Niche Construction and Evolution

Modern Evolutionary Synthesis

G. C. Williams (1992):

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

Modern Evolutionary Synthesis:

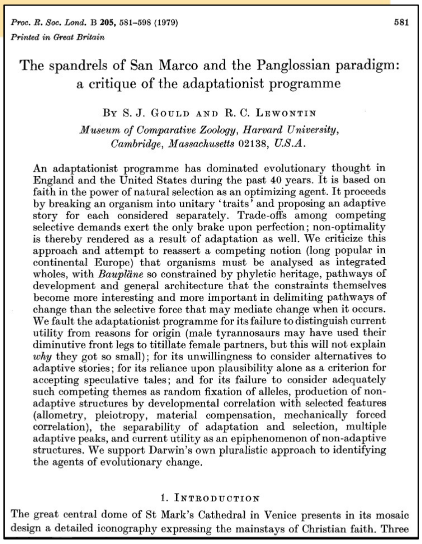
Conventional evolutionary perspective explains the organism-environment match solely in terms of natural selection. Adaptation is seen as a process by which selection shapes organisms to fit pre-existing environments (Laland & Brown 2006).

Modern Evolutionary Synthesis: criticisms

Gould & Lewontin (1979): the "Panglossian" adaptationist programme"

X Organisms as integrated entities
"sub-optimality", drift, pleiotropy, phyletic and developmental constraints

Lewontin 1983:
'Organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world'



Proc. R. Soc. Lond. B **205**, 581–598 (1979) 581
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The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

By S. J. Gould and R. C. Lewontin
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, *U.S.A.*

An adaptationist programme has dominated evolutionary thought in England and the United States during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary 'traits' and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection; non-optimality is thereby rendered as a result of adaptation as well. We criticize this approach and attempt to reassert a competing notion (long popular in continental Europe) that organisms must be analysed as integrated wholes, with *Baupläne* so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs. We fault the adaptationist programme for its failure to distinguish current utility from reasons for origin (male tyrannosaurs may have used their diminutive front legs to titillate female partners, but this will not explain *why* they got so small); for its unwillingness to consider alternatives to adaptive stories; for its reliance upon plausibility alone as a criterion for accepting speculative tales; and for its failure to consider adequately such competing themes as random fixation of alleles, production of non-adaptive structures by developmental correlation with selected features (allometry, pleiotropy, material compensation, mechanically forced correlation), the separability of adaptation and selection, multiple adaptive peaks, and current utility as an epiphenomenon of non-adaptive structures. We support Darwin's own pluralistic approach to identifying the agents of evolutionary change.

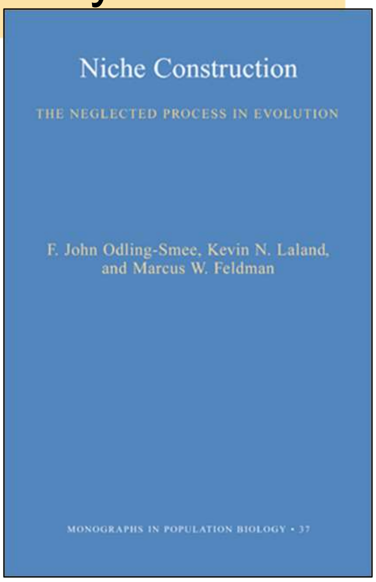
1. Introduction

The great central dome of St Mark's Cathedral in Venice presents in its mosaic design a detailed iconography expressing the mainstays of Christian faith. Three

Niche Construction Theory

F.J. Odling-Smee
1988, 1996, 1998:
"Niche construction"

Odling-Smee, Laland & Feldman 2003



Niche Construction

(Odling-Smee 1988, 1996, 1998)

Organisms change the environment through their behaviour, changing the selective pressures acting on their own and other species.

Laland & Brown 2006:
Organisms do not just build environmental components, but regulate them to damp out variability in environmental conditions

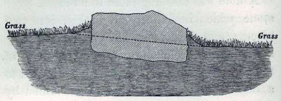
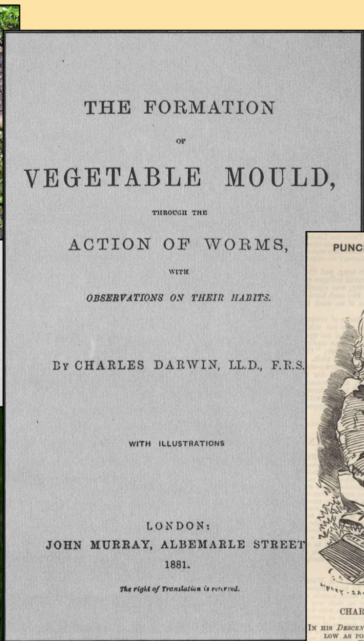


Fig. 7.

Section through one of the fallen Druidical stones at Stonehenge, showing how much it had sunk into the ground. Scale ½ inch to 1 foot.



THE FORMATION

OF

VEGETABLE MOULD,

THROUGH THE

ACTION OF WORMS,

WITH

OBSERVATIONS ON THEIR HABITS.

BY CHARLES DARWIN, LL.D., F.R.S.

WITH ILLUSTRATIONS

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1881.

The right of Translation is reserved.

Darwin, 1881

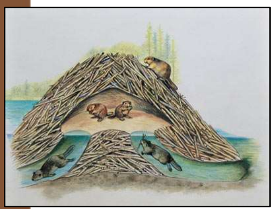
Earthworms

CHARLES ROBERT DARWIN, LL.D., F.R.S.

