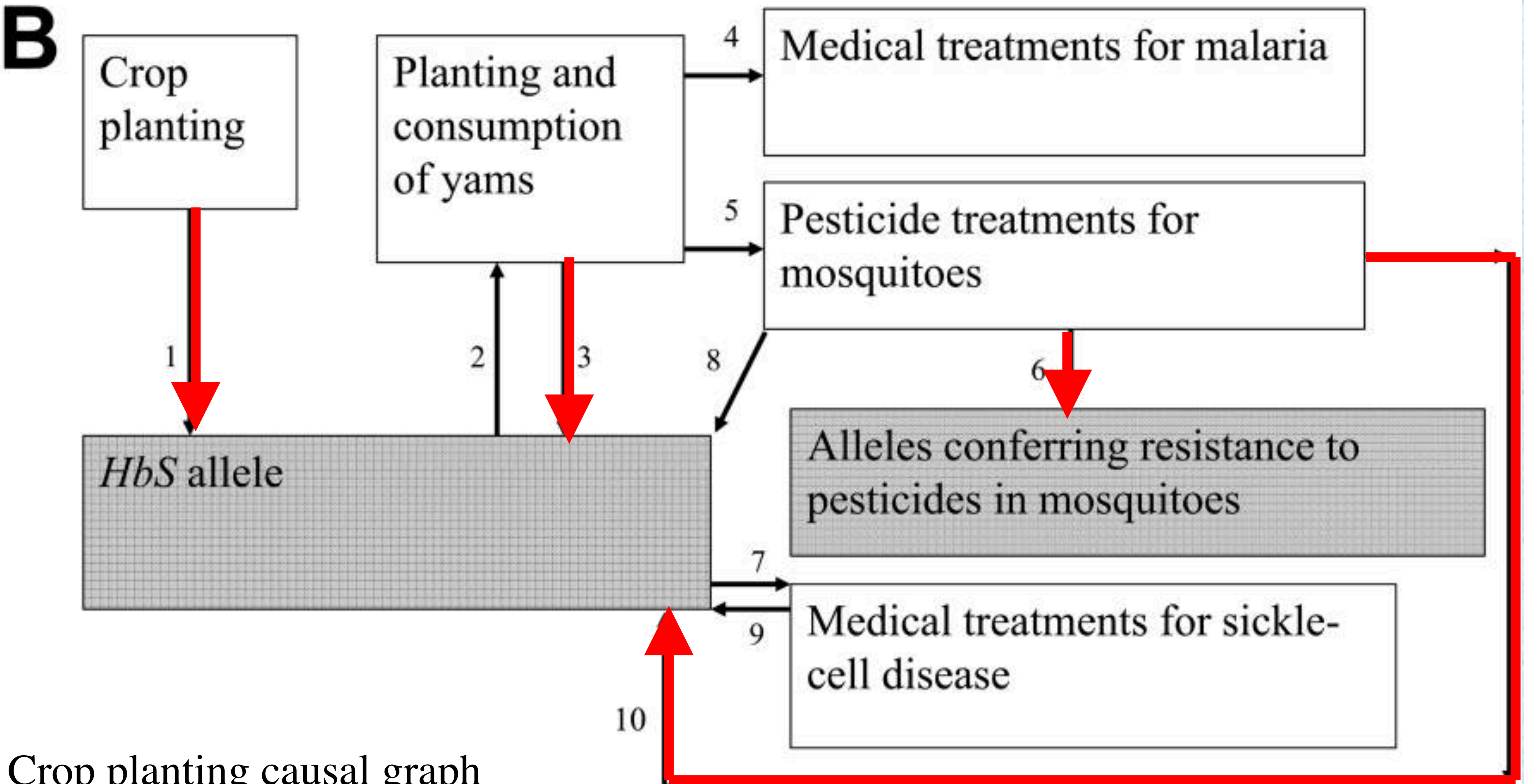
'There are causal arrows leading from genes to body. But there is no causal arrow leading from body to genes.' Dawkins (1982)



Crop planting causal graph

O'Brien M & Laland KN 2012 *Current Anthropology* 53: 434-70

'There are causal arrows leading from genes to body. But there is no causal arrow leading from body to genes.' Dawkins (1982)



