The Evolutionary Contingency Thesis

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ABSTRACT

As Stephen Gould recently put it, evolution is like a videotape that, if replayed over and over, would have a different ending every time. Last time it featured, among other things, duckbilled platypuses and human beings. And while we can be pretty sure that future replays will be every bit as humorous in their own special way, we cannot expect them to be quite as edifying. We are all, humans included, unlikely outcomes.

Gould contrasts such contingent “details” as ourselves with general “laws” that guide the course of evolution: “Invariant laws of nature. Set the channels in which organic design must evolve.” But, Gould emphasizes, “the channels are so broad relative to the details that fascinate us!” In other words, laws of nature only loosely constrain the outcomes of evolution. In this paper, I will further elaborate Gould’s thesis and further defend it. My version of the thesis may appear at first to contradict Gould’s, especially inasmuch as he emphasizes contingent “details” while I emphasize contingent generalities. Correspondingly, my version may appear stronger, though I believe he intends his to be every bit as strong. The thesis that I will defend, most briefly put, is this: all distinctively biological generalizations describe evolutionarily contingent states of nature, moreover, “highly” contingent states of nature in a sense that I will explain.

KEY WORDS: evolutionary contingency, theoretical pluralism, relative significance.

INTRODUCTION

Traditionally, there are three kind facts. First, there are the logical, conceptual, mathematical, and metaphysical necessities: facts that absolutely could not have been otherwise. (these include, for example, the fact that Rebecca is taller than Abe if Abe is shorter than Rebecca). The rest (the “contingent” facts) divide into two classes: the laws of nature (together with their contingent logical consequences) and the “accidents” (i.e., the contingent truths that do not follow from the laws alone). Among the accidents are that all of the coins in my pocket today are silver—colored and that all solid gold cubes are smaller than a cubic mile. (for the sake of argument, let’s suppose that these are truths.) what’s the difference between laws and accidents (especially considering that a law, e.g., that all solid cubes of uranium – 235 are smaller than a cubic mile, can look just like an accident [1].

Counterfactuals are notoriously context-sensitive. In Quine’s famous example, different contexts yield different answers to how Julius Caesar might have conducted the Korean War, he would have used the atomic bomb “is correct in some contexts, whereas in others, “… he would have used catapults” is correct. What is preserved under a counterfactual supposition, and what is allowed to vary, depends upon our interests in entertaining the supposition. From this feature of counterfactuals, it might be concluded that insofar as laws are distinguished from accidents by their relation to counterfactuals, the distinction between laws and accidents is also context—scientific disciplines have different interests and therefore different laws. On this view, the distinction between laws and accidents retains some degree of objectivity; given certain interests, the world helps to determine the laws. On the other hand, it might be insisted that despite the context—sensitivity of counterfactuals, the genuine laws (perhaps the laws of fundamental physics) constrain in any context what would have happened, under any nomic possibility the degree of objectivity possessed by the laws remains highly controversial.

Clearly, we have here a major philosophical difference. Lewis takes the laws as arising "from below," out of the Human mosaic; they are constituted by that mosaic. Dawkins[2], in contrast, takes the laws as governing the universe, and so as being imposed on the Human mosaic "from above"; the laws are facts over and above the facts they govern. The laws are irreducible, contingent relations among universals. Such a relation forces the Human facts to exhibit a corresponding uniformity. Whereas Dawkins thinks that the actual relations of nomic necessitation among universals would still have held had I missed my bus to work this morning, Lewis believes that in a deterministic world, this counterfactual supposition requires a "small miracle" (a single localized violation of the actual laws) to be accommodated in the least disruptive fashion, and that the laws would therefore have been different had I missed my bus to work this morning. On Lewis's view, the fact that the laws are not held sacred under counterfactual suppositions is best explained by Nan account of law according to which there is no great metaphysical gulf separating laws from accidents. On Dawkins 's view, the laws' distinctive power to explain and to support counterfactuals cannot be accounted for if laws are merely regu-

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larities, larities, even regularities belonging to Lewis's best system. They must be facts of a more exalted kind: relations among universals [2].

