Critical Review

Evolutionary Teleonomy as a Unifying Principle for the Extended Evolutionary Synthesis

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Abstract

Many people underestimate the effect that unifying principles have on the study of biology. Unifying principles are used to provide simplifying assumptions to complex problems, which allow them to be effectively tackled by the tools at hand. However, erroneous unifying principles will generate simplifying assumptions that lead towards mischaracterizations of problems which inevitably lead to invalid conclusions. The unifying principles of the current Modern Synthesis of evolution are presently being challenged by the Extended Evolutionary Synthesis. However, the Extended Evolutionary Synthesis has so far failed to provide unifying principles of its own, which has caused many to question whether or not the Extended Evolutionary Synthesis is indeed a unique synthesis of evolutionary biology. Here, the concept of evolutionary teleonomy (Ernst Mayr's concept of teleonomy applied to evolutionary processes themselves) is identified as a unifying principle of the Extended Evolutionary Synthesis. Additionally, specific examples are provided where modern research has been led astray by the unifying principles of the Modern Synthesis which would have been corrected by applying the Extended Evolutionary Synthesis with the unifying principle of evolutionary teleonomy.

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INTRODUCTION

Unifying principles have an important place in biology and, in fact, in all sciences. Unifying principles supply a default way of viewing the world. As opposed to strict laws, the primary goal of a unifying principle is to provide a mental map to researchers as to the territory that they are exploring. Laws provide invioable conditions, while unifying principles supply generalities that can be safely employed in the absence of opposing evidence. Unifying principles are used implicitly by researchers to provide simplifying assumptions, default conclusions, and research directions.

As an example, *localism* is a unifying principle of physics. That is, in physics, it is generally assumed that, all things being equal, causal entities near an event implies relatively more influence than a causal entity far away. This is not conceived of as a law—in fact there are many places where it is known to be false. However, it is a unifying principle. If a strange effect is noted, researchers do not first go check to see if the conditions on Neptune are somehow affecting an experiment in their lab. Their first reaction will be to check nearby conditions which cause the effect.

Additionally, other theories tend to be written (or rewritten) from the perspective of the unifying principle. Gravity was originally difficult to conceive of within the framework of localism, but the reconception of gravity as a warping of spacetime solved that problem.

Everyone needs a mental map of the space that they are looking into. There are an infinite number of facts available, experiments to try, and ways to understand results. Therefore, unifying principles, both stated and unstated, provide a map and guideposts to channel scientific effort in understandable (and hopefully successful) directions. They also provide the source for null models against which other hypotheses are tested [1].

These unifying principles also help a subject to be taught. Students cannot be expected to have read or experienced all of the source material of the prior generation, but well-articulated unifying principles help to synthesize the work of prior research into a form that is both understandable and actionable.

Unifying principles perform most of their work effortlessly. This is beneficial because having to explicitly justify every mental step would be costly. However, it is important to be sure that unifying principles are explicitly revisited from time to time to make sure they are leading us in positive directions. Uncovering problematic principles is an important task in order to be sure that such principles do not mislead future researchers into following a mental map whose features don't match the actual terrain.

THE MODERN SYNTHESIS

From the 1920s through the 1960s, a group of scientists developed a set of unifying principles for evolutionary theory. Known collectively as the Modern Synthesis, these ideas continue to provide the framework for evolutionary biology today. The following ideas are at the core of the Modern Synthesis:

1. Evolution at all levels results from the continual shifts in populations described by population genetics [2].
2. Genetic mutation is the result of haphazard processes, such as errors in DNA replication or the influence of cosmic X-rays. In other words, no controlling process or system guides mutation in a way that benefits organisms [3].
3. The primary directionalizing influence on organismal evolution is natural selection, which likewise is free form any controlling process or system [3].

It should be noted that while many people believe that the neutral theory of molecular evolution [4] is at odds with the Modern Synthesis, the neutral theory actually incorporates the main features of the Modern Synthesis. The neutral theory (a) is based on population genetics, (b) does not propose any guided process for mutation, and (c) holds that, to the extent that there is any guiding at all in evolution, it is indeed done by selection, and that there is no guiding mechanism behind selection itself. The main distinction of the neutral theory and is that, contrary to adaptationalism or selectionism, it downplays the importance and necessity of selection as a directionalizing influence, emphasizing instead predominant role of stochastic events in the course of evolution.