Crop planting causal graph

O'Brien M & Laland KN 2012 *Current Anthropology* 53: 434-70

“Laland … quotes me as saying

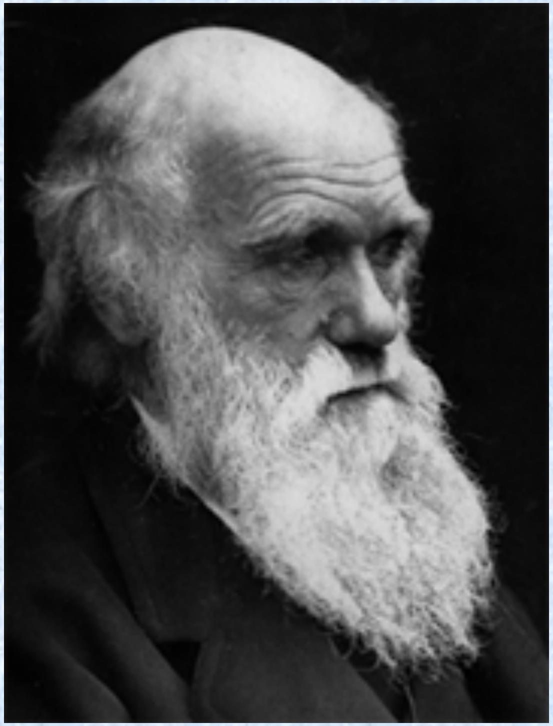
> There are causal arrows leading from genes to body. But there is no causal arrow leading from body to genes.

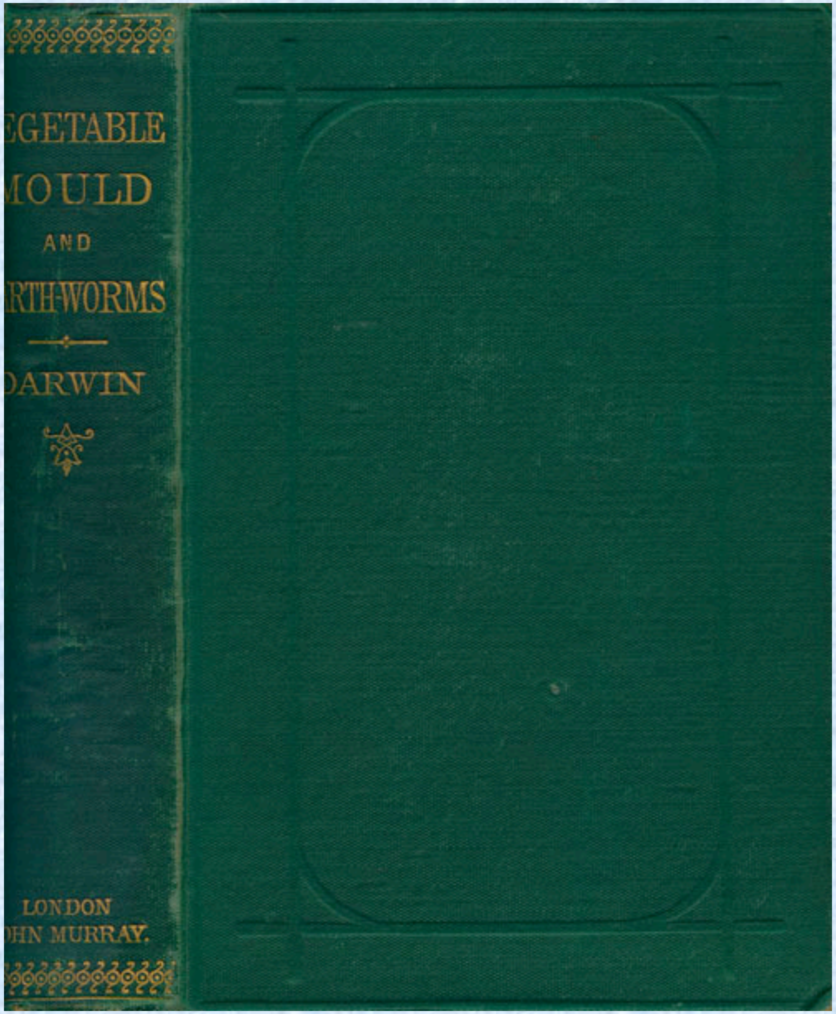
Laland, who disagrees, generously wants to absolve me from responsibility for this, saying that he is quoting out of context. But I am happy to stand by it. ‘Cyclical causation’ leaves me cold. … Attempts to argue for a reverse arrow recur through the history of biology, and always fail except in unimportant special-pleading senses.”

