COMMENT

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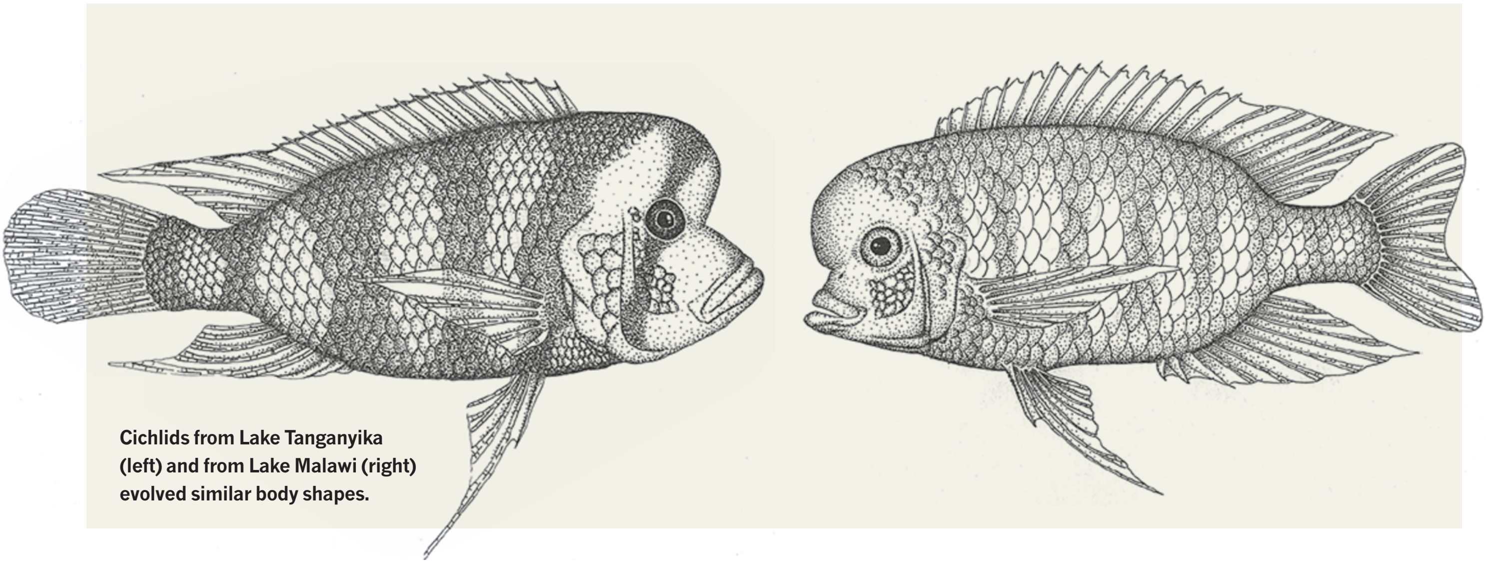


Cichlids from Lake Tanganyika (left) and from Lake Malawi (right) evolved similar body shapes.

Does evolutionary theory need a rethink?

Researchers are divided over what processes should be considered fundamental.

POINT

Yes, urgently

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

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

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

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

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

COUNTERPOINT

No, all is well

Theory accommodates evidence through relentless synthesis, say Gregory A. Wray, Hopi E. Hoekstra *and colleagues.*

In October 1881, just six months before he died, Charles Darwin published his final book. *The Formation of Vegetable Mould, Through the Actions of Worms*[11] sold briskly: Darwin's earlier publications had secured his reputation. He devoted an entire book to these humble creatures in part because they exemplify an interesting feedback process: earthworms are adapted to thrive in an environment that they modify through their own activities.

Darwin learned about earthworms from conversations with gardeners and his own simple experiments. He had a genius for distilling penetrating insights about evolutionary processes — often after amassing years of observational and experimental data — and he drew on such disparate topics as agriculture, geology, embryology and behaviour. Evolutionary thinking ever since has followed Darwin's lead in its emphasis on evidence and in synthesizing information from other fields.

A profound shift in evolutionary thinking began **PAGE 163 ▶**

ILLUSTRATION BY R. CRAIG ALBERTSON

POINT: YES, URGENTLY ▶ evolution works. We hold that organisms are constructed in development, not simply 'programmed' to develop by genes. Living things do not evolve to fit into pre-existing environments, but co-construct and coevolve with their environments, in the process changing the structure of ecosystems.

