Why Do Biologists Argue Like They Do?

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"Theoretical pluralism" obtains when there are good evidential reasons for accommodating multiple theories of the same domain. Issues of "relative significance" often arise in connection with the investigation of such domains. In this paper, I describe and give examples of theoretical pluralism and relative significance issues. Then I explain why theoretical pluralism so often obtains in biology—and why issues of relative significance arise—in terms of evolutionary contingencies and the paucity or lack of laws of biology. Finally, I turn from explanation to justification, and raise questions about the purpose and value of concerns and disagreements about relative significance.

1. Introduction. What sorts of arguments would we expect from two scientists pursuing alternative theories or models of the same domain of phenomena? Among other things, we might expect each to argue that his or her theory is *the* correct account of the domain, and that his or her rival's theory is incorrect.

And indeed, arguments in biology sometimes proceed in this way. But very often they do not. Biologists pursuing alternative accounts of a domain of phenomena are often concerned instead with whether their theory provides *a* correct (vs. *the* correct) account of the domain. Beyond that, they are often concerned to establish the "relative significance" of their theory. The relative significance of a theory within its intended domain is roughly the proportion of phenomena within the domain that the theory correctly describes. The complementary notion is "theoretical pluralism." Theoretical pluralism obtains when there are good evidential reasons for accommodating multiple, alternative theories, each with the same intended domain—in other words, when the evidence suggests that different items in the domain require explanation in terms of different theories.

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In this paper, I will first describe theoretical pluralism and relative significance issues in more detail, and give some examples. Then I will explain why theoretical pluralism so often obtains, and why issues of relative significance arise. Finally, I will turn from explanation to justification, and raise some questions about the purpose and value of concerns and disagreements about relative significance.

2. Relative Significance. To avoid confusion, I should begin by acknowledging that "relative significance" and "theoretical pluralism" have multiple meanings in the biological and philosophical literature, and that I am using them here in a restricted sense. For example, "theoretical pluralism" sometimes refers to the incorporation of multiple, coacting causal agents within one theory: a developmental theory that includes genetic and environmental factors, an evolutionary theory that includes selection and drift, etc. Faced with this sort of theoretical pluralism, biologists sometimes argue about the relative strengths of the causes that combine to bring about the phenomena of interest: genotype vs. environment in development, selection vs. drift in evolution, etc. (e.g., Mitchell 1992).

I am emphasizing a different family of issues here, and it is perhaps best to start with an illustration. Let gene regulation be the domain of phenomena in question (we might even be more specific about the domain: we might restrict it to transcription regulation in prokaryotes). Molecular geneticists currently pursue multiple theories or models of gene regulation, including the negative induction (or "lac operon") theory, the negative repression (or "trp operon") theory, positive induction and repression theories, and the attenuation theory (e.g., Lewin 1990, 240–299). Molecular geneticists are not divided with regard to which of these theories is *the correct* account of the domain. There is general agreement that each theory accounts for at least some instances of gene regulation, although the issue remains as to *what proportion* of cases each theory correctly describes, or in other words, the *relative significance* of each theory.

Of course, Jacques Monod once proclaimed that "what is true for the colon bacillus [*E. coli*] is true for the elephant" (Jacob 1988, 290), meaning that his and François Jacob's generalized negative regulation theory should be sufficient to account for all cases of gene regulation, and not just in *E. coli* where negative induction and negative repression were discovered (Jacob and Monod 1961a, 1961b; Monod and Jacob 1961). But as seems inevitable in biology, it was soon found that one theory was not sufficient, not even a synthetic theory like the generalized negative regulation theory. Multiple theories were required to cover the domain. Indeed, the generalized negative regulation theory did not even prove sufficient to cover gene regulation in *E. coli*, much less elephants.

In the case of gene regulation, as in so many other domains, *theoretical pluralism* has prevailed. That is, gene regulation, like so many other domains of biological phenomena, has proved to be heterogeneous in the sense that a plurality of theories has been proposed to account for it, different items in the domain requiring explanations in terms of different theories (and even different combinations of theories). Again, 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 needed (see also Beatty 1995).