Dawkins (2004)

EES-style thinking has already contributed constructively to several research questions, including:

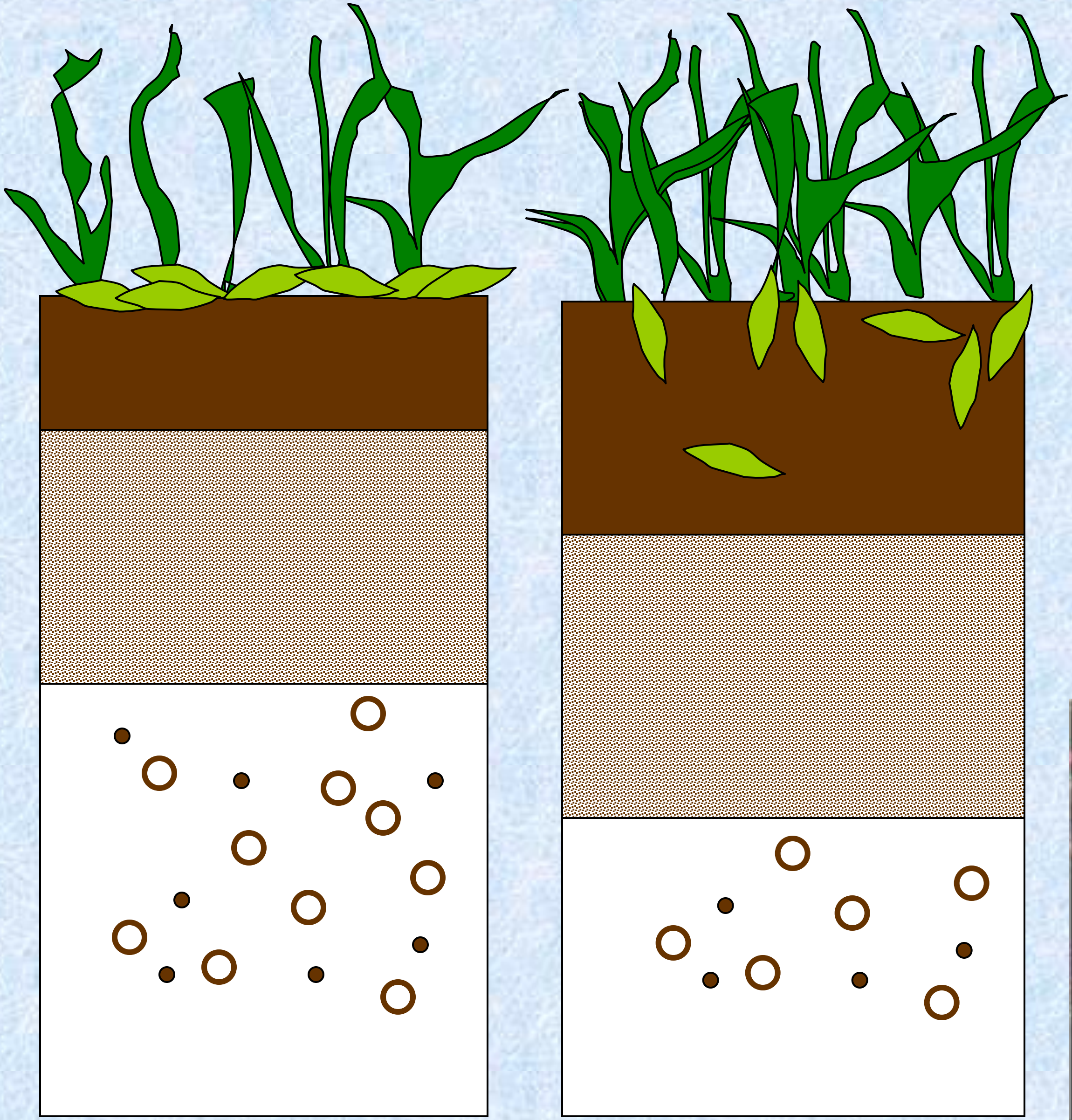
- *How do complex novel traits originate?*
- *How does inclusive inheritance affect the evolutionary process?*
- *How do macroevolutionary patterns arise?*