The concept of a natural law apparently figures prominently in physics. Do biologists also aim to discover laws? Are there distinctively biological laws (in contrast, say, to the laws governing DNA's behavior, which belong to chemistry)? They cannot take the form "All members of species S possess biological property T" because such generalizations

1 are not biological (e.g., where T is the property ; of remaining at less than light's speed); or
2 have exceptions (e.g., where the regularity is that all human beings - or that all healthy, uninjured human beings - have ten fingers: Anne Boleyn had eleven fingers); or
3 lack exceptions merely accidentally. Even if, in fact, every robin's egg is greenish-blue, that is r only because a certain mutation happened never ' to occur; had the mutation occurred, there would have been a robin's egg of a different color. Apparently, "All S's are T" does not function as a law in connection with counter- factuals.

To (3), we might reply that certain traits are necessary for a creature to live; no mutation preventing the embryological development of the human lung, would have resulted in a human being living lungless. So "All [healthy, uninjured] human beings possess lungs" has the requisite invariance under counterfactual perturbations. However, a mutation preventing lung development would not be fatal if (unlikely though this may be) it enabled human beings to produce their own oxygen.

A biological "law" is at best an accident of natural history - is not merely logically contingent, but is also evolutionarily contingent. That every robin's egg so far has been greenish-blue reflects past accidents, and as a result of future mutations and selection, there may eventually be a period r when most robins' eggs are brown. Beatty [3] concluded that whereas physical science is built '4 around laws, biology involves the application of abstract models on a case-by-case basis. For certain purposes at certain moments, a s% stem man be I usefully approximated as a"Mendelian breeding 4 group," for instance, and Mendel's "laws" are trivially true of this model since they define what a"l Mendelian breeding group" is. (As I noted earlier, physics has sometimes been interpreted in this fashion as well.) In chapter 21, by contrast, I argue that certain biological generalizations, despite having exceptions, 32 serve in biology as laws (e.g., in connection with counterfactuals). An accident of natural history can be a law of human physiology, and a law of fundamental physics can be an accidental truth in island biogeography [4-5]. Whether there are laws outside of fundamental physics, and (if so) whether the laws of fundamental physics are nevertheless distinctive in their exceptionlessness or their broad scope, remain highly controversial questions.

1. The Evolutionary Contingency Thesis and Laws of Biology

The evolutionary contingency thesis, somewhat more elaborately stated, is as follows:

All generalizations about the living world:

a) are just mathematical, physical, or chemical generalizations (or deductive consequences of mathematical, physical, or chemical generalizations plus initial conditions), or
b) are distinctively biological, in which case they describe contingent outcomes of evolution.

The first part of this claim is meant to acknowledge that there are generalizations about the living world whose truth values are not a matter of evolutionary history. Evolution has not and will not result in any forms of life that are not subject to the laws of probability, or to Newton’s laws of motion. Nor will evolution result in any carbon-based forms of life that are not subject to the principles of organic chemistry. But while these sorts of principles are true of the living world, we do not call them “biological” principles.[6] The second part of the evolutionary contingency thesis requires a lot more explanation than the first part. To begin, what is meant by the claim that all distinctively biological generalizations describe evolutionary outcomes? (After I discuss the sense in which they describe “contingent” evolutionary outcomes.)

The rule-making capacities of natural selection were of particular interest to the physicist-turned-biologist Max Delbruck, who characterized natural selection as “the overly faithful assistant of a credulous professor, the assistant being so anxious to please that he discards all those data which conflict with his master’s theory” [7]. In other words, generalizations emerge as certain traits are selected for, and as other traits— exceptions to the emerging rule—are selected against.

