Evolutionary Biology and Chemical Geology: A Timely Marriage

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For more than 150 years natural selection has been perceived to be the overwhelming force in evolution. Only in recent decades have we obtained new insights into environmental and physicochemical factors that participate with selection in a synergic way. Far from denying Darwin's theory, such neglected factors put order to the bewildering range of genotypes and morphologies found in living organisms and, more importantly, they place evolution in a planetary context where biology, geology, and chemistry can easily be integrated.

Niche Construction

The basic tenet of evolutionary biology is natural selection, viewed as the common denominator that provides a way of understanding the complexity of the world.[1] Evolution acts through inherited changes in the development of organisms. Darwin himself could not have expressed it better when, in *The Origin of Species*, he introduced the struggle for existence and followed this with a mechanism for change.[2] However, molecular genetics, with its explosive growth, has fueled our understanding of how evolution works.[3] How could anyone think that we are neglecting other mechanisms in evolution? Richard Dawkins wrote: "There is no alternative to natural selection. No other purely physical process brings about the adaptive, organized complexity of living things. The Darwinian law may be as universal as the great laws of physics".[4]

Recent analyses are changing our conception of evolution, claiming neglected processes that call the sole argument of natural selection into question. The second participant appears to be a plausible and relatively simple fact: *niche construction*.[5,6] Put in jargon-free terms, it describes the effects of an organism on its own environment.[7] Living organisms choose habitats and spend natural resources that substantially modify the environment in which they live. Moreover, through their metabolism and behavior, they may also induce irreversible chemical and physical changes in local ecosystems. Overall, such changes can augment and in some cases dominate the selection mechanisms acting on organisms. Interactions with the environment along with other cultural changes[8,9] represent additional sources of nongenetic information that can be transmitted through generations. Thus, niche construction gives rise to evolutionary feedback, each generation being influenced by the environmental changes induced by the predecessors. The defenders of this environmental effect consider it an intuitive and more obvious concept than natural selection, because it is easier to observe individual organisms engaged in niche construction than to observe them affected by selection.[5]

A series of examples nicely illustrates niche construction and its consequences. Consider, for instance, leaf-cutter ants consuming the same vegetation resource and emitting detritus. By increasing soil permeability and nutrient levels, the ants substantially alter the lives of other organisms with whom they share the ecosystem. Earthworms provide another relevant case as these organisms considerably modify both the structure and chemistry of the soils. Changes in porosity, aeration, and humidity, as well as pH and organic matter can affect plant growth.

However, the key question is how niche construction can have an evolutionary effect. Environmental changes will be able to modify selection pressures if they are persistent for long enough. If each individual inherits genes that express the same niche-constructing phenotypes, each generation will repeatedly change its environment in the same way. Thus, it is likely that some earthworm phenotypes, such as epidermis structure or the amount and type of their secretion, evolved with niche construction over generations.

Examples involving human evolution are inevitably embedded in cultural and behavioral genetics, such as the evolution of lactose tolerance. This phenomenon would have resulted from the domestication of cattle, which brought milk-based products into the diet of humans for generations, thereby inducing the appearance of genes that conferred protection against lactose. Closely related are the effects caused by the agricultural habits of human populations. Our ancestors living in tropical forests made clearings, thus favoring the amount of standing water. As an immediate consequence, mosquitoes and malaria increased. Likewise, the appearance of the hemoglobin allele that causes sickle-cell anemia in turn increased as one copy of that allele confers a certain resistance to malaria.

A third and noticeable example is provided by the emergence of infectious diseases. Novel pathogens (such as human immunodeficiency virus (HIV), severe acute respiratory syndrome (SARS), and eventually monkeypox) are believed to emerge from their natural reservoirs when ecological changes increase the pathogen's opportunities to enter the human population and to create new health hazards via human-to-

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human transmission. The evolutionary factor also contributes in terms of the adaptation of the pathogen and changes in its virulence within humans.[10]

While niche construction may certainly be appealing to environmental and atmospheric scientists, who concentrate on how human activities affect the evolution and fate of humankind, some biologists are reluctant to accept it within an extended theory of evolution. They claim that all of the relevant environmental factors are already integrated into some of the conventional evolutionary schemes, and debatable cases like lactose tolerance emerge from gene-culture coevolution.[11]