Darwin (1881) *On the formation of vegetable mould through the action of worms*

Earthworm niche construction



Without earthworms **With earthworms**

Enhanced plant yield

Less surface litter

More topsoil

More organic carbon, nitrogen and polysaccharides

Enhanced porosity, aeration and drainage

Increased invertebrate abundance and diversity

"Earthworms have no business living where they do, because they are physiologically quite unsuited for terrestrial life"

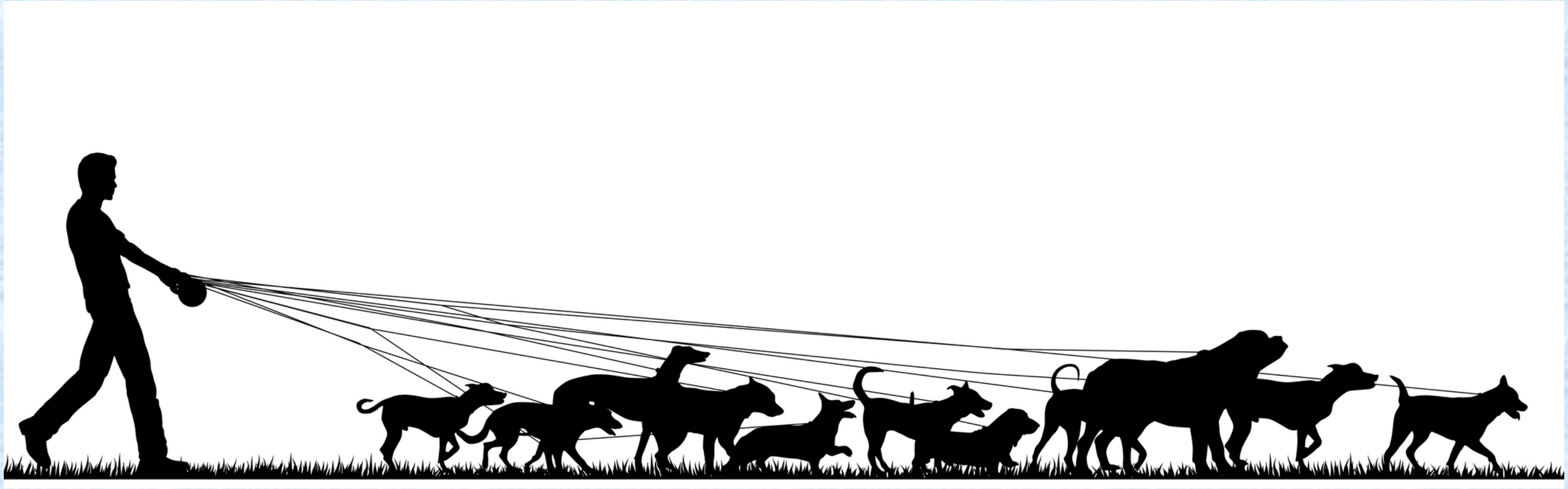
Table 7.1 **Physiological characteristics of animals living in marine, freshwater, and terrestrial habitats compared with those of the earthworm.**