IN HIS *DESCENT OF MAN* HE BROUGHT HIS OWN SPECIES DOWN AS LOW AS POSSIBLE—*I.E.*, TO "A HAIRY QUADRUPED FURNISHED WITH A TAIL AND POINTED EARS, AND PROBABLY *ARBOREAL* IN ITS HABITS"—WHICH IS A REASON FOR THE VERY GENERAL INTEREST IN A "FAMILY TREE." HE HAS LATELY BEEN TURNING HIS ATTENTION TO THE "POLITIC WORM."

Ecological Inheritance

(*Castor* spp)



When a beaver builds a dam, creating a lake and influencing river flow, this behavior not only affects the propagation of **dam-building genes**, but results in **major changes in the local environment**. It follows that **dam building by beavers must alter the selection of other beaver traits, influencing beaver evolution** (Laland & Brown 2006)

Inceptive x Counteractive Niche Construction

TABLE 2.1. Examples of the Four Categories of Niche Construction

	Perturbation	*Relocation*
Inceptive	*Organisms initiate a change in their selective environment by physically modifying their surroundings.*	*Organisms expose themselves to a novel selective environment by moving to or growing into a new place.*
	e.g., emission of detritus	e.g., invasion of a new habitat
Counteractive	*Organisms counteract a prior change in the environment by physically modifying their surroundings.*	*Organisms respond to a change in the environment by moving to or growing into a more suitable place.*
	e.g., thermoregulation of nests	e.g., seasonal migration

(Odling-Smee, Laland & Feldman 2003)

Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis
(Laland & Brown 2006)

Human behavioral ecology: **behavioral flexibility**

in response to environmental conditions that optimizes life-time reproductive success. Because humans evolved as opportunistic ecological generalists in variable environments, selection will have favored the ability to adopt the strategy that maximizes fitness in a given environment.

X

Evolutionary Psychology: **adaptive lag**

We believe the adaptive-lag hypothesis is misguided. Based on insights gained from the niche-construction perspective, we put forward the counter proposal that niche-constructing activity generally increases the match between an animal's behavior and its environment.

Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis
(Laland & Brown 2006)

Evolutionary psychologists who emphasize human adaptive lag typically stress that human psychological mechanisms are complex adaptations based on co-adapted gene complexes that are unlikely to respond quickly to selection.

BUT:

1. the genetic bases of putative evolved psychological mechanisms are unknown;
2. there is little compelling evidence that human psychological mechanisms are complex adaptations;
3. although comparatively little is known about the rates of evolutionary change of complex characters, the traits shown to respond quickly to selection are elaborate, multi-loci ones.
4. molecular genetic analyses reveal that small changes in genes, or in their promoters and enhancers, can bring about major changes in the functionality of complex characters.

Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis
(Laland & Brown 2006)

Three reasons why human niche construction should typically be adaptive:

Reason 1: Humans construct their world to **suit themselves**;

Reason 2: Humans **buffer** adaptive lag through cultural niche construction;

Reason 3: When humans are unable to buffer adaptive lag fully through further cultural niche construction, **natural selection on genes** ensues.

Reason 1:
Humans construct their world to suit themselves

Reason 1:
Humans construct their world to suit themselves

Most niche construction will increase the short-term fitness of the constructor, although it may have negative consequences for other species.

Animals do not just build structures, but regulate them to damp out variability in environmental conditions, with the result that niche construction can maintain selection pressures and preserve the adaptiveness of behavior.

Human-built environments might be different from African savanna, but many selection pressures acting on us could be broadly similar, since our constructions were built to be suited to our bodies and their needs.

Counteractive niche construction acts to **maintain environmental conditions** within tolerable limits, and in the process filters and **modifies the selection** acting on the constructor.
(ex.: earthworms).

Reason 2: Humans frequently buffer adaptive lag through cultural Niche Construction

Organisms continuously choose or manufacture a suitable environment, often in response to environmental challenges created by their ancestors.

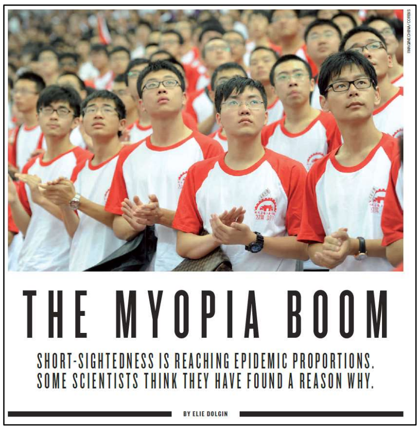
Unlike most other species, humans can respond to ancestral niche construction in two ways: through genetic evolution or through **further (usually cultural) niche construction** (ex: cities).

One consequence of the fact that cultural niche construction can damp out selection on human genes is that it can lead to increased numbers of genes in the human gene pool with potentially negative effects on fitness in the absence of these cultural activities.

Ex: the ability to manufacture prescription eyeglasses relaxed the selection pressures on genes for myopia.

Myopia and development

For many years, the scientific consensus held that myopia was largely down to genes. Studies in the 1960s showed that the condition was more common among genetically identical twins than non-identical ones, suggesting that susceptibility is strongly influenced by DNA. Gene-finding efforts have now linked more than 100 regions of the genome to short-sightedness. (...) But it was obvious that genes could not be the whole story.(...) what seemed to matter most was the eye's exposure to bright light.



