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Title: Niche Construction: The Neglected Process in Evolution

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In the natural and social sciences, there has long been an interest in the relationship between different scales of time and in how the activities of a short lifetime figure in the progress of a long history. This interest has, broadly speaking, produced two attitudes towards the individual. In one, individuals are afloat on currents of collective action on which they have minimal influence, and in the other, history is no more than a ledger inscribed with the deeds of great people.

On the side of the individual are those such as Ralph Waldo Emerson and Karl Marx. Emerson wrote: "There is properly no history, only biography"; while Marx commented: "It is not 'history' which uses men as a means of achieving - as if it were an individual person - its own ends. History is nothing but the activity of men in pursuit of their ends." On the other side are those who would diminish the impact of individuals, among them Jose Ortega y Gasset ("Man in a word has no nature; what he has... is history") and Hans-Georg Gadamer ("History does not belong to us; we belong to it").

In one case, our historical environment is an aggregate of numerous biographies; in the other, it is an omnipotent environment that shapes biographies. In the natural sciences, Charles Darwin's theory of evolution through natural selection has been thought of - wrongly, as we shall see - as a canonical instance of the environment shaping the individual. Natural selection is that process by which variation in a population is reduced through differential reproduction of variants best fitted to the local environment.

Of course, even a simple-minded reading of Darwin makes us aware of an environment with a significant biotic, organismal component. Paraphrasing Emerson, some might be tempted to say: "There is properly no environment, only organisms." But this biotic component of the environment is often deemed an average of so many organismal contributions that it amounts to an effective, static mean. As a result, it has become acceptable to assume that organisms maximise some function, typically their own reproductive output in a fixed environment, by encoding well-fitting body plans, behaviours and traits of the individual within their genes.

This monograph in a series on population biology, *Niche Construction* by John Odling-Smee, Kevin Laland and Marcus Feldman, is an effort to consider systematically the implications for evolutionary theory of a world in which organismal and environmental change are strongly coupled over short scales of time - time scales of single generations and above.

Darwin, as usual, was the great innovator in this area. He wrote two influential books on the lasting impact that organisms have on their environment: his first book, *The Structure and Distribution of Coral Reefs* (1842), and his last book, *The Formation of Vegetable Mould through the Action of Worms with Observations on Their Habit* (1881). In the latter, Darwin famously wrote, "All the fertile areas of this planet have at least once passed through the bodies of earthworms." Both books emphasise the cumulative large-scale influence of a multitude of organisms on common environments experienced by numerous species. In *Niche Construction*, Odling-Smee et al extend the Darwinian approach to provide a systematic framework for thinking about how environments are modified by organisms and the extent to which these constructed environments influence the evolution of other species.

The niche concept is one of those ideas that biology undergraduates find inveterately ambiguous. I know I did. The niche is associated largely with the work of Joseph Grinnell, Charles Elton and George Evelyn Hutchinson in the first half of the 20th century. Grinnell intended to capture that "recess" in the environment exploited by an organism while foraging. He understood that this recess is a compound of many features, which he sought to aggregate in the idea of the niche. Elton placed slightly more emphasis on the organism in its recess, and the relationships of feeding among species. In other words, the Eltonian niche extends the Grinnellian niche to include some relational features. Hutchinson gave the concept a quantitative spin by defining the niche as an "*n*-dimensional hypervolume".

What is meant, presumably, is some abstract space of requirements and interactions unique to a species or individual. Each dimension refers to factors such as water usage and nitrogen intake required by a given species of prey. In this large space of survival requirements, it is very unlikely that any two species will be identical, but they might overlap a few dimensions, in which case they are liable to compete.

Odling-Smee *et al* treat the niche functionally rather than mechanistically, as the sum of all Darwinian selection pressures to which a population is exposed. While this clarifies the idea somewhat, it is also harder to measure in practice. The authors also adopt the classification of the evolutionary biologist Walter Bock in referring to the many properties of the organism as "features" and the properties of the environment salient to the organism as "factors". Niche construction is that process by which an organism modifies the feature-factor relationship by acting on factors in its niche.

Darwinian evolution by natural selection is typically assumed to work by adaptive modifications to the feature-factor relationship through changes exclusively to organismal features. These changes are brought about through random modifications to the organismal genome (mutation, recombination and so on). But, as Odling-Smee *et al* argue, in many cases it is easier or more effective to modify the environmental factors by slightly modifying behaviour. Humans do this all the time - we wear clothes, sleep under roofs, travel on wheels and calculate with computers. Evolution in the hominid lineage has shifted from an emphasis on changing features to working on changing factors. The practice is not only commonplace in our own species, it is also widespread in nature.

About 80 pages of *Niche Construction* are dedicated to surveying niche constructing activities in the animal kingdom. We encounter the burrows of lizards, the holes of woodpeckers, spiderwebs, beaver dams, termite mounds, caddis fly cases, ant nests, bird bowers, badgers' dens and insect galls.

In this respect, this book follows in the tradition of *On the Origin of Species*, amassing a considerable body of natural historical evidence to support a hypothesis. As with Darwin's work, it is ultimately the hypothesis that the authors of *Niche Construction* would have you understand. Most of the book is dedicated to an explanation of the evolutionary and ecological implications of niche construction.

Evolutionarily, niche construction changes the selective environment and implies that the time scale of certain environmental changes are of the order of the time scale of organismal change. Organisms no longer evolve exclusively according to the dictates of a static environment, but to a degree also decree the course of their own evolution. Because some dimensions of the niche of one species overlap with the niche of another, niche construction further implies that species control the evolutionary trajectories of other species. Given that the

environment, once modified, can persist in the modified state, environmental factors are in a sense inherited. Niche construction is therefore concerned with more than building nests and dams, it is concerned with the construction of the selective context of multiple species and the emergence of environmental forms of inheritance that echo genetic forms of inheritance. The theory of niche construction presented here asks that we extend our notion of the evolutionary process to consider the larger dynamical system of species and environment, both of which are in part encoded in genes and in part heritable environmental factors.

One chapter is dedicated to the most sophisticated and prolific niche constructors of all species, humans. This is an important chapter because it exposes some of the glaring deficits of evolutionary psychology and kindred-adaptive approaches to human behaviour. Evolutionary psychology presents the modern mind as a suite of design solutions assembled in an environment of evolutionary adaptation (the EEA). What this neglects to mention is the significant contribution our ancestors made to their environments; in this sense, the EEA is an environment of evolutionary artifice.

This is not to say that components of behaviour are not targets of selection, but these targets are moving targets, and moving in a way determined partly by organisms. Given this constructed selective background, fixed design solutions are not optimal - learning and other forms of plasticity become the key to survival. It is the evolution of mechanisms promoting learning and plasticity that establish the legitimate link between evolutionary biology and the study of human behaviour and culture. Odling-Smee et al ask how biology constrains behaviour and how genetic evolution is influenced by cultural and behavioural constructs.

The latter is the idea less visited, and, to my mind, it is the hybridisation of these two approaches that is of greatest interest. One hybrid form has been the theory of gene-culture co-evolution. Cultural niche construction promises to be a more interesting approach, as it will need to include some specification of the way in which organisms modify the factors of culture and build the elements of their society. The theory will also need to specify how cultural factors persist outside of the minds of organisms and across organismal generations.

To the authors of *Niche Construction*, genes, minds and societies are all involved in various forms of construction. A better understanding of life requires that we abandon the view that organisms are account books recording in their behaviour past ages of the Earth and see them rather as builders engaged actively in the planet's construction.

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