	Animals' habitat			
Physiological activity	Freshwater	Marine	Terrestrial	Earthworm
Salt flux				
Diffusion flux *(TFF)*	−	+	∅	−
Filtration flux *(PF)*	−	− −	−	− −
Reabsorption flux *(PF)*	+++	+	+	+++
Water flux				
Osmotic flux *(TFF)*	+++	−	∅	
Evaporative flux *(TFF)*	∅	∅	−	−
Filtration flux *(PF)*	− −	−	−	− −
Reabsorption flux *(PF)*	+	+++	+	+
Excretion				
Of ammonia	Ammonia	Urea	Urea/uric acid	Ammonia/urea
Of carbon dioxide	Bicarbonate	Bicarbonate	Gaseous CO_2; bicarbonate	Calcium carbonate; bicarbonate; gaseous CO_2

Key: + = flux from environment to body; − = flux from body to environment; ∅ = no flux; *TFF* = thermodynamically favored flux; *PF* = physiological flux.

From Turner (2000) *The Extended Organism*, Table 7.1.

Genes as followers



Genes

Epigenetic inheritance

Ecological inheritance

Cultural inheritance

Parental effects

Plasticity

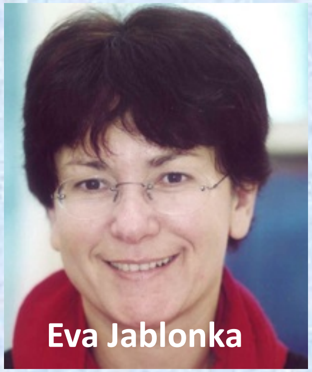
Slowly changing **Rapidly changing**

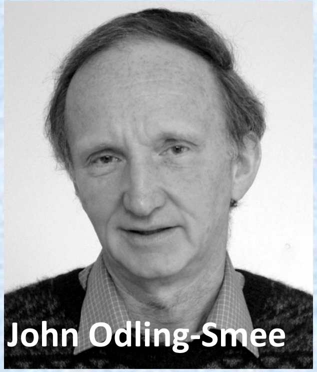
Table S1. Textbook treatments of evolutionary processes

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
Bergstrom & Dugatkin 2012. Evolution. Norton (786 pp) [157]	S,D,M,G,L,T	0	0[e]	0	0[f]	1
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
Stearns & Hoekstra 2005. Evolution. An introduction. 2nd ed. (574 pp) [158]	S,D,M,G	0	0[c]	10[b]	3	0
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.

Laland et al., 2015 Proc. R. Soc. B





We began with certain premises:

- that all fields of science and all scientists possess conceptual frameworks
- that pluralism in science at all levels is healthy
- *nullius in verba*

Could we come up with a conception of the EES that would do useful work and make a constructive contribution to evolutionary biology

EES assumptions

Classical MS core assumptions	EES core assumptions
(i) *Narrower view of causation.* 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) *Broader view of causation.* 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) *Inclusive inheritance.* Inheritance extends beyond genes to include epigenetic, physiological, ecological and cultural inheritance. Acquired characters play evolutionary roles.
(iii) *Random genetic (and phenotypic) variation.* There is 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) *Random genetic but (often) nonrandom phenotypic variation.* Developmental systems can facilitate well-integrated, functional phenotypic responses to mutation or environmental induction.
(iv) *Gene-centred.* 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.* 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.

Laland et al., 2015 Proc. R. Soc. B

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 Proc. R. Soc. B

EES assumptions and predictions

EES core assumptions
(i) *Broader view of causation.* Developmental processes share with natural selection some responsibility for the direction and rate of evolution and contribute to organism-environment complementarity.
(ii) *Inclusive inheritance.* Inheritance extends beyond genes to include epigenetic, physiological, ecological and cultural inheritance. Acquired characters play evolutionary roles.
(iii) *Random genetic but (often) nonrandom phenotypic variation.* Developmental systems can facilitate well-integrated, functional phenotypic responses to mutation or environmental induction.
(iv) *Organism-centred*. 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.