Dolgin 2015, *Nature*

Reason 3: When humans are unable to buffer adaptive lag fully through further cultural niche construction, natural selection on genes ensues.

Biological evolution can be extremely fast: significant human evolution could be measured in hundreds of years or less. Whenever human cultural processes fail to express a sufficiently effective response to an environmental change, culturally modified environments give rise to modified natural selection pressures, which may change gene frequencies

Culturally induced genetic responses to human agriculture:
Yam cultivators, malaria, and sickle-cell disease.

Culturally induced genetic responses to human pastoralism:
Lactose tolerance by adult humans

Niche Construction, Human Behavioural Ecology, and Evolutionary Psychology
(Laland 2007)

Implications for the study of human behavior

Human global population growth: evidence of adaptiveness of human Niche Construction.

It is in the Holocene* that we see the explosion in human numbers and human colonization of the globe. Population growth appears linked to agricultural practices, technological advancement, medicine etc (phenomena that are most strikingly different from the Pleistocene environments).

Post-demographic transition societies exhibit relatively stable population sizes or marginal growth or decline, indicative of largely adaptive behavior (v. Ihara & Feldman 2004, Kendal et al. 2005)

* Holocene: end of Pleistocene (11.700 y BP) to present (...Anthropocene?)

Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis
(Laland & Brown 2006)

Adaptive human behavior will be the norm and maladaptiveness the exception.

BUT processes are not instantaneous or unfailing, so humans *will* still experience some adaptive lag. Ex: our taste for salt, fat, and sugar.

Niche Construction
Laland & O'Brien 2011

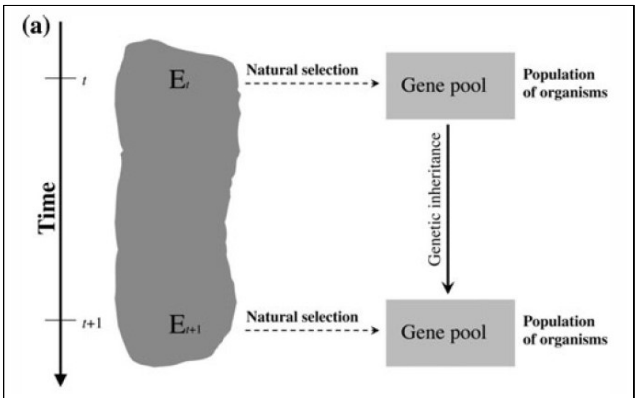
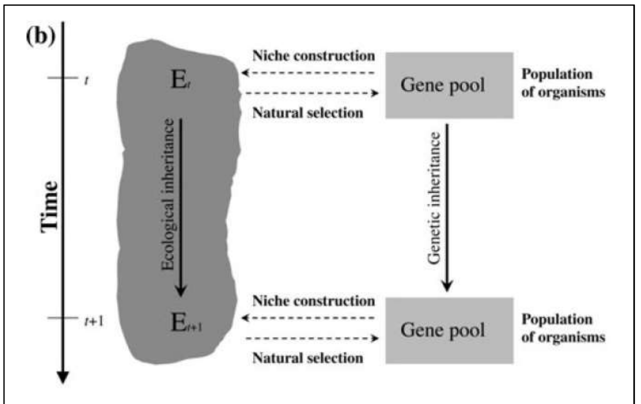


Fig. 1 Two views of evolution. Under the conventional perspective (**a**), niche construction is recognized as a product of natural selection but not as an evolutionary process. Inheritance is primarily genetic. Under the niche-construction perspective (**b**), niche construction is recognized as an evolutionary process. Here, ecological inheritance plays a parallel role to genetic inheritance

Niche Construction
Laland & O'Brien 2011



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Consequences of the Niche-Construction revision

Expanded inheritance

The niche-construction perspective adds a second general form of inheritance to the evolutionary process, stressing **two legacies** that organisms inherit from their ancestors, **genes** and **modified selective environments**. Unlike genetic inheritance, **ecological inheritance** is not a template copying system, and does not depend on replicators, but on organisms bequeathing altered environments to their offspring.

In each generation, offspring inherit a local selective environment that has, to an extent, previously been **modified**, or **chosen**, by its niche-constructing ancestors. The resulting **dual inheritance** implies that each offspring must actually inherit an **initial organism–environment relationship.**

Development and Niche Construction

K. Laland:
Niche Construction Theory is explicit about the need to treat **niche construction** as both a **developmental process** and **a cause of evolution.**

The "start-up niche"

Minimally, **parental actions and choices influence where and when offspring originate**, and in many species, they ensure that some kind of **resource package** is also present.

The niche-constructed components of the inherited niche frequently modify the range of developmental environments to which juveniles are exposed, and may subsequently transform the **norms of reaction*** of the offspring's genes.

Ex: nests, burrows, mounds, and similar structures all tend to **buffer environmental variation**, making temperature, humidity, and exposure to wind and sunlight more uniform.

Conversely, **niche construction can result in exposure to a broader range of developmental conditions as a consequence of ancestral activities** (ex: if parents relocate to a novel environment).

Laland, Odling-Smee & Gilbert 2008

[* A concept that places phenotypic plasticity in the context of a genotype-specific response]

The "start-up niche"

"Maternal Effect" and Social Information Transfer (even in asocial species)

Gilbert 1983: Monarch butterflies (*Danaus plexippus*): "Imprinting" in the choice of toxic plants for oviposition (*Asclepias* spp).