Whether niche construction should be separated from natural selection or not, the role of environments cannot be neglected at all, even at the discrete cellular level. A recent study by Buckling et al. on *Pseudomonas fluorescens* evidences the increased fitness of these bacteria in a single niche, whereas their ability to diversify into alternative environments markedly decreases.[12]

Niche construction is certainly an appealing approach, but it is not really new. Darwin in *The Origin*, although vaguely, pointed to the potential effects of organisms on their habitats. Odling-Smee et al. attribute the foundation of niche construction to Erwin Schrödinger, the famous physicist, through a lecture delivered at Cambridge in 1956, and to the evolutionary biologist Ernst Mayr in the early 1960 s.[13] In these pioneering contributions, however, it is also fair to mention another key outsider, Karl R. Popper, who addressed this phenomenon in his *Objective Knowledge*.[14] He wrote: "Animals and plants were born into a physico-chemical world, a world they never made. But although they did not make their world, these living things changed it beyond all recognition and, indeed, remade the small corner of the universe into which they were born". Popper established a metaphorical connection between the growth of knowledge and biological growth. In this regard he analyzed the cognitive structures found in the animal kingdom and compared the fitness between an organism and its environment. Nevertheless, Popper's evolutionary approach can be controversial under our modern perspective.[15]

Probably the most salient antecedent of niche construction was *The Dialectical Biologist*, the classical book by Levins and Lewontin published in the 1980s.[16] Evolution in nature can be defined by two interlocked differential equations: 1) $dO/dt = f(O,E)$ and 2) $dE/dt = g(O,E)$, where the organism (O) and the environment (E) represent the state variables. Such formulations clearly describe a scenario in which organisms and their environments are coevolving.

As iconoclastic as niche construction may be, it coincides with a renaissance of the well-known *Gaia hypothesis*,[17] (named after the ancient Greek goddess of the Earth), a thought-provoking theory suggesting that organisms and their environments evolve as a single system.[18]

As expected, the Gaia hypothesis was widely disputed by biologists, who ruled out the Earth as a living organism and therefore susceptible of natural selection. Although stronger versions of the Gaia hypothesis remain very controversial, others are fully compatible with the principles of Darwinian evolution. The Earth's living matter and the inorganic parts of the biosphere (air, oceans, and land surface) form a complex system that can be seen as a single organism having the capacity to keep our planet a fit place for life. Numerous data currently available suggest that there are direct relationships between biogenic chemicals released by living organisms and climate change.[17] Yet, the oxygen-rich atmosphere of our primitive planet would have sacrificed individual species (e.g. ancient anaerobic bacteria), opening the door to the development of higher life forms. This point is particularly noticeable because, if there is a case that illustrates the extreme effects of niche construction on a global scale, it must surely be the production of oxygen by photosynthetic organisms. The contribution of these primitive organisms to the earth's oxygen atmosphere must have taken place over innumerable generations. It is most likely that modified selection pressures, emerging from the altered atmosphere, played a significant role in biological evolution over millions of years.[5]

Niche construction should not be considered an alternative to natural selection, but simply a complementary path. Evolution is constructed from both genetic and ecological inheritance. Probably, selection pressures are always environmental.

Patterning and Selection

The intimate link between organisms subjected to natural selection and their habitats as suitable chemical laboratories introduces further questions about how early life forms evolved from organic molecules. This issue is central to the problem of organized complexity, that is, the appearance of multiple morphs (phenotypes) and their specialized functions. Among the Vitalists, the philosopher Henri Bergson, who adhered to Darwin's theory, recognized that complexity requires something more than natural selection invoking an ever-growing number of physicochemical phenomena. Nevertheless, he warned "it does not follow that chemistry and physics will ever give us the key to life".[19]

Our view of life, as we know it, invokes the standard Darwinian explanation of adaptation by natural selection. Before Darwin, numerous biologists viewed adaptations as functional modifications of naturally-occurring forms such as those found in crystals and molecules. This idea is hardly new. The comparison of biological structures with artifacts of purely inorganic or organic nature has captivated researchers throughout the ages. In the 17th century, Robert Hooke was one of the first in postulating a continuity between the nonliving and the living without invoking any vital force. He compared the generation of molds with a plantlike dendritic structure generated from silver and mercury in acid ("the silver tree"), which had been previously studied by Isaac Newton. The field, which flourished in the 19th century, called *synthetic biology* or *plasmogeny*,[20] has often been ridiculed, although it now offers clues about complexity and the significance of morphologies found in living systems. After Darwin, however, biologists saw forms as mutable assemblies of matter generated primarily by natural selection for biological function.