Proposed EES predictions
(i) Phenotypic accommodation can precede, rather than follow, genetic change, in adaptive evolution.
(ii) Novel phenotypic variants will frequently be directional and functional.
(iii) Novel, evolutionarily consequential, phenotypic variants will frequently be environmentally induced in multiple individuals.
(iv) Repeated evolution in isolated populations may be due to convergent selection and/or developmental bias.
(v) Adaptive variants propagated through selection, repeated induction, learning and non-genetic inheritance.
(vi) Rapid phenotypic evolution can be frequent and can result from the simultaneous induction and selection of functional variants.
(viii) Taxonomic diversity will sometimes be better explained by features of developmental systems (evolvability, constraints) than features of environments.
(ix) etc

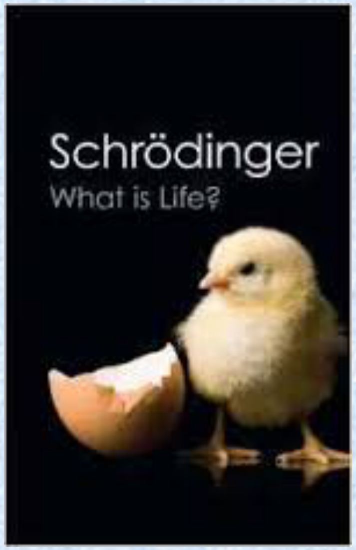
Laland et al., 2015 Proc. R. Soc. B

Central arguments of Niche Construction Theory

		Accepted 1988	Accepted 2018
1.	Organisms commonly modify environments in non-trivial ways and thereby create or alter selection.	✗	✓
2.	Niche construction can significantly modify evolutionary dynamics.	✗	✓
3.	Niche construction can support eco-evolutionary dynamics.	✗	✓
4.	Niche-constructed effects can persist beyond the lifetime of the constructor (ecological inheritance), with important consequences.	✗	✓
5.	There are two logically distinct routes to organism-environment complementarity, arising via selection or niche construction	✗	?
6.	Acquired characters can play an evolutionary role, by modifying selection pressures through niche construction.	✗	✓
7.	Evolutionary causality often begins with niche construction (plasticity first).	✗	?
8.	Organisms are active, purposive agents that co-direct (bias) the course of their evolution. Niche construction is an evolutionary process.	✗	✗

Agency

Agency is *the intrinsic capacity of individual living organisms to act …in their world, and thereby to modify their experience of it, including in ways that are neither predetermined, nor random.*



Organisms are self-building, self-regulating, highly integrated… and (crucially) “purposive” wholes which, through wholly natural processes, exert a distinctive influence and a degree of control over their own activities, outputs and local environments. Indeed, organisms must have these properties to be alive.

Niche construction **must** be orderly and directed, and constructed environments **must** bear the signature of purposive agents.

(Schrodinger, 1944; Odling-Smee 1988; Odling-Smee et al., 2003)

An extensive niche construction literature

Empirical data

TABLE 2.3. Anatomical and Behavioral Adaptations That May Be Evolutionary Responses to Prior Perturbational Niche Construction

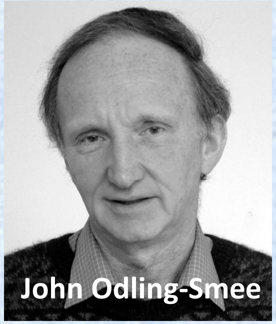
Organism	*Perturbational Behavior*	*Resource*	*Anatomical and Behavioral Adaptations to Perturbation*	*Reference*
Insects				
Soil insects	Dig burrow in soil	Burrow/ nest	Well-developed larval legs, spinose transverse bands on pupae, wings protected by hardened forewings, reduced, lost, or shed after dispersal	Gullan and Cranston (1994)
Ant lions (Myrmeleontidae)	Dig conical pit to trap ants	Pit	Jerk to create landslides, flick sand at prey	Gullan and Cranston (1994)
Potter wasps (Eumenidae)	Construct mud cell/clay pot	Mud nest	Moisten mud with regurgitated water, nest camouflage, and provisioning	Frisch (1975)
Parasitoid insects	Construct burrow to contain young/prey	Burrow	Plug burrow, provision burrow	Evans and West-Eberhard (1970), Gullan and Cranston (1994)
Mole crickets (Gryllotalpidae) and some cicadas and beetles	Construct nest for young	Burrow/ nest	Forelimbs modified for digging, lick eggs preventing mold infection	Gullan and Cranston (1994), Preston-Mafham and Preston-Mafham (1996)
Bark beetles (Passalidae and Scolytidae)	Construct nest/pupal case	Nest/ fungus	Fungus cultivation as beetle predigests wood	Preston-Mafham and Preston-Mafham (1996)
Arachnids				
Trap-door spiders (Ctenizidae) and giant trap-door spiders (Liphistiidae)	Dig tubelike burrows lined with silk	Burrow	Rakelike modified basal cheliceral segment, trap-door holding and tying behavior, trip lines,	Preston-Mafham and Preston-Mafham (1996)

