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Darwinism without populations: a more inclusive understanding of the "Survival of the Fittest"

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ABSTRACT

Following Wallace's suggestion, Darwin framed his theory using Spencer's expression "survival of the fittest". Since then, fitness occupies a significant place in the conventional understanding of Darwinism, even though the explicit meaning of the term 'fitness' is rarely stated. In this paper I examine some of the different roles that fitness has played in the development of the theory. Whereas the meaning of fitness was originally understood in ecological terms, it took a statistical turn in terms of reproductive success throughout the 20th Century. This has lead to the ever-increasing importance of sexually reproducing organisms and the populations they compose in evolutionary explanations. I will argue that, moving forward, evolutionary theory should look back at its ecological roots in order to be more inclusive in the type of systems it examines. Many biological systems (e.g. clonal species, colonial species, multi-species communities) can only be satisfactorily accounted for by offering a non-reproductive account of fitness. This argument will be made by examining biological systems with very small or transient population structures. I argue this has significant consequences for how we define Darwinism, increasing the significance of survival (or persistence) over that of reproduction.

1. Introduction

Few concepts in evolutionary theory are as central yet as ill-defined as the concept of fitness. Darwin, following Wallace's suggestion, included Spencer's expression «survival of the fittest» only in the later editions of the *Origin of Species* (starting with the fifth edition). As Paul (1988) points out, Darwin later acknowledged that "Survival of the Fittest" was a better way of expressing the main idea of the theory than the expression "Natural Selection". As Wallace commented to Darwin (see Paul, 1988, p. 416), "natural selection" had teleological or intentional overtones that Spencer's framing eschewed. The disadvantage is that using Spencer's expression seemed to link Darwin's theory to Social Darwinism: after all, many casual readers believed that Darwin (following Spencer) is interested solely in the survival of the fittest *individual organism*. This link was weakened with the rise of population genetics through the development of the Modern Synthesis by shifting the explanatory burden away from individual organisms onto allelic frequencies. While the meaning changed, the term 'fitness' remained at the core of Evolutionary Theory[1]. For better and for worse, Darwinism -defined for our purposes as a broad family of research projects centered on the idea that natural selection is the means by which adaptation is produced in the natural world- is grounded on the idea of the survival of the fittest. In defining Darwinism, I focus on selection and adaptation not because it exhausts Darwin's contribution to biology (it does not), but because these concepts provided one of the first truly compelling alternatives to arguments from (divine) design of the type offered among others by Paley, which, until Darwin, ruled our understanding of the perceived fit of organisms to their environment.

Since the fifth edition of the *Origin of Species*, the concept of fitness has occupied a significant place in the popular understanding of the theory but what does 'survival of the fittest' mean? Aside from the historical transition hinted at earlier (a shift from

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[1] Dobzhansky suggests using "adaptive value" instead of "fitness" in part to shed the Social Darwinist stigma but the shift hasn't been universally adopted (see Dobzansky, 1951, 77–79 and Paul, 1988 for discussion).

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individual organisms to alleles), there is a conceptual necessity for providing a satisfactory account of fitness. We need to understand these foundations to truly be able to assess what is the correct domain of application of evolutionary theory: what can evolve and how can we model evolution in nature?

To see why this is a real issue, one needs only look at the most often quoted framing of the process of natural selection, the one offered by Richard Lewontin (my emphasis in bold) (in Levins & Lewontin, 1985, p. 76):

A **sufficient mechanism** for evolution by natural selection is contained in three propositions:

1. There is variation in morphological, physiological, and behavioral traits among members of a species (***the principle of variation***).
2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (***the principle of heredity***).
3. Different variants leave different numbers of offspring either in immediate or remote generations (***the principle of differential fitness***).

To paraphrase this statement: variants in nature deal with varying success with their environment and if what allowed the 'lucky' variants to thrive is passed on to the succeeding variants, then evolution by natural selection will be obtain. This may seem like a contrived way of reframing Lewontin's statement, but I will argue that there is genuine advantage for such abstraction.