Development and Niche Construction: The "Ontogenetic Niche"

West & King 2008:
"At a behavioral level, the **ontogenetic niche** is the set of ecological and social circumstances inherited by individuals. Exogenetic heredity can be highly reliable, probable and stable over generations, e.g., inheriting conspecifics is as dependable as inheriting genes"

Fragaszy 2011:
For many animals, the **ontogenetic niche** prominently features **social components**, such as parents, siblings, and group mates. **The ontogenetic niche shapes individuals' opportunities for learning**, particularly for learning skills and habits characteristic of other members of their social group. Thus, this feature of constructed niches underlies traditions.

Socially Biased Learning and Niche Construction

Fragaszy et al 2013:

A complementary perspective to Socially Biased Learning framed in Niche Construction:

"Simply observing another using a tool is not enough to use a tool skillfully: enduring residual artefacts scaffold individuals' learning these skills, and thus promote the maintenance of technical traditions."

Cultural Niche Construction
Laland & Brown 2006

The feedback that niche construction generates in evolution makes a difference to how organisms evolve. This is also true for niche construction based on **learning and cultural processes**. The significance of acquired characters to evolutionary processes becomes further amplified with **stable transgenerational culture**.

By **culture**, we mean **the ability to acquire and transmit learned knowledge, beliefs, and skills** and to devise **ever more efficient solutions to problems** that build on this reservoir of **shared intelligence.**

Other animals possess **traditions** (...). Yet human cultural processes are exceptionally potent compared to those in other animals, probably because of this cumulative property.

Human evolution may be unique in that **our culture and niche construction have become self-reinforcing**.

Cultural Niche Construction
Laland & O'Brien 2011

Three domains of information acquisition

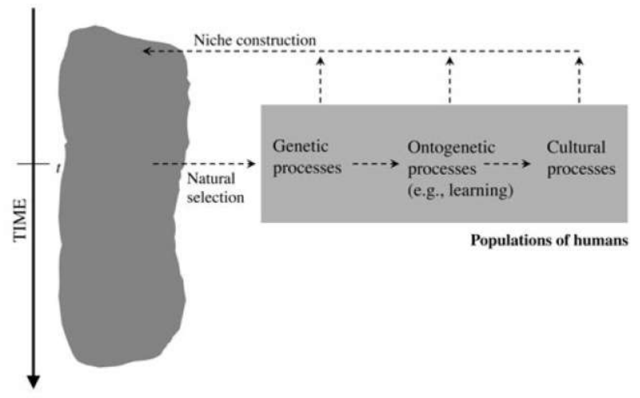


Fig. 2 Diagram showing three domains of information acquisition—genetic, ontogenetic, and cultural. Organisms, especially humans, use all three to generate information that feeds back into niche construction

Cultural Niche Construction

Laland & O'Brien 2011

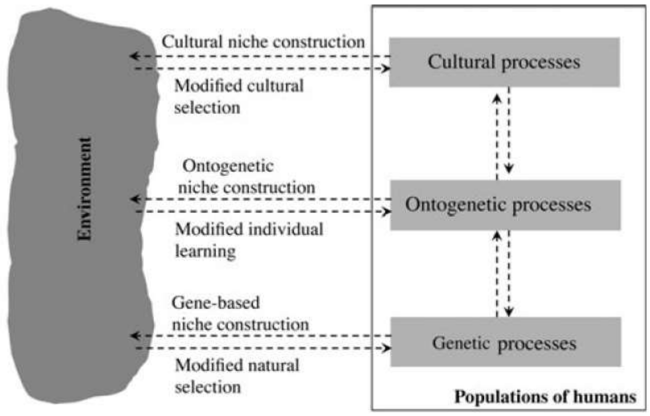


Fig. 3 Interconnectedness of the three domains of information acquisition and their roles in niche construction

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011
Cultural Niche Construction and Human Learning Environments: Investigating Sociocultural Perspectives

NCT can be applied to examine the influence of culturally constructed learning environments on the acquisition and retention of beliefs, values, role expectations, and skills.

NCT asserts that **behavior can alter the environment in ways that affect selection on heritable information**. Although NCT was originally specified by investigating how organisms' effects on the environment might influence natural selection on a gene pool, the theory is applicable to **any form of heritable information**, including epigenetic subcellular structures, socially learned patterns of behavior, and forms of symbolic representation.

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011
Cultural Niche Construction and Human Learning Environments: Investigating Sociocultural Perspectives

In cases where genetic causation of cultural variation can be discounted, cultural variation may still be subject to selection as a result of differential survival and reproduction — **demic selection** — or as a result of differential trait adoption and abandonment rates — **cultural selection**.

(Cavalli-Sforza and Feldman 1981; Feldman 2008)

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011
Cultural Niche Construction and Human Learning Environments: Investigating Sociocultural Perspectives

Learning in a culturally constructed environment is of central concern to many sociologists, cognitive scientists, and sociocultural anthropologists, albeit often from different perspectives. Four pertinent theories from these fields (as a basis for interdisciplinary investigation)

Situated learning
Activity theory
Practice theory
Distributed cognition

These theories may be addressed using a cultural niche-construction framework.

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011

Situated learning

A process by which newcomers, through ***legitimate peripheral participation***, become full participants in a community of practice, such as an apprenticeship into a particular trade, or participation in a religious community or a secular group (Lave and Wenger 1991).

The term both emphasizes learning *in situ* through participation and decentralizes common notions of mastery, pedagogy, and learning through instruction and replication.