Consider for the purposes of illustration (and for fun) a very modest generalization from physical anthropology: “Humans are relatively hairless.” That is, we have a lotless body hair than our closest ancestors. Why should this be the case? This turns out to be a highly contentious issue! But what is not disputed is that an evolutionary answer is called for. A number of different evolutionary accounts have been proposed, most of them based on natural selection.

On all these accounts, natural selection generates the relative hairlessness rule by eliminating its exceptions. But while “humans are relatively hairless” may be a slightly provocative principle, it is hardly fundamental, and so this is not a very telling case. Consider another example, which also illustrates how
distinctively biological generalizations describe evolutionary outcomes. This one has to do with the ubiquity of a particular metabolic pathway—the Krebs cycle—among aerobic organisms:

This generalization might at first seem so broad as to be just a matter of chemistry. When reformulated or drawn so as to exclude reference to aerobic organisms, and to include not only the substrates of the reactions (e.g., citrate or citric acid), but also the enzyme catalysts involved (shown in parentheses), the required reaction temperatures, the resulting generalization is just a chemical generalization (see figure 1).

Figure 1 the krebs cycle

[8]. For instance, he argued that alternative ways of metabolizing acetic acid (the starting substrate of the cycle) are not as energy efficient [3].

The case of the Krebs cycle is interesting not just because it is so fundamental, but also because, depending on how one generalizes about it, the resulting claim is either a chemical generalization whose truth value is not a matter of evolutionary history, or a distinctively biological generalization describing an evolutionary outcome [4]. Consider one more example of the rule-making capabilities of evolution by natural selection. This example is intended to anticipate questions as to whether the generalizations of evolutionary biology themselves describe evolutionary outcomes. The example concerns Mendel’s first “law” of inheritance, from which one of the central principles of evolutionary biology, the Hardy–Weinberg “law” is derived.

Mendel’s first law concerns the way in which the genes of a sexual organism are partitioned (“segregate”) among the gametes it produces. The law states that, with respect to each pair of genes of a sexual organism, 50% of the organism’s gametes will carry one representative of that pair, and 50% will carry the other representative of that pair.

The fact that Mendel’s law describes an evolutionary outcome is especially interesting because one of the central principles of evolutionary biology, the so-called Hardy–Weinberg “law” of gene frequency change, is a straightforward deductive consequence of Mendel’s “law.” Hence, the Hardy–Weinberg “law” of evolution itself describes an evolutionary outcome [9–10]. As population geneticist Marcy Uyenoyama has so plainly put it, “Just as the meiotic mechanism [of gamete formation] directs evolution through its effects on the pattern of inheritance, the process of genetic transmission itself evolves by natural selection” [11].

Admittedly, as Bas van Fraassen complains, philosophers of science are better at illustrating this distinction than explaining it [12]. A common sort of illustration (van Fraassen’s own, p. 27; see also Hempel 1966, pp. 54–58) contrast the following two generalizations:

1. All solid spheres of enriched uranium (U235) have a diameter of less than one hundred meters.
2. All solid spheres of gold (Au) have a diameter of less than one hundred meters.

Suppose both claims are true. Still, there seems to be more to the former than the latter, by virtue of which we might accord the former but not the latter the status of law (or perhaps in this case it would be better to suggest that the first generalization describes an “instance” of a more general law). The critical mass of uranium excludes the possibility of such a large sphere of the substance. But nothing that we know about gold excludes the
possibility of such a large sphere of that material. Now if on these grounds we accord to the former claim but not to the latter the status of law (or “instance” of a law), then we acknowledge that there is more to being a law than just being true. That something more has to do with what nature necessitates or precludes [10].

The weaker sense has to do with the fact that the conditions that lead to the evolutionary predominance of a particular trait within a particular group may change, so that the predominance of the trait declines. Somewhat more colloquially: what the agents of evolution render general, they may later render rare. Two sources of this kind of contingency are mutation, and natural selection in changing environments.

