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Reductionism in Evolutionary Biology: A Perceptional Artifact?

THE PROBLEM

What is a genotype-phenotype map? Gene loci produce gene products, gene products interact and these "epigenetic" interactions create and maintain living things, organisms with phenotypes: in some convoluted way, genetic information is mapped onto phenotypes. To characterize this map is to characterize living things and different subdisciplines in biology focus on its different aspects. In evolutionary biology, one unsolved problem is central: how deep can natural selection penetrate this web of epigenetic interactions? Do the effects of natural selection always reach the individual gene, the basis of the epigenetic system, or do they act on a higher level of epigenetic organization? Whatever the answer is, it will determine the level of organization that should be the focus of our research efforts. Maybe, however, no one-for-all solution exists. Different case studies might yield different answers, some favoring genes as the "unit of selection," some favoring higher level entities. This, in and by itself, is not a problem. A problem is that limitations in available

1993 Lectures in Complex Systems, Eds. L. Nadel and D. L. Stein,
SFI Studies in the Sciences of Complexity, Lect. Vol. VI, Addison-Wesley, 1995

methods seem to create a perceptional artifact, the assumption—more implicit than pronounced—is that the proper level of focus is the individual gene. A brief overview of a debate related to the problem will be given; reasons for the persistence of the problem will be discussed.

THE DEBATE, ITS CONCEPTS . . .

There are defenders of the idea that higher levels of genetic organization than the individual gene, in the limit, the whole genome, are the relevant players in evolution. For example, Lewontin[12] concludes the review of a formidable amount of experimental data and theory with the statement:

> The fitness at a single locus, ripped from its interactive context, is about as relevant to real problems of evolutionary genetics as the study of the psychology of individuals isolated from their social context is to an understanding of man's sociopolitical evolution. In both cases context and interaction are not simply second-order effects to be superimposed on a primary monadic analysis. Context and interaction are of the essence.

From the other side of the ideological fence, Williams[15] writes:

> No matter how functionally dependent a gene may be, and no matter how complicated its interactions with other genes and environmental factors, it must always be true that a given gene substitution will have an arithmetic mean effect on fitness in any population. One allele can always be regarded as having a certain selection coefficient relative to another at the same locus at any given point in time. Such coefficients are numbers that can be treated algebraically, and conclusions inferred from one locus can be iterated over all loci. Adaptation can thus be attributed to the effect of selection acting independently at each locus.

WHOM ARE WE TO BELIEVE?

The debate gained widespread public attention with Dawkins'[4,5,6] advocacy of gene selectionism. If nothing else, his contributions have led to conceptual advances: he introduced the concept of the "replicator" to the debate, a concept that was subsequently used and extended by others to a canonical terminological framework. In this terminology, natural selection takes place in a world of "replicators" and "interactors," implying the distinction between "units of selection" and "levels of selection."

According to Dawkins[4] a "replicator" is "any entity in the universe which interacts with its world, including other replicators, in such a way that copies of itself are made." DNA molecules, dividing cells, and asexually reproducing multicellular organisms, along with their genomes, may qualify as replicators, but sexually reproducing organisms and their genomes may not. Sexual reproduction is quite another matter, since genetic recombination is involved.

Hull introduces the concept of the "interactor" and defines it[8] as "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential." The individual organism is the prototypic example of an interactor, but there may well be interactors on different levels of organization, such as cell lineages within multicellular organisms. Within such lineages, selective processes may occur, favoring cells that divide more rapidly than others. Here, the dividing cell is the interactor within the organism as its environment. The interplay between different levels of interaction may profoundly affect the evolutionary potential of each level, as emphasized by Buss.[3]

Given these terms, the process of natural selection is defined as "a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them."[8] In these terms, a "unit of selection" is any level of organization that qualifies as a replicator, and a "level of selection"[2] is any level of organization on which interaction can occur. Note that interactors and replicators may, but need not necessarily, designate different things. In the above example of cell lineages, cells are interactors as well as replicators. Their genome is a replicator, but not an interactor. And the multicellular organism in which they proliferate, provided that it is sexually reproducing, is an interactor but not a replicator.

. . .AND SOME SHORTCOMINGS

The definition of the replicator, as given above, harbors a conceptual problem. If replicators were always replicated with perfect accuracy, we would not be here to think about them. Changes in genetic replicators are what allows evolution. Since the definition of replicators is purely structural, every change, be it through mutation or recombination, creates a new replicator. And those replicators that are most abundant in a population because they convey higher fitness onto their carriers are most likely to be hit by mutations and, thus, extinguished. Considering its transience, Dawkins'[6] standpoint—that the beneficiary of all adaptation is the replicator—seems somewhat contrived. The strictly structural replicator concept may be too Platonic an idea to be perfectly fit for evolution. Here is a further argument for its inadequacy: if we do not want to seem prejudiced, we have at least to admit the possibility that phenomena typical for other "many body" systems occur in organisms. For example, the information necessary to produce a character