Reconsidering the logical structure of the theory of natural selection

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Natural selection has been criticized as a tautology. This would be a major problem for evolutionary biology, if true, because tautological statements can’t be falsified and, therefore, can’t be scientific. There is merit to this critique insofar as the theory of natural selection is indeed generally described in a tautological manner. However, natural selection can be described non-tautologically if we’re careful. Natural selection should be defined as the theory that attempts to predict and retrodict evolutionary change through environmental forces acting upon organisms. However, this re-framing comes at a cost: it reveals, based on our current knowledge of evolutionary forces, the lack of ability to make accurate predictions about expected changes except in the most simple of circumstances. I suggest that evolutionary biologists should work to develop “principles of evolution,” based on an expanded and more focused research program designed to identify common trends in evolution, which will ultimately allow us to make more accurate predictions and retrodictions about evolution.

Framing the Tautology Problem

Tautologies and circular statements are always true and are thus not useful as theories because they can’t be falsified. A tautology is a statement that is true by necessity. Tautologies often take the form “a equals b,” but b reduces to a, so really “a equals a.” Similarly, circular statements include components that rely on each other mutually for their definition, taking the general form “a is true because b is true and b is true because a is true.” Tautologies and circular statements cannot be falsified, because they are always true, so they are not scientific under a Popperian view of science.

In this paper, I agree that natural selection, as the prevailing theory of how evolutionary change occurs, is generally described in a manner that is tautological or circular. I suggest below, however, how to save natural selection from tautology or circularity. This comes at a cost, which is to accept that natural selection theory is not currently predictive in the way that mature scientific theories should be. I also suggest a rough outline of how natural selection theory may become more predictive.

Darwin first described natural selection in The Origin of Species in a way that is tautological. The full title of his seminal book is On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life. The sub-title is itself a tautology because “natural selection,” “preservation of favored races” and “struggle for life” all reduce to the same concept, if we accept...
that “struggle” includes reproduction as well as survival. A equals a equals a. Tautologies can sometimes be useful in terms of describing the same concept with different words that give more information about key ideas (I just did it by using the terms “concept” and “ideas,” which are exactly the same thing in this context). However, in describing the prevailing theory of evolution, we must avoid tautology at all costs because tautology renders the theory empty.

In *Origin*, Darwin describes natural selection as the “preservation of favorable variations and the rejection of injurious variations…” But this is again a tautology because “preservation” and “favorable” reduce to the same thing (what is preserved is defined as being favorable and what is favorable is defined as that which is preserved), and “rejection” and “injurious” reduce to the same thing under the same reasoning process. A equals a.

Similarly, Herbert Spencer’s phrase, “survival of the fittest,” used frequently as a short definition of natural selection by Darwin (in later editions of *The Origin*) and many others since, is a tautology and circular because “survival” and “fittest” reduce to the same concept. What survives? The fittest. What organisms are the fittest? Those that survive. A equals a. I examine further below the tricky concept of fitness.

For a more modern description of natural selection, Ayala (2008) writes: “Natural selection – i.e. differential multiplication – can accomplish adaptation because a favorable mutation that has occurred in one individual may thus spread to the whole species in a few generations…” Parsing this sentence, we see that “Natural selection,” “differential multiplication,” “favorable,” “accomplish adaptation,” “may thus spread,” are all ways of saying the same thing: more offspring are produced in some situations. Even more simply, all these phrases say, essentially, is that *there is some biological change occurring*, with no explanation as to how. A equals a equals a equals a. The “how” is what natural selection theory is supposed to provide, but providing mutually inter-defined terms does not do so.

To most encountering this critique for the first time, there is a shake of the head and a refusal to acknowledge that such a serious problem could have persisted in evolutionary theory for this long. It seems that the root of this (wrong) conclusion is the deceivingly common-sense feeling that adaptations and natural selection are not the same concept. They are indeed different in some ways, but they reduce to the same concept. We know intuitively that an opposable thumb, for example, is an adaptation to our environment because it’s so useful in our normal (human) lives. And we know that being able to run faster than potential predators is an obvious adaptation for a deer, through observation. So of course these types of adaptations will spread through the population in a process that we label “natural selection;” that is, nature, as the sum of various forces in the environment of the organism or population at issue, favors (selects) these adaptations.