Suppose that relative hairlessness owes its prevalence to the fact that it was favored under particular circumstances by natural selection—relative hairlessness being selected against—selection acting, as Delbruck suggested, “like the overly faithful assistant” who “discards all those data which conflict with his master’s theory.” Is there anything naturally necessary about the circumstances under which relative hairlessness was favored—something that could not change? Is the professor really so single minded? And are the loyalties of the professor’s assistant really so unswerving?[13].

Different organisms would be expected to make different demands on the several resources of the cycle and thus control the cycle in different ways in accordance with their individual metabolic “life-styles.” It seems reasonable to assume that the evolutionary paths to different organismshave been accomplished by the evolution of distinctive regulatory and other individual functionalfeatures in the CAC [the Krebs cycle].

And there are many pairs of genes, in many species, that do not segregate in a 50:50 fashion; in these cases there is instead a marked bias in the production of gametes containing one rather than the other representative of the pair [14]. As Graham Bell [15] recently acknowledged, many of his fellow evolutionary biologists who contemplate such issues actually find it easier to imagine circumstances in which unequal segregation of alleles among gametes would prevail than to imagine the circumstances which would favor evolution by natural selection of 50:50 segregation ratios a la Mendel.

The different reproductive contraptions of orchids had evolved, Darwin believed, from a common form (the original orchid species), in response to a common problem (the need for cross fertilization), and at least originally under virtually the same circumstances (e.g., the sameness of available insects). Sometimes this part of the flower had been modified to entice or trap insects, sometimes another part had been modified to do the job. Even when the same parts had been modified to do that job, they did it in very different ways. Among the various orchid species, presumably derived from one, Darwin thus conceived the evolution of reproductive mechanisms occurring over and over again with no generally determined outcome except cross-fertilization. And this was to be expected on the basis of chance variations and the possibility of functional equivalence. Selection acts on whatever opportunities present themselves, with never the same order of useful modifications arising, and with equally functional results.

The problem of formulating any particular law of gene expression is therefore the problem of stating it in such a way that it would not be rendered false by further evolutionary change with respect to interacting genes. And that requires that we state a sufficiently inclusive set of genetic and environmental conditions. An appropriately conditionalized law of gene expression might then be rendered inapplicable by evolution—the conditions of the law no longer being met—but it might not be rendered false by evolutionary change.

What would such a law look like? It seems that one would be in a better and better position to know whether the set of conditions was sufficiently inclusive the more and more one knew about the chemical pathways leading from the sequence of nucleotidesbases that make up the genes in question, to a physical-chemical specification of the phenotype in question. I suspect this is why Hull included the biochemical reactions linking genes to phenotypes in his schema of a law of gene expression.

Suppose that complete chemical pathways from genotypes to phenotypes could be formulated; and suppose that generalizations about these were indeed laws; still, I see no reason to regard them as distinctively biological laws. That is, I see no compelling reason to regard a description of a chain of chemical reactions—no matter that the reactants and products include DNA, RNA, and lots of enzymes—as “biological” generalizations.

So to summarize this part of the discussion, the closer one’s generalizations about gene expression come to describing sequences of chemical reactions, the more certain one can be that they are laws, because one can be more certain that no evolutionary outcomes can contradict them. But at the same time, the generalizations will become less and less distinctively biological [16].

Schaffner and Kauffman and others are surely right to stress that there are more or less contingent generalities in biology. The present formulation of the evolutionary contingency thesis may be misleadingly simplistic in this regard.

2. Theoretical Pluralism and Relative Significance Controversies

I want to switch now from articulating the evolutionary contingency thesis, to applyng it. In particular I want to consider its bearing on the explanatory ideals of biology, especially on the “theoretical pluralism” so
characteristic of biology, and also on the nature of controversy in biology, specifically the "relative significance" controversies that are so prevalent in the life sciences.