Examples of theoretical pluralism and relative significance controversies occur at every level of investigation in biology. Consider for now just genetics and evolutionary biology. As already discussed, molecular geneticists have wondered and argued about the extent of applicability of a variety of models of gene regulation (see also Yanofsky 1981, 1992). Molecular geneticists have also explored the degree of universality of the genetic code (e.g., Osawa 1995), and the degree of generality of RNA-to-DNA vs. DNA-to-RNA models of the transfer of genetic information (e.g., Crick 1970; see also Darden 1995, 145–154). Classical geneticists have raised questions about the ubiquity of Mendelian inheritance, arguing that non-Mendelian mechanisms, leading to the biased segregation of alleles, are possibly very common (e.g., Crow 1979).

Evolutionary biology is rife with relative significance controversies. For instance, evolutionary biologists have argued about whether selection theories have greater applicability to microevolutionary changes than neutral theories, and which of the alternative selection theories is the most significant, and which of the alternative neutral theories is most important (e.g., Lewontin 1974, Kimura 1983, Gillespie 1991). Evolutionary biologists have argued about whether gradualist, adaptationist theories of macroevolution have greater applicability than the punctuated equilibrium theory (e.g., Gould 1980, Lande 1980). Evolutionary biologists and systematists have argued about the extent of applicability of each of the multitude of theories of speciation, from each of the various forms of sympatric speciation, to parapatric speciation, to each of the various forms of allopatric speciation (e.g., Otte and Endler 1989).

These issues may in principle be resolved by theoretical synthesis, e.g., by formulating one overarching theory that includes all the current alternatives as special cases. Or the issues may be resolved by restricting each of the alternative theories to a more narrowly characterized domain for which it is the single correct account (Allchin 1994, Darden

1996). But until then, the domains in question remain heterogeneous with respect to the theories that have been proposed to account for them. Moreover, it is by no means clear that progress lies in the direction of a singular theory for each domain. For example, Charles Yanofsky emphasizes "the dazzling progress that has been made" *since* the time when Jacob and Monod were defending a more unitary account of the domain of gene regulation (Yanofsky 1992, 22). Similarly, Seymour Cohen reflects on the multitude of alternative biochemical pathways that have been discovered, and concludes that the earlier "notion of the 'unity of biochemistry' . . . reflects a primitive stage in the development of the discipline" (Cohen 1963, 1025).

3. Accounting for Relative Significance Disputes. That theoretical pluralism often obtains and relative significance issues so often arise may be the fact of the matter, but what makes it so? One reason is that there are so few (if any) laws of biology. To engage in a relative significance dispute is to acknowledge that theoretical pluralism obtains with respect to the domain in question, which in turn means that none of the alternative theories proposed to account for that domain provides *the correct* account of it. Each of the alternatives fails within its intended domain, which is to say that none of the alternatives constitutes a law with respect to the domain. If Mendel's "law" of heredity were really a law, then biologists would not worry about how often non-Mendelian inheritance occurs. If it were to be agreed that gene regulation is always a matter of negative induction or repression, then proponents of positive regulation and attenuation theories would give up arguing for the relative significance of their views. If evolutionary biologists were all to accept as a matter of natural law that all speciation events are allopatric speciation events, then there would no point to arguing the importance of sympatric speciation.

But to attribute theoretical pluralism and questions about relative significance to the paucity or lack of laws in biology is really just to restate the problem, not to explain it. So why, again, are there so few if any domains of biology for which one theory suffices, and in connection with which there are relative significance issues?

There are probably many factors. One involves the contingencies of evolutionary history. Consider, for instance, that the various mechanisms of gene regulation are products of evolution (Yanofsky 1992, 8, 12–13, 19). If the negative induction theory were *the correct* account of gene regulation, that would be because evolution had resulted in only one gene regulation system. Similarly, if Jacob and Monod's generalized negative induction and negative repression theory of gene regulation were the correct account, that would be because evolution had resulted in only two gene regulation mechanisms. But evolution has resulted in a *variety* of gene regulation mechanisms, for which a variety of gene regulation theories are appropriate.

Similarly, evolution has resulted in a *variety* of reproductive systems, consistent with a variety of mechanisms of speciation. Faced with this variety, evolutionary biologists do not argue about which mechanism of speciation is the correct one; rather, they argue about the relative significance of each account.