The number of biologists calling for change in how evolution is conceptualized is growing rapidly. Strong support comes from allied disciplines, particularly developmental biology, but also genomics, epigenetics, ecology and social science[1,2]. We contend that evolutionary biology needs revision if it is to benefit fully from these other disciplines. The data supporting our position gets stronger every day.

Yet the mere mention of the EES often evokes an emotional, even hostile, reaction among evolutionary biologists. Too often, vital discussions descend into acrimony, with accusations of muddle or misrepresentation. Perhaps haunted by the spectre of intelligent design, evolutionary biologists wish to show a united front to those hostile to science. Some might fear that they will receive less funding and recognition if outsiders — such as physiologists or developmental biologists — flood into their field.

However, another factor is more important: many conventional evolutionary biologists study the processes that we claim are neglected, but they comprehend them very differently (see 'No, all is well'). This is no storm in an academic tearoom, it is a struggle for the very soul of the discipline.

Here we articulate the logic of the EES in the hope of taking some heat out of this debate and encouraging open discussion of the fundamental causes of evolutionary change (see Supplementary Information; go.nature.com/boffk7).

Plasticity: commodore butterflies emerge with different colours in dry (left) and wet seasons.

ORANGE: PETER CHADWICK/SPL; BLUE: LAWRENCE LAWRY/SPL

CORE VALUES

The core of current evolutionary theory was forged in the 1930s and 1940s. It combined natural selection, genetics and other fields into a consensus about how evolution occurs. This 'modern synthesis' allowed the evolutionary process to be described mathematically as frequencies of genetic variants in a population change over time — as, for instance, in the spread of genetic resistance to the myxoma virus in rabbits.

In the decades since, evolutionary biology has incorporated developments consistent with the tenets of the modern synthesis. One such is 'neutral theory', which emphasizes random events in evolution. However, standard evolutionary theory (SET) largely retains the same assumptions as the original modern synthesis, which continues to channel how people think about evolution.

The story that SET tells is simple: new variation arises through random genetic mutation; inheritance occurs through DNA; and natural selection is the sole cause of adaptation, the process by which organisms become well-suited to their environments. In this view, the complexity of biological development — the changes that occur as an organism grows and ages — are of secondary, even minor, importance.

In our view, this 'gene-centric' focus fails to capture the full gamut of processes that direct evolution. Missing pieces include how physical development influences the generation of variation (developmental bias); how the environment directly shapes organisms' traits (plasticity); how organisms modify environments (niche construction); and how organisms transmit more than genes across generations (extra-genetic inheritance). For SET, these phenomena are just outcomes of evolution. For the EES, they are also causes.

Valuable insight into the causes of adaptation and the appearance of new traits comes from the field of evolutionary developmental biology ('evo-devo'). Some of its experimental findings are proving tricky to assimilate into SET. Particularly thorny is the observation that much variation is not random because developmental processes generate certain forms more readily than others[3]. For example, among one group of centipedes, each of the more than 1,000 species has an odd number of leg-bearing segments, because of the mechanisms of segment development[3].

In our view, this concept — developmental bias — helps to explain how organisms adapt to their environments and diversify into many different species. For example, cichlid fishes in Lake Malawi are more closely related to other cichlids in Lake Malawi than to those in Lake Tanganyika, but species in both lakes have strikingly similar body shapes[4]. In each case, some fish have large fleshy lips, others protruding foreheads, and still others short, robust lower jaws.

SET explains such parallels as convergent evolution: similar environmental conditions select for random genetic variation with equivalent results. This account requires extraordinary coincidence to explain the multiple parallel forms that evolved independently in each lake. A more succinct hypothesis is that developmental bias and natural selection work together[4,5]. Rather than selection being free to traverse across any physical possibility, it is guided along specific routes opened up by the processes of development[5,6].

Another kind of developmental bias occurs when individuals respond to their environment by changing their form — a phenomenon called plasticity. For instance, leaf shape changes with soil water and chemistry. SET views this plasticity as merely fine-tuning, or even noise. The EES sees it as a plausible first step in adaptive evolution. The key finding here is that plasticity not only allows organisms to cope in new environmental conditions but to generate traits that are well-suited to them. If selection preserves genetic variants that respond effectively when conditions change, then adaptation largely occurs by accumulation of genetic variations that stabilize a trait after its first appearance[5,6]. In other words, often it is the trait that comes first; genes that cement it follow, sometimes several generations later[5].