Odling-Smee et al (2003)

Table 2 | **Genes identified as having been subject to recent rapid selection and their inferred cultural selection pressures**

Genes	Function or phenotype	Inferred cultural selection pressure	Refs
LCT, MAN2A1, SI, SLC27A4, PPARD, SLC25A20, NCOA1, LEPR, LEPR, ADAMTS19, ADAMTS20, APEH, PLAU, HDAC8, UBR1, USP26, SCP2, NKX2-2, AMY1, ADH, NPY1R, NPY5R	Digestion of milk and dairy products; metabolism of carbohydrates, starch, proteins, lipids and phosphates; alcohol metabolism	Dairy farming and milk usage; dietary preferences; alcohol consumption	6,7,16,41,63, 102,118, 144,145
Cytochrome P450 genes (*CYP3A5, CYP2E1, CYP1A2* and *CYP2D6*)	Detoxification of plant secondary compounds	Domestication of plants	6,63,146,147
CD58, APOBEC3F, CD72, FCRL2, TSLP, RAG1, RAG2, CD226, IGJ, TJP1, VPS37C, CSF2, CCNT2, DEFB118, STAB1, SP1, ZAP70, BIRC6, CUGBP1, DLG3, HMGCR, STS, XRN2, ATRN, G6PD, TNFSF5, HbC, HbE, HbS, Duffy, α-globin	Immunity, pathogen response; resistance to malaria and other crowd diseases	Dispersal, agriculture, aggregation and subsequent exposure to new pathogens; farming	6–8,14,16,50, 63,148,149
LEPR, PON1, RAPTOR, MAPK14, CD36, DSCR1, FABP2, SOD1, CETP, EGFR, NPPA, EPHX2, MAPK1, UCP3, LPA, MMRN1	Energy metabolism, hot or cold tolerance; heat-shock genes	Dispersal and subsequent exposure to novel climates	14,150
SLC24A5, SLC25A2, EDAR, EDA2R, SLC24A4, KITLG, TYR, 6p25.3, OCA2, MC1R, MYO5A, DTNBP1, TYRP1, RAB27A, MATP, MC2R, ATRN, TRPM1, SILV, KRTAPs, DCT	The externally visible phenotype (skin pigmentation, hair thickness, eye and hair colour, and freckles)	Dispersal and local adaptation and/or sexual selection	9,14,63,97, 101,151
CDK5RAP2, CENPJ, GABRA4, PSEN1, SYT1, SLC6A4, SNTG1, GRM3, GRM1, GLRA2, OR4C13, OR2B6, RAPSN, ASPM, RNT1, SV2B, SKP1A, DAB1, APPBP2, APBA2, PCDH15, PHACTR1, ALG10, PREP, GPM6A, DGKI, ASPM, MCPH1, FOXP2	Nervous system, brain function and development; language skills and vocal learning	Complex cognition on which culture is reliant; social intelligence; language use and vocal learning	6,7,14,63, 68–70,78,149
BMP3, BMPR2, BMP5, GDF5	Skeletal development	Dispersal and sexual selection	6,63
MYH16, ENAM	Jaw muscle fibres; tooth-enamel thickness	Invention of cooking; diet	80,113