Under what circumstances could we reasonably expect a single theory to suffice for a domain of biological phenomena? To expect a single mechanism underlying an entire domain of biological phenomena, we would have to assume that one mechanism evolved in a common ancestor of all the taxa covered by the domain, and that the mechanism has been maintained in each of those taxa ever since, and/or we would have to assume that the very same mechanism arose independently and has been maintained in all the taxa covered by the domain. In other words, we would have to assume *extreme phylogenetic conservativism*, and/or extremely strong and remarkably similar selection pressures resulting in *extreme parallel evolution*. This is precisely how Francis Crick explained the universality of the genetic code: once the code was established in a particular lineage, any change in the code would have had enormous, cascading effects, resulting in changes in the amino acid sequences of many, many previously adaptive proteins. Such a change could not conceivably be beneficial overall. Thus, the code became, in Crick's words, a "frozen accident" (Crick 1968).

To the extent that the outcomes of evolution are not so conservative or restricted, it is less likely that there will be singular accounts of the domains of biological phenomena. And this is precisely what investigators of the *non-universality* of the genetic code now argue: "the genetic code, formerly thought to be frozen, is, in fact, in a state of evolution," (Osawa 1995, i, 73).

To the extent that the outcomes of evolution are not so constrained, then, biologists will often be faced with a variety of alternative mechanisms, described by a variety of alternative theories or models, and they will be forced to deal with issues of relative significance.

4. Justifying Concerns About Relative Significance. Surely that conclusion does not follow. Even if evolution in independently evolving lineages leads to multiple mechanisms underlying many or most domains of biological phenomena, and hence even if a variety of theories or models is required to cover most domains, biologists would still not be forced to deal with issues of relative significance. For instance, biologists might choose to concentrate their time and energy on determining which theories or models apply in which particular cases, without worrying about tallying all the cases to which a particular theory or model applies. And/or they might concentrate on discovering new theories or models that have some applicability, without worrying about how much applicability.

The contingencies of evolutionary history merely provide the *occasion* for relative significance disputes. There are still *normative* issues to consider—issues having to do with whether relative significance disputes are worthwhile. There are some aspects of relative significance issues that lead me to question their worth.

Consider for instance the following passage from the transcript of a conference convened to discuss which of two selectionist theories—H. J. Muller's "classical" theory vs. Theodosius Dobzhansky's "balance" theory—provides the most significant account of evolutionary change (see also Lewontin 1974, Beatty 1987). At issue here is whether evolution occurs "mainly" in the manner of Dobzhansky's theory:

> DOBZHANSKY: Excuse me, but there is one word which may cause trouble, if I may point this out; "mainly," in question 3. You say "mainly." Would you agree to change it to "substantially," "substantial fraction?" "Mainly" may be misunderstood as meaning 99 per cent.
>
> CROW: By "mainly," I mean more than half. . . .
>
> DOBZHANSKY: Could we say 40 to 60 per cent?
>
> CROW: Is "more than half" all right?
>
> LEWONTIN: That's not 40 to 60 per cent. . . .
>
> NEEL: But at least it makes the question less ambiguous. . . .
>
> DOBZHANSKY: Why not say "substantially" [Laughter] It means all sorts of—50 per cent is not a sacred percentage, is it?
>
> CROW: I don't favor it, particularly. Let's say "substantially."
>
> GLASS: I think "substantially" is just as vague as "mainly."
>
> NEEL: And to put an exact figure in gives us something to shoot at, so let's say "more than half."
>
> LEWONTIN: My only objection to that, Jim, is that, precisely by giving you something to shoot at, it may be giving you a false target. People may start to argue whether it is 40 or 60 per cent, which may not be worth arguing about.
>
> NEEL: Is that any worse than arguing about what "mainly" or "substantially" mean? (Macy Foundation 1963, 369–370)

There are several points of concern raised here. The classical/balance controversy is by no means unique with regard to the vagueness of the quantifiers used to demarcate the relative significance of alternative hypotheses. Typical quantifiers include terms like "main," "major," "principal," "important," "minor," "insignificant," and "unimportant." What exactly does it mean to call one account the "major," as opposed to a "minor," account? (This problem and some of the other problems that I consider below also arise in the case of disagreements about the "relative strengths" of combined causes, as discussed at the beginning of §2.)