"Theoretical pluralism" has to do with the number of theories or mechanisms that are believed to be required to account for a domain of phenomena (see also Beatty 1994). A proponent of theoretical pluralism with respect to a particular domain believes that the domain is essentially heterogeneous, in the sense that a plurality of theories or mechanisms is required to account for it, different items in the domain requiring explanations in terms of different theories or mechanisms. There is no single theory or mechanism even a single synthetic, multi-causal theory or mechanism that will account for every item of the domain. This is not merely a matter of insufficient evidence for a single theory; rather, it is a matter of the evidence indicating that multiple accounts are required [17].

Theoretical pluralism contributes to, and is reflected by, a certain kind of controversy - the so-called "relative significance" dispute. What is at issue in a relativeseignificance dispute is the extent of applicability of a theory or mechanism within a domain - roughly, the proportion of items of the domain governed by the theory or mechanism - not whether the theory or mechanism in question is the correct account of the domain.

Ecologists debate the extent of applicability of alternative theories of community structure, from competition theory, to predation and abiotic factor theories, to random colonization models [18]. Again, these are all disputes about the extent of applicability of alternative theories or mechanisms within a particular domain, not whether this or that account is the universally true one within that range.

I believe there are reasons to be a theoretical pluralist with respect to every domain of distinctly biological phenomena, and reasons to anticipate relative significance controversies within every domain. The main reason is that the contingencies of evolutionary history preclude the existence of laws of biology. It is not surprising that a biologist should be more interested in the extent of applicability of a theory within its intended domain than in its possible universality within that domain. Not expecting universal generalizations to hold within a domain, biologists expect instead to have recourse to a plurality of theories to cover it.

The theoretical pluralism so prevalent in biology contrasts strikingly, I believe, with a traditional ideal, namely, to explain a domain of phenomena in terms of as few as possible different mechanisms, and best of all one single mechanism. This ideal was expressed particularly well by Newton, and so I will call it the Newtonian tradition.

Newton elaborated it most succinctly in the first two of his three "rules of reasoning in philosophy". According to the first rule, "We are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances." As Newton clarified the rule, "To this purpose the philosophers say that Nature does nothing in vain, and more is in vain when less will serve; for Nature is pleased with simplicity and affects nothing in vain."

Judging by their acceptance of theoretical pluralism, and by their waging of relativeseignificance disputes, many biologists seem not overly impressed by this rule of reasoning. Indeed, by their promotion of theoretical pluralism they seem to repudiate the Newtonian ideal. This pluralism is also characteristic of the recent anthology and state-of-the-art summary, Speciation and its Consequences, edited by Otte and Endler [12].

Recently summarized the trend toward theoretical pluralism in ecology, away from the ideals of the sixties and early seventies when ecologists like Robert MacArthur envisioned that all of ecology would ultimately be "embodied in a small number of simple laws." Recent anthologies, for example the anthology on community ecology edited by Diamond and Case [7] proclaim pluralism in the preface and throughout. The editors explicitly distance themselves from the ideals of Newtonian mechanics:

The Newtonian tradition may prevail more in the physical sciences (at least in thenon-historical - e.g., non-geological, non-cosmological - physical sciences). The difference between that tradition, and the tradition of relative significance controversies that prevails in biology, is well illustrated by the following Sidney Harris cartoon of two physicists (they're not mathematicians - mathematicians don't wear white coats).

The assumption behind the cartoon - what makes it funny - is that physicists are not supposed to argue about such matters. But what makes us think these are physicists? Well, if they were not, it would not be funny. Imagine that they are evolutionary biologists arguing about theories of speciation, or theories of the rate of evolutionary change. Now this is not a joke. It is rather the fact of the matter. To some it is the sad fact of the matter. Which leads me to temper my remarks about theoretical pluralism in biology.

It is important not to exaggerate the differences between the biological and physical sciences. The Newtonian tradition has considerable appeal in biology as well, and not only in the more ahistorical branches of biology, like molecular biology.