While these principles of the Modern Synthesis are not held by every biologist, they do represent the majority view, making them the default background position for research in evolutionary biology.

THE EXTENDED EVOLUTIONARY SYNTHESIS

A loose-knit group of biologists has over the last decade been calling for a new synthesis to replace the Modern Synthesis. The new thinking, now referred to as the *Extended Evolutionary Synthesis*, gained prominence as a result of a workshop held at the Konrad Lorenz Institute for Evolution and Cognition Research in 2008. The workshop resulted in a book titled *Evolution, the Extended Synthesis* [5].

Among the new ideas (not included in the Modern Synthesis) are the following, as described by Pigliucci and Müller [6]:

- Contingency as a more primary actor in determining possible mutations
- Shifting focus from individual genes to gene networks
- Various new kinds of inheritance, including transgenerational epigenetic inheritance, niche inheritance, and cultural inheritance
- The influence of developmental biology on the theory of evolution
- The analysis of evolvability itself

Many other scientists have subsequently chimed in, some to say a new synthesis is absolutely necessary [7], some to say that the Modern Synthesis is just fine as it is [8], and others to say they don't see a distinction between the two.

Laland et al. [7] list the features that they think make the Extended Evolutionary Synthesis distinct. These include:

1. Extended inheritance: organisms inherit more than just genes and more than just by physical inheritance. Organisms not only have genetic and epigenetic inheritance, they have inheritance of behavior based on the nurturing of parents and biological communities.
2. Reciprocal causation: organisms shape their environment, which then acts on themselves.
3. Non-random phenotypic variation: organisms are biased in certain evolutionary directions rather than others, as reflected by available evolutionary phenotypes.
4. Variable rates of change: the effects of mutations are non-linear, and therefore have the potential for saltational effects.
5. Organism-centered perspective: organisms themselves have a larger causal role in the Extended Evolutionary Synthesis, as opposed to the gene-centered approach of the Modern Synthesis.
6. Macro-evolutionary processes: the additional modes of inheritance will also lead to additional macro-evolutionary processes.

This list maintains the cautious approach typically taken by those favoring the Extended Evolutionary Synthesis, making it unclear whether it deserves to be treated as a new synthesis. Is this really new, or are they merely tweaking around the edges?

The architects of the Extended Evolutionary Synthesis are adamant about the need for a new synthesis but highly cautious about how it is described. Pigliucci and Müller sum it up like this [6]:

> The concepts we bring together in this volume for the most part do not concern population dynamics, our understanding of which is improved but not fundamentally altered by the new results. Rather, the majority of the new work concerns problems of evolution that had been sidelined in the MS and are now coming to the fore ever more strongly, such as the specific mechanisms responsible for major changes of organismal form, the role of plasticity and environmental factors, or the importance of epigenetic modes of inheritance. This shift of emphasis from statistical correlation to mechanistic causation arguably represents the most critical change in evolutionary theory today.

Essentially, according to these authors what is new about the Extended Evolutionary Synthesis is that it takes what used to be "black box" pieces that it could not look into, and opens them up to make them central to evolution. However, according to them, it does not fundamentally alter any past grounding principle of the Modern Synthesis.

Taking the underlying principles of the Modern Synthesis seriously, we will see that the Extended Evolutionary Synthesis quietly but drastically alters them. However, the architects of the Extended Evolutionary Synthesis appear to be holding too tightly to past principles to be frank about the most interesting aspects of their proposal.

TELEONOMY AND EVOLUTION

To understand the way in which the Extended Evolutionary Synthesis differs from the Modern Synthesis we need to look at the concept of teleonomy and its role in the theory of evolution.

For more than a century, biology has struggled with the concept of teleology. Teleology is the orientation of objects (often organisms) towards *ends*. That is, organisms have purposes which are reflected in their behaviors. What makes biology unique as a subject is that while the study of rocks or atoms rarely makes reference to purpose, the study of biology is almost exclusively concerned with purpose.

The understanding of organs within an organism is based on purpose. The understanding of the genome is based on purpose. When asking about a mountain, few people would ask, "what is that mountain there for?" However, the most fundamental question about an organ or organ system in biology is "what is the purpose of it?"