What exactly did Darwin mean in the first edition of the *Origin*, where he wrote that, "I am convinced that Natural Selection has been the main but not the exclusive means of modification" (Darwin [1859] 1966, 6). And why exactly did he change this in the sixth edition to read, "the most important, but not the exclusive means of modification" (Darwin 1872, 4)?

Two of my favorite relative significance quantifiers are the solid and dotted arrows in Crick's famous diagram of the central dogma (Crick 1970). The arrows represent the direction of flow of genetic information; their continuity reflects the significance of that direction. For instance, the flow of information from DNA to RNA is represented by a solid arrow, which represents a "general" transfer of information, while the flow of information from RNA to DNA is represented by a dotted arrow, which represents a "special" case.

But suppose we could state the alternative positions precisely, and even come up with fairly precise estimates of the relative significance of each alternative. What would we have learned from determining these precise numbers? Suppose that there are only two alternative accounts of a particular domain, describing two alternative mechanisms, and that their relative significances are hypothesized to be 45% and 55% respectively. What if upon extensive investigation (and this is another problem—how extensive would it have to be?), the answer turned out to be just the reverse, 55% and 45%? How interesting would that be (as Lewontin suggests above in connection with the classical/balance controversy)?

One might think that differences so small would not be worth arguing about, but that it would be worth arguing about more extreme differences—like 90% vs. 10%. It does seem the case that participants in relative significance disputes often take highly polarized positions. As Gould and Lewontin acknowledge concerning the tendency toward polarization in relative significance controversies,

> 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 congrat-

> ulate yourself for being such an ecumenical chap. (Gould and Lewontin 1979, 585)

But the question remains, why should extreme differences in relative significance be worth arguing about, and small differences not?

Is it possible that biologists defending extreme relative significance positions are trying to come as close as possible to defending laws? If they cannot reasonably defend a theory as *the correct* account of its intended domain—if they acknowledge that it fails in its intended domain—at least they can argue that it is *by far the most important* account of that domain.

But why exactly should biologists be aiming for (if falling short of) theoretical unity? We have good evolutionary reasons for not expecting *the correct* account of every domain of biology. The evolutionary assumptions that would lead us to expect a singular account—*extremely* strong phylogenetic conservativism and/or *extremely* strong parallel evolution—are too extreme to be realistic with regard to many, if not most (if not all) biological domains. The evolutionary assumptions that would lead us to expect that we will find one account of a domain that is, if not the correct account, then nonetheless *by far the most important account*, are only somewhat more moderate. Nonetheless, as Kenneth Schaffner argues, there may be domains where we would expect—for good evolutionary reasons—one account to be more prevalent than any alternative, as in the case of the genetic code (Schaffner 1993, 121–122). But do we know a priori, before we consider the issue evolutionarily, that a particular domain will require one or only a few theories to account for it, in which case it would be reasonable to aim for theoretical unity, or for only a few alternative theories?

David Hull has suggested an interesting argument in favor of aiming for theoretical unity, even if we eventually fall short. Theoretical pluralism might reflect more about the state of our ignorance than about the state of nature: there may actually be 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 know for sure. Nonetheless, we should aim for unitary or unifying theories. Then, if a particular domain is really, inescapably heterogeneous, we will ultimately be forced to deal with theoretical pluralism. But if we begin by advocating theoretical pluralism, then we may never find the unitary or unifying theories that might actually be true. We might rest happy with multiple accounts when a unitary account is possible and could be discovered with a little more effort (Hull 1987, 178).

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 a premise that is implicit in what I have said so far, but deserves to be made explicit. That is, scientific methodology, including injunctions to seek unitary accounts of each and every domain, should be scientifically (in this case evolutionarily) informed. 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 gene regulation, or a unitary account of speciation—unless we have reason to believe that the outcomes of evolution are *highly* constrained in the manner previously discussed?