Numerous other biologists are pluralists, but only reluctantly, as if pluralism falsifies the Newtonian ideal. For example, Ghiselin concludes a review of mechanismsof the evolution of sex by admitting that, "Perhaps we shall have to accept a pluralistic assemblage of explanations." And again, "From the point of view of having an adequate explanation for all the data, we may have to accept more than one hypothesis." And as James and Carol Gould admit, "we have, it seems, an embarrassment of plausible hypotheses to account for the..."
evolution and maintenance of [sex]’’ [19]. Many natural historians reveal the limits of their tolerance for theoretical pluralism by conducting their relative significance arguments in the manner described.

In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but circumscribe its domain of action so narrowly that it cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an ecumenical chap. There are other means by which biologists try to eliminate or contain theoretical pluralism. One important means is by splitting a heterogeneous domain, governed by multiple theories, into two or more homogeneous sub-domains, each governed by only a couple of theories or perhaps even a single theory. For example, the evolution of sex can be partitioned into two sub-domains, the origin of sex and the maintenance of sex. Some biologists believe that the DNA-repair hypothesis will be the account of the origin of sex, while multiple theories may be needed to explain the maintenance of sex. Similarly, attempts are often made to distinguish the domain of microevolutionary changes within which selectionist theories are most significant, from the domain in which neutralist theories are most important [20]. Interestingly, while Diamond [7] (quoted above) promotes theoretical pluralism in community ecology, they nonetheless seriously entertain the possibility that “one can at least partition communities among a modest number of types and devise a model for each type” [7] strategy of domain partitioning.

But the fact that tactics like these are employed to contain theoretical pluralism indicates that theoretical pluralism is indeed widespread, however much some biologists with Newtonian inclinations may regret it. I can imagine an argument for adhering to the Newtonian ideal, independently of its romantic qualities. That is, one might suggest that theoretical pluralism reflects more about the state of our ignorance than about the state of nature: there may actually be laws of biology, and a unitary or unifying theory for each domain of biological phenomena, but we have yet to discover these important generalizations. Whether theoretical pluralism reflects the nature of the biological world, or the state of our ignorance, we cannot at present know. Nonetheless, we should aim for unitary or unifying theories.

This is a difficult argument to counter. The best I can do is to offer an alternative argument (or rather, sketch of an argument), which rests on the following premise: scientific methodology, including injunctions to seek unified accounts of each and every domain, should be scientifically (in this case evolutionarily) informed. This is, for example, the assumption that structures Elliott Sober’s analysis of the evolutionary grounds underlying the parsimony criterion in phylogenetic systematics.

Similarly, why should we adhere to a methodology that dictates the search for unitary accounts of each domain of biological phenomena—e.g., a unitary account of inheritance, or a unitary account of carbohydrate metabolism, or a unitary account of cell growth, or a unitary account of speciation—unless we have reason to believe the outcomes of evolution are highly constrained?

If I have stressed the factors that broaden the range of evolutionary possibilities, that is not because I think they are intrinsically more interesting or important than the factors that limit the range. But unless we believe that the outcomes of evolution are always severely constrained, then perhaps we should be on the lookout for multiple accounts of each domain. Only a naive Newtonian would rest satisfied with a unitary account, when, with a little more effort, a multiplicity of accounts might be found!

3. Conclusion

I will summarize very briefly. Gould contrasts the ‘‘laws in the background’’ with the ‘‘contingent details’’ in the foreground of biology. What this means to me is that there may be genuine laws that are relevant to biology (e.g., laws of physics and chemistry), but those laws are not distinctively biological. What is distinctively biological are the contingent details, allowed but not necessitated by the presumed laws. The details can have most any degree of generality—and the degrees of generality of those details may change over time. And all the while evolution is making new rules and breaking old rules, the rules of evolution are themselves changing.

This evolutionary contingency thesis bears upon a number of other issues in philosophy of biology, including the explanatory ideals manifested in ‘‘theoretical pluralism,’’ and the nature of ‘‘relative significance’’ controversies. Just as a scientific hypothesis derives support from the phenomena it successfully explains, so, too, the evolutionary contingency thesis derives support from these other general features of biology that it makes sense of.

REFERENCES