Studies of fish, birds, amphibians and insects suggest that adaptations that were, initially, environmentally induced may promote colonization of new environments and facilitate speciation[5,6]. Some of the best-studied examples of this are in fishes, such as sticklebacks and Arctic char. Differences in the diets and conditions of fish living at the bottom and in open water have induced distinct body forms, which seem to be evolving reproductive isolation, a stage in forming new species. The number of species in a lineage does not depend solely on how random genetic variation is winnowed through different environmental sieves. It also hangs on developmental properties that contribute to the lineage's 'evolvability'.

In essence, SET treats the environment as a 'background condition', which may trigger or modify selection, but is not itself part of the evolutionary process. It does not differentiate between how termites become adapted to mounds that they construct and, say, how organisms adapt to volcanic eruptions. We view these cases as fundamentally different[7].

Volcanic eruptions are idiosyncratic events, independent of organisms' actions. By contrast, termites construct and regulate their homes in a repeatable, directional manner that is shaped by past selection and that instigates future selection. Similarly, mammals, birds and insects defend, maintain and improve their nests — adaptive responses to nest building that have evolved again and again[7]. This 'niche construction', like developmental bias, means that organisms co-direct their own evolution by systematically changing environments and thereby biasing selection[7].

INHERITANCE BEYOND GENES

SET has long regarded inheritance mechanisms outside genes as special cases; human culture being the prime example. The EES explicitly recognizes that parent–offspring similarities result in part from parents reconstructing their own developmental environments for their offspring. 'Extra-genetic inheritance' includes PAGE 164 ▶

COUNTERPOINT: NO, ALL IS WELL ▶ during the 1920s, when a handful of statisticians and geneticists began quietly laying the foundations for a dramatic transformation. Their work between 1936 and 1947 culminated in the 'modern synthesis', which united Darwin's concept of natural selection with the nascent field of genetics and, to a lesser extent, palaeontology and systematics. Most importantly, it laid the theoretical foundations for a quantitative and rigorous understanding of adaptation and speciation, two of the most fundamental evolutionary processes.

In the decades since, generations of evolutionary biologists have modified, corrected and extended the framework of the modern synthesis in countless ways. Like Darwin, they have drawn heavily from other fields. When molecular biologists identified DNA as the material basis for heredity and trait variation, for instance, their discoveries catalysed fundamental extensions to evolutionary theory. For example, the realization that many genetic changes have no fitness consequences led to major theoretical advances in population genetics. The discovery of 'selfish' DNA prompted discussions about selection at the level of genes rather than traits. Kin selection theory, which describes how traits affecting relatives are selected, represents another extension[12].

Nonetheless there are evolutionary biologists (see 'Yes, urgently') who argue that theory has since ossified around genetic concepts. More specifically, they contend that four phenomena are important evolutionary processes: phenotypic plasticity, niche construction, inclusive inheritance and developmental bias. We could not agree more. We study them ourselves.

But we do not think that these processes deserve such special attention as to merit a new name such as 'extended evolutionary synthesis'. Below we outline three reasons why we believe that these topics already receive their due in current evolutionary theory.