It has been argued that the assumption of theoretical unity has blinded scientists to the limitations of particular theories within their intended domains. For instance, James Crow has suggested that mildly biased segregation of alleles may be much more common than is supposed, but has not often been noticed because investigators have not been looking for non-Mendelian segregation (Crow 1979, 146). Similarly, in criticizing the notion of "the unity of biochemistry," Seymour Cohen argues that, "Such an underestimation or oversimplified view of the significance and ubiquity of a single [metabolic] path has tended to and still does restrict the search for new paths and an evaluation of their functional role" (Cohen 1963, 1025–1026).

Consider another problem. Suppose that we had stated a relative significance postion precisely, and that we had doggedly pursued it, and that we had tallied the hypothesized proportion of instances of the theory within its intended domain. Suppose for instance that we had a reliable tally of the proportion of taxa for which the iconic genetic code is correct. Why would we consider this proportion to be telling? Why, for instance, would we consider it to represent any more than a highly contingent fact of evolutionary history on earth up to the present day? What would it tell us about "tomorrow," in an evolutionary sense? Why would we expect that evolutionary trend to continue?

Well, one might not care so much whether the trend continues—whether it is anything like a timeless truth. One might have more pressing, more immediate interests in the relative significances of the alternative theories or models of a domain. Consider a researcher whose main concern is to account for a particular phenomenon within a domain, say gene regulation at a particular locus, or the origin of a particular species. Facing a variety of alternative possible accounts, the researcher needs to decide where to begin. Imagine a graduate student with three years to initiate and complete his or her research, or any researcher on a 3-year, non-renewable grant, and hence little time to waste. Would not he or she be well advised to *start* by considering those several theories generally agreed to be most significant within the domain—that is, unless he or she had reason to suspect a special case scenario?

Consider a researcher facing a pressing medical or environmental problem. Time is of the essence. But there are a variety of possible alternative accounts of the threat to consider, and correspondingly a variety of possible solutions. Where to start? Again, would not such a researcher be wise to start with those theories generally agreed to be the most significant within the domain—again, unless he or she had reason to suspect a special case etiology?

Note that the role of relative significance claims in the latter two scenarios is not so much explanatory as heuristic, serving more as a guide to research on particular cases, rather than as an explanation of them. But perhaps relative significance disputes are "worth" waging for altogether different reasons—more socio-professional than cognitive.

For instance, is it possible that such controversies are not only about the relative significance of theories, but also about the relative significance of the *proponents* of those theories? Is the significance of an investigator within his or her community proportional to the relative significance of the theory that he or she pursues? Does this have anything to do with the polarization that characterizes so many relative significance disputes?

It may indeed be the case that relative significance debates are about the significance of the debaters, but it is by no means obvious why that should be so. The professional rewards for discovering even a very rarely applicable model may be great. Presumably Howard Temin and David Baltimore received the Nobel Prize not for showing that RNA *generally* serves as the template for the formation of DNA, but for demonstrating quite clearly that genetic information at least *sometimes* flows in that direction.

Consider another possible socio-professional role played by relative significance controversies, especially highly polarized ones, namely, in the recruitment of young scientists into an area of study. Is it perhaps difficult to recruit young scientists into an area where theories or models are perceived to accumulate like stamps in a stamp collection, or where the most general issues in contention have to do with whether theory A applies 45% of the time and B applies 55% of the time, or whether A applies 55% of the time and B 45%? Is a field in which the alternatives vie for 90–95% of the domain a more attractive field, everything else being equal?

Again, this is by no means obvious. It is not obvious, for instance, why a young scientist would be attracted to an area in which the primary objective is just to tally instances in favor of one or another alternative theory, rather than to another area in which the emphasis is on the discovery of new, somewhat applicable models, or on the discovery of the solution to particularly vexing phenomena within the domain under investigation. One might well have judged the area of gene regulation to be more exciting and promising rather than less so as the number of models of gene regulation increased, and as it became apparent that there was more than one mechanism to be discovered and elaborated (Yanofsky 1992, 22).

5. Conclusion. I have raised many questions and answered very few. But I hope at least to have drawn attention to a common issue in biology. Relative significance issues are common enough to warrant philosophical analysis. Their prevalence can be understood in part in terms of the prevalence of theoretical pluralism, which can in turn be understood in part in terms of evolutionary contingency. But to explain relative significance concerns in this way is not to justify them. We need to explore their justifications, and we also need to know more about possible motivations for pursuing these issues, above and beyond their possible justifications.

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