Only in recent decades have we moved toward a different perspective that offers new insights into the subtle equilibrium between patterning versus competition.[21] The key issue here is self-organization and how it contributes to order at both the micro- and macroscopic levels.[22] Chemists often consider self-organization as a molecular aggregation process giving rise to elegant, yet functional, supramolecular architectures. What is crucial is the fact that living organisms, as nonequilibrium (open) systems, exhibit spatio-temporal patterns that are reminiscent of those observed in nonliving systems. Disparate patterns, such as snowflake formation, the synchronous flashing of fireflies, or spiral waves in the Belousov–Zhabotinsky reaction, share some underlying principles. A large class of oscillating systems that interact with each other and modify each other's phase or frequency will reach a synchronous state; this represents an example of self-organization.[23]

However, the term "complexity" in open systems still lacks any precision.[21,24] One might define structural complexity as patterns with repeating yet variable subunits; although disordered structures could be regarded as being as complex as repeating ones. Moreover, functional complexity may refer to systems whose dynamic properties cannot be explained by the behavior of the individual components, like in bacteria colonies.[24] Complexity emerges via cooperative behavior and where the microscopic interactions will ultimately lead to a macroscopic organization with efficient adaptation to resist adverse conditions. Just like in oscillating chemical reactions, there is no plan, no instructions about the pattern that emerges. What exists is a set of physical relationships among the components of the system that result in a dynamically stable state.[25] The overall picture is not shaped by selection, but by abiotic physicochemical laws that include, to name a few, surface tension, capillary forces, diffusion kinetics, anisotropic growth, or molecular folding mediated by noncovalent interactions.[26]

This perspective brings to mind the idea that, at least for primitive forms of life, function often follows form rather than the opposite.[26a] The idea has also a bearing on the discussion of the biological significance of artificial morphologies. Thus, consider that self-assembled silica-carbonate structures, generated by an abiotic mechanism, are almost identical to ancient biogenic microfossils;[27,28] or the fact that some self-assembled molecular containers may be topologically very similar to enzymes and viruses, and exhibit a few primitive regulatory strategies featured by natural systems.[29]

Although a definition of life is controversial, the above-mentioned systems should not be considered to be alive; rather they represent a transition from nonliving to living matter, or more precisely, the appearance of forms when only nonliving molecules were present.[30,31] This echoes the crucial point of how and when selection played a greater role than thermodynamics in the observed distribution of phenotypes.[30] If niche construction has been neglected, the role of prior thermodynamics and chemical kinetics has been partly neglected. Again, this argument does not negate selection. Abiotic, molecular forms would have been subjected to natural-selection pressures in subsequent evolution of living matter, thereby giving rise to heritable variations. A notorious example may be provided by the molecular motors on which life depends, such as F_1F_0ATPase.[32] Essentially, it is no more than a thermodynamic machine driven by Brownian motion. The F_1 component generates a power stroke using ATP as its fuel, whereas the F_0 counterpart is a Brownian ratchet that uses the binding and release of protons.

Conclusion

In conclusion, a grand theory of evolution requires no more than extending evolutionary biology into evolutionary geology, thereby highlighting the symbiotic effects of organisms on their environment coupled with natural selection. In doing so, we are simply enhancing Darwin's theory. A touch of modern plasmogeny might help to unravel how geology—through inorganic and carbon-rich materials—contributed to creating the primeval morphologies found in living organisms. As Knoll concludes in a recent work: "If there is one lesson that paleontology offers to evolutionary biology, it is that life's opportunities and catastrophes are tied to Earth's environmental history".[33]

Keywords: environmental effect · molecular evolution · morphogenesis · natural selection · self-organization

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