But most adaptations are not so obvious as those I’ve just described, and many are not at all obvious. The large majority of adaptations can, as a consequence, only be assessed as adaptations by examining how they play out in the game of life; that is, by examining how many offspring result from organisms that enjoy the ostensibly adaptation. Is a slightly darker shade of fur in a field mouse an adaptation to its particular environment? Is a slightly longer wing an adaptation to a hawk in its particular environment? We could only know in these cases, and in the vast majority of potential adaptations, what actually is adaptive by looking at the results in terms of survival and reproduction of the organisms possessing the trait(s). Thus, defining adaptations in relation to natural selection, and vice versa, results in tautology.

One of the few biologists to tackle this issue head on, Stephen Jay Gould, would have disagreed with what I have just written were he still with us. However, I think it is clear that his arguments are insufficient to save natural selection from tautology, Bethell (1976) writes, in a popular article on the subject:

Darwin made a mistake in proposing his natural-selection theory, and it is fairly easy to detect the mistake. We have seen that what the theory so grievously lacks is a criterion of survival that is independent of survival. If only there were some way of identifying the fittest beforehand, without always having to wait and see which ones survive, Darwin’s theory would be testable rather than tautological.

In a 1976 rebuttal to Bethell, Gould (1976) writes (emphasis in original):

... Darwin was justified in analogizing natural selection with animal breeding. In artificial selection, a breeder’s desire represents a “change of environment” for a population. In this new environment, certain traits are superior a priori; (they survive and spread by our breeder’s choice, but this is a result of their fitness, not a definition of it). In nature, Darwinian evolution is also a response to changing environments. Now, the key point: certain morphological, physiological and behavioral traits should be superior a priori as designs for living in new environments. These traits confer fitness by an engineer’s criterion of good design, not by the empirical fact of their survival and spread. It got colder before the woolly mammoth evolved its shaggy coat.

But Gould’s “a priori defense” clearly fails. How can we know what constitutes fitness as an a priori matter? It seems, rather, that the only way we can know what constitutes fitness, as a general matter, is by operationalizing the definition of fitness, that is, by looking at what actually survives in actual populations. We can conduct lab experiments and bioengineering experiments to attempt to measure various possible adaptations and their fitness, but we can never know what a given trait’s actual impact on fitness is until we examine it in actual populations, either in the lab or in the wild. This is not a priori.

We are back to tautology: the fittest survive and those that survive are the fittest. There is nothing a priori about survival and adaptation because literally every environment, organism and population is different. I suggest below that it is possible to develop “principles of evolution” that may constitute a more general theory of evolution, but it seems we are far from having a firm set of such (predictive)
principles at this point. And my suggested principles of evolution will never amount to a priori principles. To the contrary, they will be developed only through rigorous empirical work—the opposite of a priori.

Lipton and Thompson (1988)\textsuperscript{10} attempt a more spirited defense of natural selection against charges of circularity by arguing that natural selection explanations are recursive rather than circular and are a type of filter explanation. For example, to answer the question "why are polar bears white?" a filter explanation says "because there is a filter that makes them white." The filter is then to be specified through examination of the environment and polar bear populations. Lipton and Thompson disavow the very common practice of defining natural selection or adaption in reference to fitness because they recognize explicitly that such explanations are indeed circular and thus empty. But when we examine their attempt to sidestep circularity or tautology by appealing to recursivity and filter explanations we see that filter explanations, as a category, a meta-theory, reduce to a simple posit that there is some natural cause (the filter) that led to the traits at issue. And positing that there is some natural cause for the trait at issue is not helpful as a theory, other than to make a basic distinction between natural selection and supernatural theories of evolution. This distinction itself is important, to be sure—particularly in the context in which Darwin wrote—but it does not qualify natural selection as a general theory without a great deal more development. Lipton and Thompson themselves discuss how theories can be over-general because they don’t always exclude possible explanations, but their own filter theory explanation of natural selection is itself far too underspecified for the reasons just stated. To be useful as hypotheses, filter explanations must specify the details of the filter posited.