In Aristotle's view of causation, final (i.e., teleological) causes are just as fundamental as efficient causes. The growth of science in the 18th and 19th centuries, however, began to lessen the role of teleological causes, eventually excluding them from science altogether [9]. Bacon, for instance, believed that reliance on teleological causation tied causal explanation too closely to man's own nature, making it harder to describe the universe as it really is.

While Bacon's ideas were generally kept to physics through the early part of the 19th century, the idea of evolution by natural selection seemed to remove teleology from biology as well. There was nothing in natural selection that referred to purpose—only to reproduction. The whole of evolution was therefore devoid of purpose. If teleology was not needed in physics, and now it is not needed in biology, then it seems like there is no need for it at all.

Thus, the whole concept of purpose fell out of favor with biologists. It was thought of as an old-fashioned concept—a leftover relic that would soon go the way of alchemy. By the beginning of the twentieth century, biologists were actively avoiding any sort of purpose-oriented language, sometimes to the point of ridiculousness.

As reported by Pittendrigh [10],

> Biologists for a while were prepared to say a turtle came ashore *and* laid its eggs, but they refused to say it came ashore *to* lay its eggs [emphasis in original].

In other words, biologists were careful not to ascribe any purposefulness to organisms out of fear of being labelled a teleologists, thereby having their views tainted with Aristotelian causation. Despite the fact that it is obvious that turtles do indeed come to shore for the purpose of laying their eggs, biologists were uncomfortable with stating that plainly.

In order to alleviate the situation, Pittendrigh [10] and later Mayr [11] suggested using the term *teleonomy* instead of teleology to describe this sort of purposive behavior.

Mayr suggested that we can use the term teleonomy to represent something that operates according to a purpose *because of a program*. Specifically, Mayr [11] says

> It would seem useful to restrict the term teleonomic rigidly to systems operating on the basis of a program, a code of information. Teleonomy in biology designates "the apparent purposefulness of organisms and their characteristics," as Julian Huxley expressed it.

That is, to the extent that organisms operate according to their genetic programming, "purpose" can simply refer to the actions of the program behind the organism.

Thus, Pittendrigh and Mayr devised a way to include purposive behavior and descriptions within biology without invoking the Aristotelian worldview generally associated with purpose in causation.

However, Mayr was concerned with the fact that someone may try to tie the new teleonomy with the old teleology through evolution. That is, they may try to explain the existence of the program-directed purposiveness by reference to a teleological system (i.e., a divine purpose or something similar). However, the Modern Synthesis that was developing at that time had a ready answer to this—evolution itself cut any teleological connection between the organism and any higher organizing principle. Because evolution proceeded by random or happenstance changes (i.e., non-teleological changes), there was no linkage between the results of evolution and any purposes within nature.

Simpson [12] stated it this way:

> Only three processes are known to [change the genetic pool]: mutation, fluctuation in genetic frequencies, and differential reproduction. The first two of those processes are not oriented toward adaptation. They are in that sense essentially random, and are usually inadaptive, although they may rarely and coincidentally be adaptive. By "differential reproduction" is meant the consistent production of more offspring, on an average, by individuals with certain genetic characteristics than by those without those particular characteristics...

Mayr [11] made similar arguments, and further stating:

> If an organism is well adapted, if it shows superior fitness, this is not due to any purpose of its ancestors or of an outside agency, such as 'Nature' or 'God,' who created a superior design or plan.

As pointed out by Merlin [3], this view was not unique to Mayr, but instead was held by all of the founders of the Modern Synthesis. Organisms do have purposes, but they didn't *arrive* at their purposes through a purpose. Note that here, Mayr explicitly decries not only the influence of *outside* purposes (i.e., divine teleology) in evolution, but also the influence of *inside* purposes (i.e., biological purposes present within ancestors).

UNIFYING THE EXTENDED EVOLUTIONARY SYNTHESIS WITH EVOLUTIONARY TELEONOMY

So what does this have to do with the Extended Evolutionary Synthesis? Quite a bit, it turns out.

We can summarize the point of view of the Modern Synthesis regarding teleonomy as follows:

1. Organisms exhibit purposiveness because of teleonomy
2. Evolution lacks any teleonomic driver

The Extended Evolutionary Synthesis, however, seems to run directly counter to this point of view in many respects. The sections below will examine several of them in turn.