Intuitively the notion of fit between an organism and the problems posed by the environment has always been part of Darwinism. This is not always the case in the explicit scientific models themselves. Whereas the meaning of fitness was originally set out in ecological terms (i.e. the fittest individual organisms survive in their environment), it took a statistical turn in terms of reproductive success of population variants throughout the 20th Century. While this turn doesn't eliminate the ecological characterization of fitness it explicitly pushes it in the background. If there is random variation among the traits of organisms and if some variant traits fortuitously confer advantages on the organisms that bear them then those organisms will live to have more offspring, which in turn will bear the advantageous traits, thereby increasing the frequency of the trait bearers (and their genes) in the population. Fitness is then explicitly described in populational terms: 'good' traits are replicated in a population so the fitter entity is the one with the most descendants. In other words, fitness is usually about differential reproductive success. I will examine various reasons why this account is unsatisfactory (or at least in need of revision). My proposal has three major motivations:

1- *Urgency for our understanding of contemporary evolution*. At least some biological organisms' evolution cannot be adequately understood if we focus exclusively on reproductive success. In this paper, I will focus on one clonal species to show the limitations of a reproductive account of fitness. I will argue that since these clonal organisms are doing something 'right' without reproduction we need to see how our understanding of fitness can be modified.

2- *Urgency for our understanding of past evolution*. The facts that most of life of Earth has not been sexually reproducing and that all sexually reproducing species have evolved from asexual reproducing species behoves us to modify our understanding of evolution so that it can adequately chart out not just the last 500 million years of evolution (about the time sexual reproduction arose) but the 3.5 billion years before that. It's not the case that all clonal species pose a problem for replication accounts, but rather that many do. We will see that for many clonal species, selection acts on the parts of a growing individual, not a growing population of individuals.

3- *Urgency for our understanding of the origin of life*. Our best current understanding of evolutionary theory is basically making the claim that at some point in the history of life on Earth, entities started reproducing and that that permitted evolution by natural selection to kick in. It might be fruitful to examine how evolutionary theory recast in terms of persistence (my proposal) might be able to explain how life itself arose as the result of the evolution of physical and chemical forms into more persistent biotic forms. Many projects related to inquiry about self-organization or evolution and thermodynamics have been making similar claims, but many lack a unified account of fitness.

A full account of usages of the term fitness will not be offered here (See Rosenberg and Bouchard, 2008). What I will offer here are examples of the difficulty of identifying populations, and difficulties establishing reproductive success for some biological systems and how these should inform our understanding of 'survival of the fittest' and of Darwinism.

I argue that, moving forward, Darwinism should look back at its ecological roots and focus on survival (or persistence) in order to be more inclusive in the type of systems it examines. This move is necessary for the motivations 2 and 3 highlighted above. Reproducing entities have evolved from non-reproducing entities. The question remains as to whether this transition was itself the result of evolution by natural selection or not. How we define fitness is an important component of the answer to this question. I will briefly explore this point at the beginning and end of this paper. The first motivation will occupy a large part of this paper. Many biological systems (e.g. clonal species, colonial species, multi-species communities) can only be satisfactorily accounted for by offering a non-reproductive account of fitness. Such an account will be sketched out in terms of the differential persistence of lineages. I have provided a fuller account of this idea elsewhere (see Bouchard, 2004, 2008) but here I will develop a specific part of this broader argument: extremely small population structures show that that growth and reproduction are not as distinct as we often believe. If this is the case, then it's not so much populations that are needed (contra Lewontin's characterization of the process of evolution) but collections of components. This has deep implications for how we can explain the adaptive change in many biological systems. This will be the core of the argument presented here.

2. Where do replicators come from?

As I stated earlier, one of the main explanatory benefits of Darwin's theory of evolution is the way it provides an explanation for adaptation (i.e. how well organisms seem to fit the demands imposed by their environment). I want to show that one does not need populations per se to get evolution by natural selection (although one needs ensembles or collections of something: and as we shall see the distinction between population and ensembles is not trivial). Further, I will develop some ideas about how to think about fitness in general. Focusing on ensembles instead of populations also changes the role of reproduction. This will be presented not merely as a clever semantic shift, but as a way to understand actual cases of adaptive changes that are not well accounted for by standard accounts of evolution by natural selection.

Under many contemporary interpretations of the theory of evolution by natural selection focused on replicator based explanations, evolution is the accumulation of change in allelic frequencies