Situated learning emphasizes the importance of the interaction between the learner and the constructed learning environment. Similarly, ecological psychologists use the notion of ***affordance***, which is a measure of the properties of the environment relative to the learner.

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011

Activity theory

Cultural-historical activity theory: the effect of the constructed learning environment on the learner.

Vygotsky: the "**Zone of Proximal Development**":
"the distance between the actual developmental level as determined by independent problem solving and the level of potential development as determined through problem solving under adult guidance or in collaboration with more capable peers".

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011

Distributed cognition

Donald (2000): **Hybrid mind hypothesis**: semantic memory systems can be augmented by ''extended'' storage: "The memory repositories of culture allow our species to transmit across generations the codes, habits, institutional structures, and symbolic memory systems that are needed to operate a significant portion of the processes of modern cognition in human culture".

Sociocultural systems: human agents + nonhuman artifacts.

Wheeler & Clark (2008): Structured learning environments as extended cognitive systems: "Non-organic props and aids, many of which are either culturally inherited tools or structures manipulated by culturally transmitted practices, might themselves count as proper parts of extended cognitive processes".

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011

Practice theory

Practice theory was born out of an historical debate among sociocultural anthropologists over the persistence and stability of structure in a social system:

Structural functionalists and cognitive structuralists (Durkheim, Lévi-Strauss) favored a top-down perspective, where social structure retains its form through the imposition of sanctions upon individuals and can be analyzed horizontally as a function of structural relations.

X bottom-up arguments, consistent with an historical (vertical) analysis of a social system.

Development and Niche Construction: Cultural Niche Construction

Kendal JR 2011

Sociocultural Theories may be addressed using a cultural niche-construction framework

A common theme of situated learning, activity theory, practice theory, and distributed cognition is the emphasis that **learning is a process of construction of knowledge and beliefs that is structured by the cultural environment**. However, there appears to have been little attempt in the literature to relate all four theories in the context of both a developmental and an evolutionary framework.

Niche Construction and cumulative culture

Niche Construction and the Toolkits of Hunter–Gatherers and Food Producers (Collard, Buchanan, Ruttle & O'Brien 2011)

X

34 hunter–gatherer / 45 small-scale food-producing populations.

[ethnographic data + proxies for risk of resource failure/ Regression Analysis]

Explaining toolkit size (*subsistants*) and complexity (*technounits*) differences:

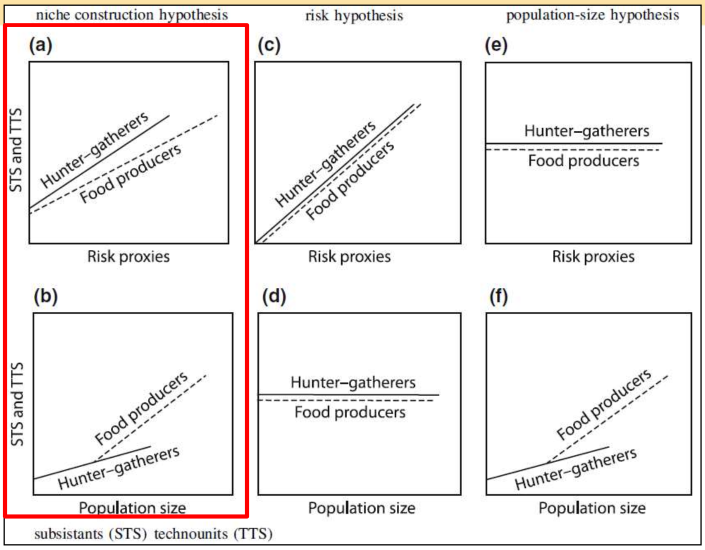
H1: **risk of resource failure** (the greater the risks, the larger/+complex toolkit)

H2: toolkit diversity and complexity are driven by **population size**

H3 (NCT): subsistence toolkits of **small-scale food producers** (**more potent niche constructors**) should be less influenced by **risk of resource failure** and more influenced by **population size** (**having on average larger populations**) than the subsistence toolkits of **hunter–gatherers**.

Niche Construction and cumulative culture

Niche Construction and the Toolkits of Hunter–Gatherers and Food Producers (Collard, Buchanan, Ruttle & O'Brien 2011)



Is Non-genetic Inheritance Just a Proximate Mechanism? Mesoudi et al 2013

Lewontin (1970): general aspects of Darwinian evolution: variation, inheritance, and differential fitness: **genetic evolution is but one specific theory that fulfills these criteria**.

The specialized assumptions of the MS, such as **natural selection**, **recombination**, and **undirected genetic mutation**, are not sufficient to explain the adaptive dynamics of evolution, and must be expanded to include a suite of additional **developmental, epigenetic, behavioral**, and **cultural processes**.

An evolutionary theory that encompasses **multiple interacting inheritance systems** and the interactions between them is far more compatible with sociocultural phenomena, in both humans and non-human species alike, than a gene-centric evolutionary theory.

Is Non-genetic Inheritance Just a Proximate Mechanism? Mesoudi et al 2013

The **human behavioral and social sciences** have been highly critical of gene-based approaches to the study of human behavior such as sociobiology or, more recently, evolutionary psychology.
This is largely because the phenomena that social/behavioral scientists study — the cultural dynamics of languages, technology, religious beliefs, socio-political institutions, and so on — are not under direct genetic control, and can only be explained as **cultural adaptations that arise through cultural evolution**.