Modes of inheritance

One of the primary areas where the Extended Evolutionary Synthesis differs from the Modern Synthesis is in the number of modes of inheritance available for evolutionary action. These modes of inheritance, however, each appear to incorporate some amount of teleonomy in their operation.

The first mode of inheritance we will examine is niche inheritance. Niche inheritance is the idea that organisms construct niches which themselves provide an evolutionary influence over organisms. That is, the organisms are constructing the means to their own evolution.

What is the driver of this niche construction? The consensus is that the genetic program within an organism dictates to the organism how to construct its own environment. Likewise, we know that these environments are there for the benefit of the organisms *and their offspring*.

Thus, we have a program within an organism that is affecting its evolution. This directly contradicts Mayr's notion that "If an organism is well adapted, if it shows superior fitness, this is not due to any purpose of its ancestors or of an outside agency." In fact, according to niche inheritance, the adaptation of an organism to its environment is precisely *because* of the teleonomic purposes of the organism's ancestors. Thus, in the action of niche inheritance evolution is being directed at least in part by teleonomy.

Sexual selection is similar. In sexual selection, organisms, according to their internal programs, choose mates to *produce the most healthy offspring*. Thus, their internal genetic programs (i.e., the organism's teleonomy) are guiding their evolutionary results.[1] Sexual selection works precisely because the end results of evolution are what the genetic program is looking for. Organisms choose healthy mates (sexual selection) in order to have (teleonomy) healthy offspring (Evolutionary Teleonomy).

This also occurs in epigenetic inheritance. Organisms have the ability to modulate their genes through epigenetic influences. These are all modulated by existing programs within the organism. Therefore, the inputs in one generation, guided through a teleonomic program, directly affect the evolutionary outputs in the next.

Developmental biology

In the Extended Evolutionary Synthesis, developmental biology is shown to play an important role in evolution. Specifically, the developmental pathways that undergird ontogeny canalize the effects of genetic evolution. In other words, organisms develop in such a way as to take advantage of mutations that occur within them. They have mechanisms of action which cause potentially happenstance mutations to reveal themselves in ways that are developmentally consistent.

For instance, during bone development, chondrocytes secrete factors that encourage blood vessel formation [13]. This means that the blood vessels and bone structures do not need to be separately coded within the genome. They

[1] It may be pointed out that sexual selection has always had a prominent place in evolutionary theory, even during the development of the Modern Synthesis. This is true. However, it was not recognized often or at all the way in which the nature of sexual selection undermined, and was actually directly contradictory to, the nature of selection as presented by the theory. Increasingly relying on sexual selection means putting additional pressure on internal inconsistencies in the way in which terms and ideas in the Modern Synthesis were thought of and applied, and shows that the underlying, unifying principles are less sound (and less unifying) than usually understood.

are linked in such a way that changes to the structure of the bones will automatically cause a matching change to blood vessel formation to make sure that the new shape is properly vascularized.

Thus, there is a program (a teleonomy) that partially directs the evolution of an organism by making sure that certain changes are matched by other changes.

Evolvability

Another important subject in the Extended Evolutionary Synthesis is that of evolvability. Evolvability is essentially the idea that different genetic features of an organism have different edit distances from an ancestor genome. Edit distance, however, is affected not only by the raw number of base pairs which need changing, but also the mechanisms of change available to the organism. When the mechanisms of change (i.e., programs or teleonomy within the organism that direct the generation of mutations) align with the pathways of evolvability (i.e., selectable features), the organism is demonstrating a very direct type of Evolutionary Teleonomy.

This branch of the Extended Evolutionary Synthesis aligns (both in terms of advocates and in terms of ideas) with what has become known as the "third way".[2] Shapiro [14], Caporale [15], and Noble [16] show that many systems within organisms can direct the evolution of specific genes. These evolvability systems are encoded by the genome, targeted by gene products, and produce effects that benefit the evolution of offspring. In every way they match the concept of Evolutionary Teleonomy.