We have, then, 2 components to the theory of natural selection under Lipton and Thompson’s approach: 1) a general statement about the nature of filter theories as recursive but not circular explanations of evolutionary change; 2) the detailed development of such filter theories. However, part 1) is, as just described, nothing more than an assertion that there is some cause for the evolutionary changes at issue, a truism. Part 2) is crucial in terms of natural selection becoming a general theory. But if part 1) does no work, what is it that unites the set of part 2) filter theories into a general theory? We can say that it is their nature as filter theories, but we have just seen that calling them “filter theories” doesn’t actually do anything to distinguish them from other scientific theories or hypotheses, which are, by definition, causal theories. Thus the set of filter theories that may eventually comprise a general theory of natural selection display little to nothing to distinguish them from other causal theories that may or may not be classifiable under the “natural selection” rubric. We need to look elsewhere for solutions.

**Honing in on the Problem**

It’s helpful at this point to consider some of the key concepts in evolutionary biology today: natural selection, fitness and adaptation. I offer the following definitions, as they are generally framed:

1. Adaptations are new traits that lead to increased fitness for organisms and populations
2. Increased fitness leads, through the process of natural selection, to increased survival and reproduction ("survival of the fittest")
3. Natural selection is the process whereby adaptations spread throughout a population by differential reproduction

These definitions should appear sound to most readers. However, on closer inspection we see that each of the definitions/ descriptions hinges on the other in a manner that is entirely circular. (1) Adaptation is defined through reference to fitness; (2) fitness is defined through reference to natural selection; (3) Natural selection is defined through reference to adaptations. And we are back to the beginning of the circular chain.

These are not entirely new arguments. Numerous writers have criticized natural selection as a tautology or circular argument, including Butler (1882),\textsuperscript{11} T. H. Morgan,\textsuperscript{12} Waddington (1960),\textsuperscript{13} MacBeth (1971),\textsuperscript{14} Bethell (1976)\textsuperscript{15} and more recently Rosenberg and Bouchard (2008).\textsuperscript{16}

The tautology/circularity charge, if true, is fatal to natural selection as a theory of how biological change occurs. This is an exceedingly nuanced issue yet it is surprising that so few biologists and philosophers of biology have tackled the issue head on. I suggest in the next section a possible resolution.

**Toward Resolution**

Responses to the tautology critique have varied from no response (the most common) to Gould’s appeal to “a priori engineering principles,” to Lipton and Thompson’s filter theory approach, to an explanation of fitness as “expected fitness” rather than actual fitness. I’ve addressed above how Gould’s and Lipton and Thompson’s approaches fail. However, the “expected fitness” approach, often described as the “propensity approach” or “propensity interpretation” of fitness, goes part way toward resolving the issues I’ve described. Resolving the tautology problem for natural selection requires that we more closely examine the concept of fitness.

Brandon and Ramsey (2007)\textsuperscript{17} defend the propensity interpretation of fitness, which was developed specifically to resolve the tautology problem:

The prime motivation [for introducing the propensity interpretation] was to make room for an explanatory theory of natural selection, which is tantamount to solving the so-called “tautology problem.” This problem arises from a casual inspection of the phrase “survival of the fittest” and then asking what defines the fittest. If the answer is those that reproduce the most, then it seems we are explaining a phenomenon, differential reproduction, in terms of itself, which is no explanation at all.”

The propensity interpretation of fitness allows statements such as: “We expect population A to grow by x percent
as a result of a y percent increase in seed stock.” The “x percent growth” prediction is the “expected fitness” of population A. This re-framing allows a definition of (testable) natural selection as follows:

Natural selection is a theory that predicts differential survival and reproduction of organisms with the highest expected fitness.

The propensity interpretation does indeed save natural selection from tautology because “expected fitness” does not reduce to “survival,” because the former is defined as a theoretical expectation and the latter is defined based on empirical observation. Nevertheless, there are additional perils lurking in this approach, particularly as they relate to the concept of expected fitness – a companion concept necessarily inter-related to the concept of natural selection. And we are far from the point, based on today’s knowledge of evolutionary processes, of being able to make accurate predictions about expected fitness.