Is Non-genetic Inheritance Just a Proximate Mechanism? Mesoudi et al 2013

Is Non-genetic Inheritance Just a Proximate Calibration Mechanism?

Phenotypic plasticity occurs when phenotypes vary in response to **environmental variability** in the absence of corresponding DNA variation, and such direct proximate responses may entail **epigenetic** or **individual learning** mechanisms.

X

Non-genetic inheritance, in contrast, occurs when variable information that is unrelated to DNA sequence variation is transmitted across successive generations of individuals, such as occurs with **epigenetic inheritance** and **cultural transmission/social learning.**

Is Non-genetic Inheritance Just a Proximate Mechanism? Mesoudi et al 2013

If the function of phenotypic plasticity is to track environmental change that cannot be anticipated by genes, then there simply must be a partial decoupling between genes and phenotypic plasticity, otherwise the latter would never have evolved. This applies even more to transgenerational non-genetic inheritance. Once information can be inherited non-genetically, it can significantly transform evolutionary dynamics through reciprocal feedback between the different inheritance systems. This goes far beyond mere proximate ''calibration.'' Gene-culture coevolution is the best-understood example.

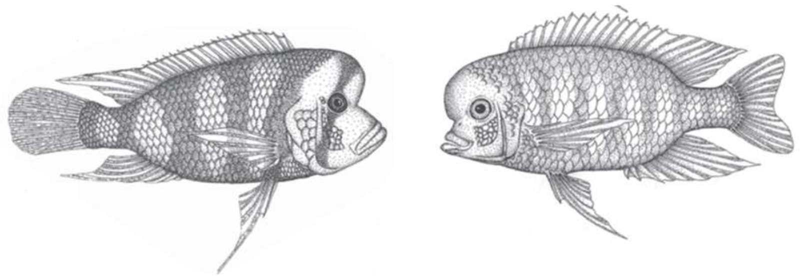
Is Non-genetic Inheritance Just a Proximate Mechanism? Mesoudi et al 2013

A Corroboration of the
Extended Evolutionary Synthesis

The existence and scope of non-genetic inheritance systems, including epigenetic inheritance, niche construction/ecological inheritance, and cultural inheritance -alongside certain other theory revisions - necessitates an extension to the neo-Darwinian Modern Synthesis (MS) in the form of an Extended Evolutionary Synthesis (EES).

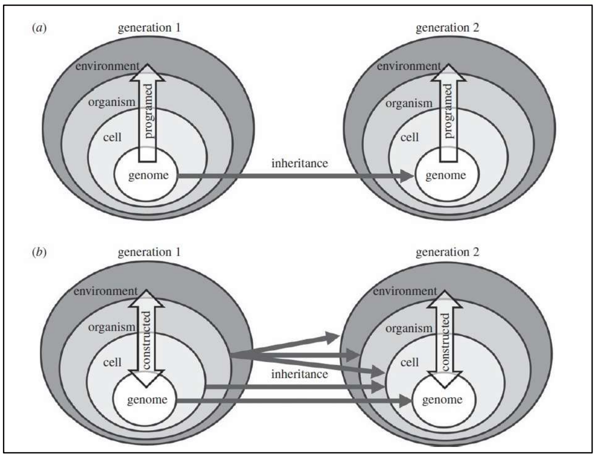
The extended evolutionary synthesis
Laland *et al* 2015

EES: an extension of the Modern Synthesis or a different framework?



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**.

The extended evolutionary synthesis
Laland *et al* 2015



Programmed x Constructive development
Reciprocal causation

The extended evolutionary synthesis

Laland *et al* 2015

- Evolutionary developmental biology
- Developmental Plasticity
- Inclusive inheritance
- Niche Construction theory

Table 1. A comparison of the core assumptions of the classical MS and the EES.

classical MS core assumptions	EES core assumptions
(i) *The pre-eminence of natural selection.* 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) *Reciprocal causation (organisms shape, and are shaped by, selective and developmental environments).* Developmental processes, operating through developmental bias and niche construction, 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 encompass (transgenerational) epigenetic inheritance, physiological inheritance, ecological inheritance, social (behavioural) transmission and cultural inheritance. Acquired characters can play evolutionary roles by biasing phenotypic variants subject to selection, modifying environments and contributing to heritability
(iii) *Random genetic 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) *Non-random phenotypic variation.* Developmental bias, resulting from non-random mutation or phenotypic accommodation, means that some phenotypic variants are more likely than others. Developmental systems facilitate well-integrated, functional phenotypic responses to mutation or environmental induction
(iv) *Gradualism.* Evolution via mutations of large effects is unlikely because such mutations have disruptive pleiotropic effects. Phenotypic transitions typically occur through multiple small steps, leading to gradual evolutionary change	(iv) *Variable rates of change.* Variants of large effect are possible, allowing for rapid evolutionary change. Saltation can occur either through mutations in major regulatory control genes expressed in tissue-, module- or compartment-specific manner, or when developmental processes respond to environmental challenges with change in coordinated suites of traits, or through nonlinear threshold effects
(v) *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	(v) *Organism-centred perspective.* Developmental systems can facilitate adaptive variation and modify selective environments. 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
(vi) *Macro-evolution.* Macro-evolutionary patterns are explained by micro-evolutionary processes of selection, drift, mutation and gene flow	(vi) *Macro-evolution.* Additional evolutionary processes, including developmental bias and ecological inheritance, help explain macro-evolutionary patterns and contribute to evolvability