Teleonomy in the Extended Evolutionary Synthesis

As is evident, Evolutionary Teleonomy plays a central, unifying role in nearly every aspect of Extended Evolutionary Synthesis.[3] Additionally, teleonomy itself also meshes more naturally with other ways in which biology is analyzed. In nearly every other aspect of biology, the presumption of function is used as a heuristic for understanding how biological systems work. This teleonomic presumption was removed during the Modern Synthesis, but further developments in the theory of evolution over the last several decades show that Evolutionary Teleonomy should be returned to a central place in evolutionary thinking.

HOW EVOLUTIONARY TELEONOMY AIDS BIOLOGICAL REASONING

I noted in the Introduction the importance of unifying principles within a discipline. Ultimately, human beings must be able to reason and make logical connections, even when not all of the facts are in. Therefore, theory development is of utmost importance, because it provides a rubric by which we supply information when it cannot be obtained explicitly. The Modern Synthesis is not merely a label, but is in fact a mode of supplying facts not in evidence. If the synthesis has a strong alignment with the truth about the world, this can lead to great strides. However, if the synthesis is not strongly aligned with truth, then it will lead us astray in important areas, often without notice.

An excellent example of this occurs in a recent paper by Graur [17]. A number of datasets and population-genetics equations are combined in that paper with a goal of determining the functional fraction of the human genome.[4] To do this work, Graur needed to estimate the deleterious mutation rate per base pair in the genome. How did he come up with this estimation?

First, he decided on a mutation rate, using a rate on the order of 1.0×10^{-8} based on data from Scally [19]. Then, to calculate the fraction of mutations that are deleterious, he divided mutations into three categories—synonymous mutations (mutations that don't change the amino acid sequence), missense mutations (mutation that change a single amino acid), and nonsense mutations (mutation that generate a premature stop codon, thereby preventing expression of the full gene).

Graur argues that synonymous mutations don't affect selection, and therefore should be categorically classified as non-deleterious, and that nonsense mutations do affect selection, and therefore should be categorically classified as deleterious.

This provides an lower and upper bound for the fraction of deleterious mutations as between 4% and 76% respectively. Thus, the location on this rather large range where the actual deleterious mutation fraction lies is determined by the frequency with which missense mutations are deleterious. For the purpose of this argument, we will not take issue with Graur's assumptions and calculations up to this point, and merely assume them to be correct.

So, the question is, what percentage of the missense mutations are deleterious? This is where the unifying principles of the Modern Synthesis come into play. Graur combines two different statistics, which, if the Modern Synthesis were true, would be valid. However, if the Modern Synthesis is not true, then statistics cannot be combined the way Graur combines them. We will assume that the individual statistics themselves are correct.

[2] A listing of the advocates for the "third way" position can be found at http://www.thethirdwayofevolution.com/people.

[3] Some of the areas of Extended Evolutionary Synthesis, such as "reciprocal causation" and "organism-centered perspective" are a little fuzzier, but it is clear that Evolutionary Teleonomy fits in with these quite well. Evolutionary Teleonomy is specifically about reciprocal causation (organisms directing their own evolution), and it is difficult to be more organism-centered than saying that the organism itself is one of the causative factors in evolution.

[4] A reviewer amusingly noted that perhaps, following the practices in the early 20th century noted by Pittendright [10] (with the turtle example in Section), we should not say that Graur combined the datasets with a *goal* of determining the functional fraction of the human genome, but rather we should just say that he combined the datasets *and then* determined the functional fraction of the human genome. Purpose seems to lie behind almost every action of biological organisms, as has been pointed out by Turner [18].

The first statistic is the data about what fraction of *all possible* missense mutations are deleterious. For this, Graur uses Soskine and Tawfik's estimate that 40% of the total possible missense mutations are deleterious [20]. He then applies this to the number of missense mutations that occur in the human genome, which is estimated as being 72% of the mutations.

But are these two numbers combinable in that way?

Soskine and Tawfik's number is the fraction of *all possible* missense mutations that are deleterious [20]. But are the missense mutations that *actually occur* in the genome the same as the set of all possible missense mutations? If the Modern Synthesis is true, then we could at least say that the range of actually occurring mutations should not be preferentially inside or outside the set of all possible missense mutations. In that case, we would be able to use the percentage fraction of the total missense mutations as a stand-in for the ones that actually occur. If we presume that the genome is only accidentally (i.e., non-teleonomically) mutating, then the lack of a preference for deleterious or non-deleterious mutations can be reasonably modeled as a sampling from that set.