With respect to the propensity interpretation of fitness, Rosenberg and Bouchar (2008) state that evolutionary theory’s “reliance on the concept of ‘fitness’ makes it imperative that conceptual problems threatening the explanatory legitimacy of this notion be solved.” And: “[F]ar from providing the theoretical meaning of fitness, the probabilistic propensity ‘definition’ is a set of an indefinitely large number of operational measures of fitness.” They conclude: “The problem of defining fitness remains.”

Beatty and Finsen (1989)18 conclude similarly: “We are not sure whether a radically revised interpretation of fitness is necessary. But it does seem to us that certain gross oversimplifications of the propensity interpretation deserve more serious attention. We most certainly do not propose to return to the interpretation of fitness that the propensity interpretation was designed to replace. Whatever fitness is, it is not actual offspring contribution, although it was long misconceived as such.”

“Whatever fitness is...” is the key phrase here. Beatty and Finsen undertake a detailed examination of the many different propensity interpretations, which they label the “multiple propensities problem,” demonstrating that “the greater ability to leave offspring” is itself impossible to define in a non-arbitrary way. This is the case because what timeframe should one consider in such an analysis? One generation, 2, 3, infinite? Different statistical approaches yield different answers. Beatty and Finsen illustrate this problem with the following image: is A or B more fit; does A or B have a higher propensity for survival and thus higher fitness?

The seemingly inescapable conclusion (my own, not Beatty and Finsen’s, who hold out some hope of a non-arbitrary approach) is that “expected fitness” cannot be defined in a non-arbitrary way – but this isn’t itself a fatal problem if we recognize that “expected fitness” is simply the biologist’s tool for making predictions about expected evolution in actual organisms or populations, rather than some property that inheres in organisms or populations.

Summing up: we are saved from tautology by the propensity interpretation(s), and its reliance on “expected fitness,” but with a cost: we must acknowledge that there is no a priori property or value of fitness or expected fitness – as Gould and others have argued. The way in which we define fitness or expected fitness is necessarily arbitrary. This is a substantial but not a fatal problem, so we have made progress. In dealing with arbitrariness, we simply need to be clear how we are defining fitness or expected fitness in each circumstance, allowing for useful comparisons across different studies, as well as conceptual coherence. Moreover, for natural selection to earn its reputation as a powerful theory of how evolution occurs, the theory must be developed far more than it has to date, with a focus on testing and improving evolutionary predictions.

Along these lines, Orzack (2010)19 has called for an Adaptationism Project akin to the Human Genome Project. This project would conduct and collect rigorous studies from around the world and establish in as many real circumstances as possible whether natural selection was the primary agent in observed evolutionary change, a fact that is simply assumed by adaptationists.

Developing natural selection as a theory will require developing a detailed set of filter theories for particular circumstances. These sub-theories will, after testing in numerous experiments, eventually allow development of what may be labeled “principles of evolution.” The good news is that increasingly sophisticated computer models are being developed that should, with good empirical data, allow for the development of the suggested principles more readily than without these powerful new tools. It may be the case, however, that many aspects of evolution in actual populations will remain forever unknowable due to the inherent complexity in such populations. Once we are able to develop models for accurately predicting the course of evolution in actual populations (if not all), natural selection may fairly be described as a general theory of evolution.

While the details of the proposed principles of evolution are beyond the scope of this paper, and certainly beyond my current knowledge, it does seem clear that a new synthesis of evolutionary theory will be far more pluralist than today’s focus on adaptation and natural selection would suggest. I have proposed the outlines of a Generalized Agentic Selection theory as a complement to natural selection in Hunt (2011).20 An in-progress paper fleshes out these ideas. The present critique refers only to natural selection and doesn’t delve into the issues surrounding the origin of variation. The Modern Synthesis posits that variation is random, but it seems that an increasing number of non-random sources of variation, such as Shapiro’s21 natural genetic engineering, or Kirschner and Gerhart’s “facilitated variation,”22 must also be considered if we are to create a more predictive theory of evolution.

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No potential conflicts of interest were disclosed.

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