ADAMTS, ADAM metalloproteinase with thrombospondin motif; *ADH*, alcohol dehydrogenase; *ALG10*, asparagine-linked glycosylation 10; *AMY1*, salivary amylase 1; *APEH*, *N*-acylaminoacyl-peptide hydrolase; *APOBEC3F*, apolipoprotein B mRNA-editing enzyme, catalytic polypeptide-like 3F; *APBA2*, amyloid β precursor protein-binding, family A, member 2; *APPBP2*, amyloid β precursor protein-binding protein 2; *ASPM*, abnormal spindle, microcephaly associated; *ATRN*, attractin; BMP, bone morphogenetic protein; *CCNT2*, cyclin T2; *CDK5RAP2*, cyclin dependent kinase 5 regulatory subunit-associated protein 2; *CENPJ*, centromere protein J; *CETP*, cholesteryl ester transfer protein; *CSF2*, colony stimulating factor 2; *CUGBP1*, CUG triplet repeat, RNA-binding protein 1 ; CYP, cytochrome P450; *DAB1*, disabled homologue 1; *DCT*, dopachrome tautomerase; *DEFB118*, defensin β118; *DGKI*, diacylglycerol kinase ι; *DLG3*, discs, large homologue 3; *DSCR1*, Down syndrome critical region 1; *DTNBP1*, dystrobrevin-binding protein 1; *EDAR*, ectodysplasin A receptor; *EGFR*, epidermal growth factor receptor; *ENAM*, enamelin; *EPHX2*, epoxide hydrolase 2; *FABP1*, fatty acid-binding protein 1; *FCRL2*, Fc receptor-like 2; *FOXP2*, forkhead box P2; *G6PD*, glucose-6-phosphate dehydrogenase; *GABRA4*, γ-aminobutyric acid A receptor, subunit α4; *GDF5*, growth differentiation factor 5; *GLRA2*, glycine receptor α2; GRM, glutamate receptor, metabotropic; Hb, haemoglobin; *HDAC8*, histone deacetylase 8; *HMGCR*, HMG coenzyme A reductase; *IGJ*, immunoglobulin joining chain; KRTAP, keratin-associated protein; *LCT*, lactose; *LEPR*, leptin receptor; *LPA*, lipoprotein A; *MAN2A1*, mannosidase, alpha, class 2A, member 1; MAPK, mitogen-activated protein kinase; *MATP*, membrane-associated transporter protein; MC, melanocortin; *MCPH1*, microcephalin 1; *MMRN1*, multimerin 1; *MYH16*, myosin, heavy chain 16; *MYO5A*, myosin VA; *NCOA1*, nuclear receptor coactivator 1; *NPPA*, natriuretic peptide precursor A; NPY, neuropeptide Y; *OCA2*, oculocutaneous albinism II ; OR, olfactory receptor; *PCDH15*, protocadherin 15; *PHACTR1*, phosphatase and actin regulator 1; *PLAU*, plasminogen activator, urokinase; *PON1*, paraoxonase 1; *PPARD*, peroxisome proliferator-activated receptor δ; *PREP*, prolyl endopeptidase; *PSEN1*, presenilin 1; RAG, recombination activating gene; *RAPSN*, receptor-associated protein of the synapse; *RAPTOR*, regulatory-associated protein of mTOR; *SCP2*, sterol carrier protein 2; *SI*, sucrase-isomaltase; *SILV*, silver homologue; *SKP1A*, S-phase kinase-associated protein 1; SLC, solute carrier; *SNTG1*, syntrophin γ1; *SOD1*, superoxide dismutase 1; *STAB1*, stabilin 1; *STS*, steroid sulfatase; *SV2B*, synaptic vesicle glycoprotein 2B; *SYT1*, synaptotagmin 1; *TJP1*, tight junction protein 1; *TNFSF5*, tumour necrosis factor superfamily, member 5; *TRPM1*, transient receptor potential cation channel, subfamily M, member 1; *TSLP*, thymic stromal lymphopoietin; TYR, tyrosinase; TYRP1, tyrosinase-related protein 1; *UBR1*, ubiquitin protein ligase E3 component n-recognin 1; *UCP3*, uncoupling protein 3; *USP26*, ubiquitin-specific peptidase 26; *VPS37C*, vacuolar protein sorting 37 homologue C; *XRN2*, 5′–3′ exoribonuclease 2; ZAP, ζ-associated protein kinase.



Laland, Odling-Smee & Myles (2010) *Nature Reviews Genetics* 11: 137-48