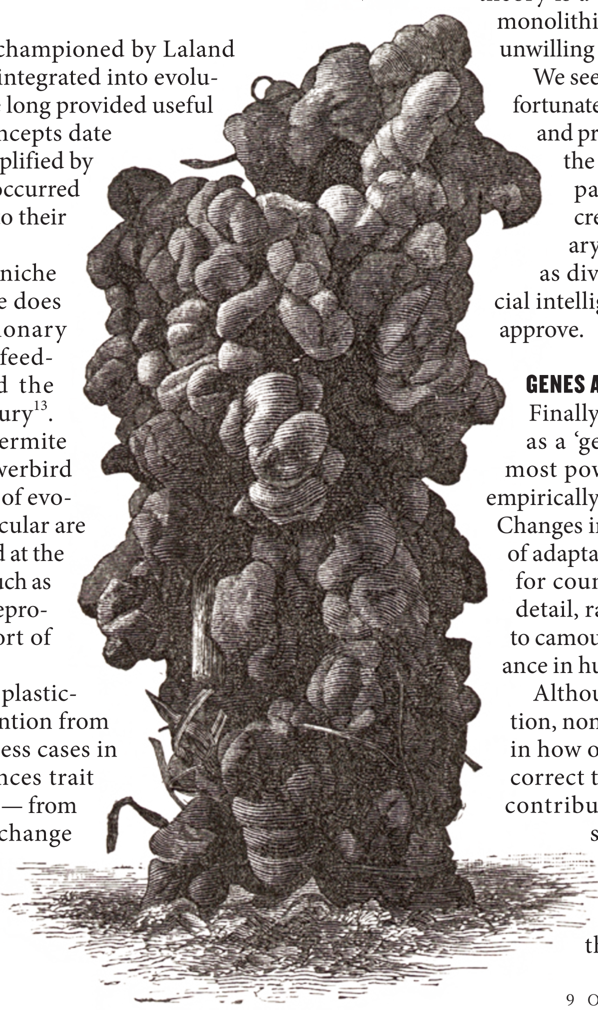
NEW WORDS, OLD CONCEPTS

The evolutionary phenomena championed by Laland and colleagues are already well integrated into evolutionary biology, where they have long provided useful insights. Indeed, all of these concepts date back to Darwin himself, as exemplified by his analysis of the feedback that occurred as earthworms became adapted to their life in soil.

Today we call such a process niche construction, but the new name does not alter the fact that evolutionary biologists have been studying feedback between organisms and the environment for well over a century[13]. Stunning adaptations such as termite mounds, beaver dams, and bowerbird displays have long been a staple of evolutionary studies. No less spectacular are cases that can only be appreciated at the microscopic or molecular scale, such as viruses that hijack host cells to reproduce and 'quorum sensing', a sort of group think by bacteria.

Another process, phenotypic plasticity, has drawn considerable attention from evolutionary biologists. Countless cases in which the environment influences trait variation have been documented — from the jaws of cichlid fishes that change shape when food sources alter, to leaf-mimicking insects that are brown if born in the dry season and green in the wet. Technological advances in the past decade have revealed an incredible degree of plasticity in gene expression in response to diverse environmental conditions, opening the door to understanding its material basis. Much discussed, too, was a book[5] by behavioural scientist Mary Jane West-Eberhard that explored how plasticity might precede genetic changes during adaptation.

So, none of the phenomena championed by Laland and colleagues are neglected in evolutionary biology. Like all ideas, however, they need to prove their value in the marketplace of rigorous theory, empirical results and critical discussion. The prominence that these four phenomena command in the discourse of contemporary evolutionary theory reflects their proven explanatory power, not a lack of attention.



JOHN VAN WYHE/DARWIN-ONLINE.ORG.UK

A worm cast pictured in Charles Darwin's final book.

MODERN EXPANSION

Furthermore, the phenomena that interest Laland and colleagues are just four among many that offer promise for future advances in evolutionary biology. Most evolutionary biologists have a list of topics that they would like to see given more attention. Some would argue that epistasis — complex interactions among genetic variants — has long been under-appreciated. Others would advocate for cryptic genetic variation (mutations that affect only traits under specific genetic or environmental conditions). Still others would stress the importance of extinction, or adaptation to climate change, or the evolution of behaviour. The list goes on.

We could stop and argue about whether 'enough' attention is being paid to any of these. Or we could roll up our sleeves, get to work, and find out by laying the theoretical foundations and building a solid casebook of empirical studies. Advocacy can take an idea only so far.

What Laland and colleagues term the standard evolutionary theory is a caricature that views the field as static and monolithic. They see today's evolutionary biologists as unwilling to consider ideas that challenge convention.

We see a very different world. We consider ourselves fortunate to live and work in the most exciting, inclusive and progressive period of evolutionary research since the modern synthesis. Far from being stuck in the past, current evolutionary theory is vibrantly creative and rapidly growing in scope. Evolutionary biologists today draw inspiration from fields as diverse as genomics, medicine, ecology, artificial intelligence and robotics. We think Darwin would approve.

GENES ARE CENTRAL

Finally, diluting what Laland and colleagues deride as a 'gene-centric' view would de-emphasize the most powerfully predictive, broadly applicable and empirically validated component of evolutionary theory. Changes in the hereditary material are an essential part of adaptation and speciation. The precise genetic basis for countless adaptations has been documented in detail, ranging from antibiotic resistance in bacteria to camouflage coloration in deer mice, to lactose tolerance in humans.

Although genetic changes are required for adaptation, non-genetic processes can sometimes play a part in how organisms evolve. Laland and colleagues are correct that phenotypic plasticity, for instance, may contribute to the adaptedness of an individual. A seedling might bend towards brighter light, growing into a tree with a different shape from its siblings. Many studies have shown that this kind of plasticity is beneficial, and that it can readily evolve if there PAGE 164 ▶

POINT: YES, URGENTLY

the transmission of epigenetic marks (chemical changes that alter DNA expression but not the underlying sequence) that influence fertility, longevity and disease resistance across taxa[8]. In addition, extra-genetic inheritance includes socially transmitted behaviour in animals, such as nut cracking in chimpanzees or the migratory patterns of reef fishes[8,9]. It also encompasses those structures and altered conditions that organisms leave to their descendants through their niche construction — from beavers' dams to worm-processed soils[7,10]. Research over the past decade has established such inheritance to be so widespread that it should be part of general theory.