The extended evolutionary synthesis

Laland *et al* 2015

Classical MS assumptions	EES core assumptions
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The extended evolutionary synthesis

Laland *et al* 2015

Classical MS assumptions	EES core assumptions
(iv) *Gradualism*. Evolution via mutations of large effects is unlikely because such mutations have disruptive pleiotropic effects. Phenotypic transitions typically occur through multiple small steps, leading to gradual evolutionary change	(iv) *Variable rates of change*. Variants of large effect are possible, allowing for rapid evolutionary change. Saltation can occur either through mutations in major regulatory control genes expressed in tissue-, module- or compartment-specific manner, or when developmental processes respond to environmental challenges with change in coordinated suites of traits, or through nonlinear threshold effects
(v) *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	(v) *Organism-centred perspective*. Developmental systems can facilitate adaptive variation and modify selective environments. 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
(vi) *Macro-evolution*. Macro-evolutionary patterns are explained by micro-evolutionary processes of selection, drift, mutation and gene flow	(vi) *Macro-evolution*. Additional evolutionary processes, including developmental bias and ecological inheritance, help explain macro-evolutionary patterns and contribute to evolvability

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Phenomena such as developmental bias or niche construction do not directly change gene frequencies (as selection, drift, gene flow and mutation), and hence are not viewed as causes of evolutionary processes.

Table 2. Two alternative interpretations of developmental bias, developmental plasticity, inclusive inheritance and niche construction.

	a traditional interpretation	the EES interpretation
developmental bias	sources of bias in phenotypic variation treated as phylogenetic or developmental constraints. Such constraints are important components of optimality models and in analyses of contemporary evolution (e.g. in attempts to quantify the G matrix in quantitative genetics), which may explain why populations are poorly adapted	sources of bias in phenotypic variation considered an important evolutionary process, which does not only constrain but also facilitate and direct evolution. Developmental bias is a major source of evolvability and explanation of its mechanisms, prevalence and direction are crucial to understand evolutionary diversification
developmental plasticity	conceptualized as a genetically specified feature of individuals (i.e. a reaction norm) that can evolve under selection and drift. Focus is on the conditions that promote adaptive evolution of plastic versus non-plastic phenotypes. The primary evolutionary role of plasticity is to adjust phenotypes adaptively to variable environments. Plastic responses regarded as pre-filtered by past selection	considers reducing plasticity to a genetic feature to be explanatorily insufficient. Retains an interest in adaptive evolution of plasticity, but also focuses on how plasticity contributes to the origin of functional variation under genetic or environmental change, and how the mechanisms of plasticity limit or enhance evolvability, and initiate evolutionary responses. Many plastic responses viewed as reliant on open-ended (e.g. exploratory) developmental processes, and hence capable of introducing phenotypic novelty
inclusive inheritance	heredity defined to exclude non-genetic inheritance. Cultural inheritance treated as a special case. Transmission genetics considered explanatorily sufficient for the evolution of adaptations. Causal effects of parents on offspring are referred to as parental (maternal) effects, which are shown to have a variety of consequences for evolutionary trajectories and may be adaptations	heredity defined to include all causal mechanisms by which offspring come to resemble their parents. Phenotypes are not inherited, they are reconstructed in development. Non-genetic mechanisms of inheritance contribute to heritability and facilitate the origin and spread of environmentally induced novelties
niche construction	aspects of niche construction studied under different labels (e.g. extended phenotypes). Environmental states modified by organisms viewed as no different from independent environmental states and treated as a background condition. Niche construction typically reduced to genetically controlled aspects of phenotypes, or adaptations	views evolutionary causation as reciprocal and hence that organisms co-evolve with their environments. Environments modified by organisms viewed as qualitatively different from independent environmental states. Niche construction treated as a process that directs evolution by non-random modification of selective environments. Niche construction may result from acquired characters, by-products and the accumulated outputs of multiple species

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EES is not just an extension of the MS but a distinctively different framework for understanding evolution.

Table 3. A comparison of predictions made by a traditional interpretation and the EES.

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 hence novel phenotypes, will be random in direction and typically neutral or slightly 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) adaptive evolution typically proceeds through selection of mutations with small effects	(iv) 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	(v) repeated evolution in isolated populations may be due to convergent selection and/or developmental bias
(vi) adaptive variants are propagated through selection	(vi) in addition to selection, adaptive variants are propagated through repeated environmental induction, non-genetic inheritance, learning and cultural transmission
(vii) rapid phenotypic evolution requires strong selection on abundant genetic variation	(vii) 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) heritable variation will be unbiased	(ix) 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	(x) 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