However, if the genome is in any way *active* (i.e., teleonomic) in the picking of mutations, then there is no present way to combine these two data points. As we have shown in previous sections, there is significant evidence that genetic evolution is at least partially teleonomic. Therefore, these data points cannot be combined.[5]

A reviewer pointed out that Graur's assumption that synonymous mutations were neutral is also a problematic point, as studies have shown that there are significant reasons to think that synonymous mutation sites are subject to selection. The question of whether or not synonymous mutations affect selection is a fascinating subject all its own which is also highly relevant to the notion of Evolutionary Teleonomy. Chamary et al. [21] show that, due to effects such as intron splicing and mRNA stability, synonymous mutations do in fact affect substitution. Nonetheless, that paper still suffers from the kind of issues we demonstrated for Graur's paper. Namely, they are presuming that random distributions of mutations are a sufficient proxy for actual distributions of mutations, under the assumption that mutations are not biased towards a particular beneficial outcome. Chamary et al. [21] show that there are sites in the genome that appear to be invariant, and they *assume* that this is due to selection pressure, when it might also be attributed to organisms undergoing mutation at lower rates in areas where it is potentially detrimental. The idea that the distribution of mutations themselves could be guided by internal mechanisms was not even considered by the authors.

Thus, we can see that unifying principles are not only used within education (teaching people about their subject), but are used directly in reasoning about the subject. The concept of Evolutionary Teleonomy can be helpful simply by giving editors and reviewers a way of referring to a class of considerations that researchers can take into account in their publications. "Have you considered the impact that Evolutionary Teleonomy would have on your results and assessments?"

Additionally, Evolutionary Teleonomy gives guidance about potentially useful directions of evolutionary research. Because research has been dominated by the Modern Synthesis for so long, many fields are ripe for re-examination along the lines of Evolutionary Teleonomy, and the term provides a unifying way of speaking about and understanding these undertakings. The question, "To what extent is the organism itself driving its own evolution?" is an important one that has been overlooked for a century or more, and Evolutionary Teleonomy provides a unifying theme for addressing it and similar questions.

The concept of Evolutionary Teleonomy also normalizes the mode of inference for the biological sciences. The field of Systems Biology, for instance, generally works from the presumption of function in any system it studies. That does not mean that it must conclude that all systems are functional, but the default mode of inference is that a biological system is likely to be functional unless specific reasons can be given that it is not. This is true up and down the biological sciences—the sociological structure of organisms, the gross morphology of organisms, the organs of organisms, the cellular structure of organisms, etc., are all presumed to be geared towards the benefit of the organism or the species as a whole unless specific reasons are found otherwise. If something has an unknown function, it is simply classified as such.

The exception, due to the effect of the Modern Synthesis, is evolutionary systems. The concept of Evolutionary Teleonomy normalizes evolution with respect to the rest of the biological sciences. Evolutionary Teleonomy does not say that all evolutionary processes are necessarily functional, but rather that we cannot discount the possibility of their function without specific evidence, and certainly cannot use the presumption of their non-function in constructive use of multiple datasets such as done by Graur.

CONCLUSION

The unifying principles of a subject perform several important functions. They serve as powerful aids for education and intuition while also providing a basis for inferences based on incomplete data. Throughout the twentieth century, the Modern Synthesis dominated as the unifying principle for biological evolution, focused on the idea that evolution *happens to* an organism, and that the organism itself does not have a significant causative effect in its own evolution. The Extended Evolutionary Synthesis claims to provide a new way of looking at evolution, but has failed to generate a set of unifying principles for biologists. We have proposed Evolutionary Teleonomy—the idea that organisms can actively

[5] There are many other issues with the Graur paper, not the least of which is the way in which technology offsets the necessary fertility replacement rates in humans. Nonetheless, the issue chosen was due to its specific reliance on the unifying principles of the Modern Synthesis.

affect their evolution on every level—as the new foundational principle of evolutionary biology. Evolutionary Teleonomy unifies many of the independent topics of the Extended Evolutionary Synthesis under a single, understandable label.

As has been demonstrated, these principles have real effects on the way that biological facts are used and applied in biological research, and using the wrong principles will lead to incorrect results.

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