Mathematical models of evolutionary dynamics that incorporate extra-genetic inheritance make different predictions from those that do not[7–9]. Inclusive models help to explain a wide range of puzzling phenomena, such as the rapid colonization of North America by the house finch, the adaptive potential of invasive plants with low genetic diversity, and how reproductive isolation is established.

> *"There is more to inheritance than genes."*

Such legacies can even generate macro-evolutionary patterns. For instance, evidence suggests that sponges oxygenated the ocean and by doing so created opportunities for other organisms to live on the seabed[10]. Accumulating fossil data indicate that inherited modifications of the environment by species has repeatedly facilitated, sometimes after millions of years, the evolution of new species and ecosystems[10].

BETTER TOGETHER

The above insights derive from different fields, but fit together with surprising coherence. They show that variation is not random, that there is more to inheritance than genes, and that there are multiple routes to the fit between organisms and environments. Importantly, they demonstrate that development is a direct cause of why and how adaptation and speciation occur, and of the rates and patterns of evolutionary change.

SET consistently frames these phenomena in a way that undermines their significance. For instance, developmental bias is generally taken to impose 'constraints' on what selection can achieve — a hindrance that explains only the absence of adaptation. By contrast, the EES recognizes developmental processes as a creative element, demarcating which forms and features evolve, and hence accounting for why organisms possess the characters that they do.

Researchers in fields from physiology and ecology to anthropology are running up against the limiting assumptions of the standard evolutionary framework without realizing that others are doing the same. We believe that a plurality of perspectives in science encourages development of alternative hypotheses, and stimulates empirical work. No longer a protest movement, the EES is now a credible framework inspiring useful work by bringing diverse researchers under one theoretical roof to effect conceptual change in evolutionary biology. ■

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COUNTERPOINT: NO, ALL IS WELL

is genetic variation in the response[14]. This role for plasticity in evolutionary change is so well documented that there is no need for special advocacy.

Much less clear is whether plasticity can 'lead' genetic variation during adaptation. More than half a century ago, developmental biologist Conrad Waddington described a process that he called genetic assimilation[15]. Here, new mutations can sometimes convert a plastic trait into one that develops even without the specific environmental condition that originally induced it. Few cases have been documented outside of the laboratory, however. Whether this is owing to a lack of serious attention or whether it reflects a genuine rarity in nature can be answered only by further study.

Lack of evidence also makes it difficult to evaluate the role that developmental bias may have in the evolution (or lack of evolution) of adaptive traits. Developmental processes, based on features of the genome that may be specific to a particular group of organisms, certainly can influence the range of traits that natural selection can act on. However, what matters ultimately is not the extent of trait variation, nor even its precise mechanistic causes. What matters is the heritable differences in traits, especially those that bestow some selective advantage. Likewise, there is little evidence for the role of inherited epigenetic modification (part of what was termed 'inclusive inheritance') in adaptation: we know of no case in which a new trait has been shown to have a strictly epigenetic basis divorced from gene sequence. On both topics, further research will be valuable.

All four phenomena that Laland and colleagues promote are 'add-ons' to the basic processes that produce evolutionary change: natural selection, drift, mutation, recombination and gene flow. None of these additions is essential for evolution, but they can alter the process under certain circumstances. For this reason they are eminently worthy of study.

> *"What matters is the heritable differences in traits, especially those that bestow some selective advantage."*

We invite Laland and colleagues to join us in a more expansive extension, rather than imagining divisions that do not exist. We appreciate their ideas as an important part of what evolutionary theory might become in the future. We, too, want an extended evolutionary synthesis, but for us, these words are lowercase because this is how our field has always advanced[16].

The best way to elevate the prominence of genuinely interesting phenomena such as phenotypic plasticity, inclusive inheritance, niche construction and developmental bias (and many, many others) is to strengthen the evidence for their importance.

Before claiming that earthworms "have played a more important part in the history of the world than most persons would at first suppose"[11], Darwin collected more than 40 years of data. Even then, he published only for fear that he would soon be "joining them"[17]. ■

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