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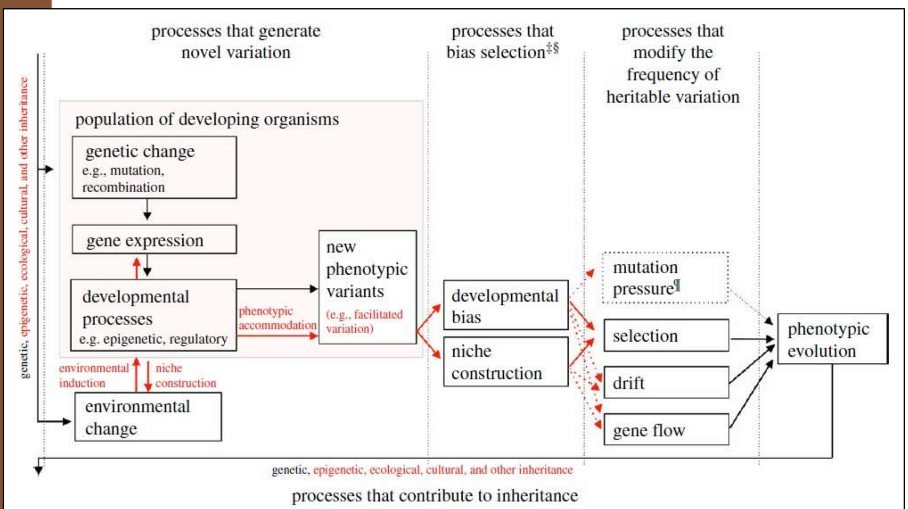
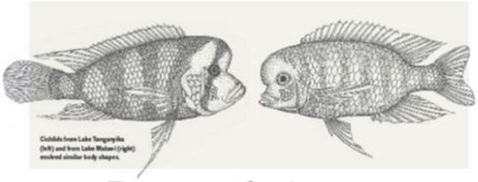


COMMENT



Does evolutionary theory need a rethink?

Researchers are divided over what processes should be considered fundamental.

POINT

Yes, urgently

COUNTERPOINT

No, all is well

Nature, Oct. 2014

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PUTTING THE EXTENDED EVOLUTIONARY SYNTHESIS TO THE TEST

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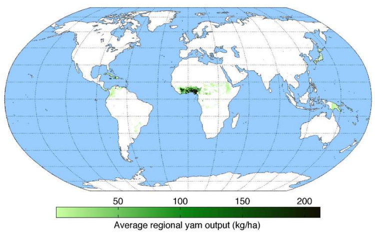
Cultural Niche Construction and Gene-Culture Coevolution

Agriculture, malaria
and Sickle-Cell Disease
Jackson 1996

Pastoralism and adults' lactose absorption
Aoki 1986

Cultural Niche Construction and Gene-Culture Coevolution

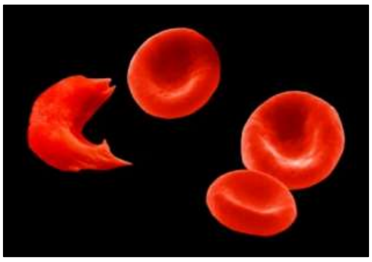
Yam cultivators in West Africa: clearings increased the amount of standing water, breeding grounds for mosquitoes, increased the prevalence of malaria.



Agriculture, malaria
and sickle-cell disease
Jackson 1996

Cultural Niche Construction and Gene-Culture Coevolution

Natural selection pressures in favor of an increase in the frequency of the sickle-cell S allele because, in the heterozygous condition, the S allele confers protection against malaria.



Agriculture, malaria and sickle-cell disease
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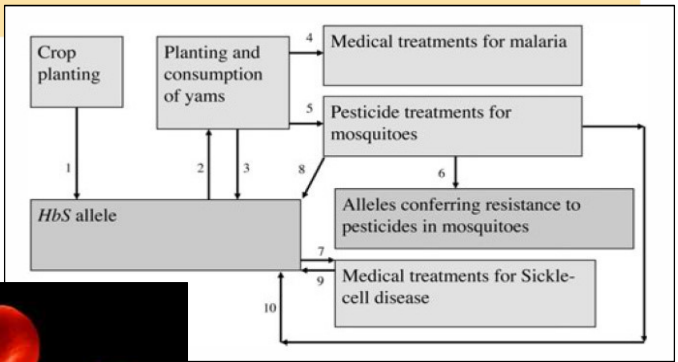
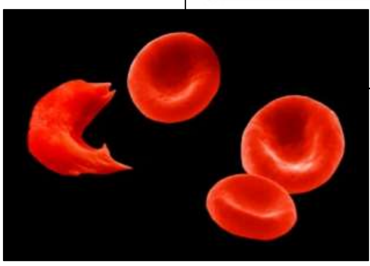
Cultural Niche Construction and Gene-Culture Coevolution





Agriculture, malaria and sickle-cell disease
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Aoki 1986

Pastoralism and lactose tolerance by adult humans

Pastoralism and lactose tolerance by adults

Lactase genes' silencing and sibling competition

x Mutation ~10ky, Turkey → Eurasia, to Great Britain, Scandinavia, the Mediterranean, India (stopping only at the Himalayas)

Other independent mutations for lactose tolerance: 1 in Middle East, 3 in Africa (Tishkoff et al 2007) [**not** in the Americas, Australia, or the Far East].

Extremely fast spread; 80-100% (European populations)

BUT fermentation → lactose-free yogurt → → → hard cheese

Eurasia and parts of Africa: humans fermenting the lactose out of dairy for thousands of years before lactose tolerance was widespread. **Why was milk consumption so beneficial?**

Pastoralism and lactose tolerance by adults

Everywhere that agriculture and civilization went, lactose tolerance came along. ´"Agriculture was worst mistake in human history". Jared Diamond (1997)

Less varied/healthy diet → disease
(first Neolithic farmers: tooth decay, anemia, low bone-density)

Civilization → Cities → rapid spread of infectious diseases.
Lactose tolerance → vitamin D and calcium deficiencies?
Pardis Sabeti: milk boosted women's fat stores & fertility?
Milk = fresh drinking water (pathogen-free)?
Tishkoff et al 2007: 4 different mutations (1 in Eurasia, 3 in Africa)

Next lecture:

Gene-Culture Coevolution (cont.)