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Integration without Unification: An Argument for Pluralism in the Biological Sciences

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ABSTRACT: In this article, we consider the tension between unification and pluralism in biological theory. We begin with a consideration of historical efforts to establish a unified understanding of evolution in the neo-Darwinian synthesis. The fragmentation of the evolutionary synthesis by molecular evolution suggests the limitations of the general unificationist ideal for biology but not necessarily for integrating explanations. In the second half of this article, we defend a specific variety of pluralism that allows for the integration required for explanations of complex phenomena without unification on a large scale.

Keywords: integration, unification, pluralism, evolutionary synthesis, molecular evolution.

Biology studies complex, developing, and evolving organisms and populations. Developing sea urchins, division of labor in social insect colonies, and predator-prey interactions, for example, are all compositionally and dynamically complex. Their behavior depends on multiple levels of organization and multiple causal components. Additionally, ever since Niko Tinbergen's articulation of four questions and Ernst Mayr's distinction between ultimate and proximate causes, there is general recognition of multiple levels of analysis (function, cause, development, evolution) or questions (why and how) that can be brought to bear to explain a biological property or behavior. This generates a plurality of models and explanations aiming to get scientific traction on the "blooming buzzing confusion" that constitutes life (James 1911, p. 50). But how are we to understand the pluralism of contemporary bi-

ological practice? Is it a mark of the immaturity of biological theory? Will today's pluralism give way to a grand unified theory of biology in the image of Newtonian physics? Or does pluralism indicate a healthy competition among biologists about what is the singular true account of why a system behaves the way it does? Or is it something altogether different?

In this article, we will consider the tension between unification and pluralism in biological theory. We begin with a consideration of historical efforts to create unification in biology on a large scale through the neo-Darwinian synthesis. The fragmentation of the evolutionary synthesis with the rise of molecular evolution suggests the limitations of the unificationist ideal for biology. In the second half of this article, we will defend a specific variety of pluralism that allows for the integration required for explanations of complex phenomena without unification on a large scale.

The Fragmentation of the Evolutionary Synthesis

Theodosius Dobzhansky's well-worn declaration that "nothing in biology makes sense except in the light of evolution" was a testament to his faith in the unifying power of the evolutionary synthesis (Dobzhansky 1973). From the late 1930s, Dobzhansky, Ernst Mayr, and G. G. Simpson organized a loose array of biologists interested in evolution into members of a new discipline of evolutionary biology. The circumstances of this neo-Darwinian or evolutionary synthesis are still a matter of debate among historians, but certainly a unified understanding of the foundational principles of evolutionary biology was the goal of the synthesis's architects (Smocovitis 1996). As Dobzhansky put it, biology without evolution "becomes a pile of sundry facts some of them interesting or curious but making no meaningful picture as a whole" (Dobzhansky 1973, p. 125).

While historians rightly emphasize the discipline-building work of getting paleontologists and geneticists to communicate and agree about the processes of evolution, the hallmark of the evolutionary synthesis in terms of

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biological theory was the developing consensus about the primacy of natural selection (Provine 1988; Cain 1993; Smocovitis 1996). The rising panselectionist belief that natural selection was the most important mechanism of evolutionary biology was dubbed the "hardening" of the synthesis by Stephen Jay Gould (Gould 1983). A hardened synthesis provided a foil for biologists' intent of setting themselves apart from the "evolutionary orthodoxy." While, in fact, there was never complete agreement among evolutionary biologists about the importance and power of natural selection, there was enough agreement to make divergence from the perceived orthodoxy seem revolutionary. Motoo Kimura took advantage of these perceptions in his advocacy of the neutral theory of molecular evolution, beginning in 1968 (Kimura 1968; Dietrich 1994).

As molecular biology rose in prominence in the 1960s, molecular evolution emerged from the intersection of fields such as evolutionary genetics, systematics, biochemistry, molecular biology, anthropology, and microbiology. As biologists began to compare biochemical similarities and differences in order to make evolutionary inferences, they began to entertain the idea that not all molecular changes had been subject to natural selection (Zuckerlandl and Pauling 1965; Dietrich 1994). The possibility of neutral mutations had been previously posited by Dobzhansky and others but was not taken seriously as an alternative to natural selection (Dobzhansky 1955). When Motoo Kimura, Jack King, and Tom Jukes began to advocate the importance of neutral mutations and random drift in 1968 and 1969, attitudes about drift and neutrality began to shift (Kimura 1968; King and Jukes 1969). Many molecular evolutionists with biochemical training were willing to accept neutral mutations on the basis of detected biochemical differences and molecular variability, but many biologists trained in evolutionary biology and steeped in the evolutionary synthesis were much more skeptical (Dietrich 1998).

The controversy between the neutralists and selectionists that emerged in the 1970s and arguably continues to this day is usually understood as pitting drift against selection. Even though the neutral theory includes a significant role for natural selection, it is perceived as opposing panselectionism because it also advocates a significant role for neutrality and drift at the molecular level. The juxtaposition of neutrality and panselectionism was beautifully captured by Alexey Kondrashov when he recently wrote,

Once upon a time, the world seemed simple when viewed through the eyes of evolutionary biologists. All genomes were tightly controlled by various forms of natural selection. ... This idyllic world began to crumble in 1968, when Kimura

made his modest proposal that most allele substitutions and polymorphisms do not substantially affect an organism's fitness and are governed, not by positive or balancing selection, but by random drift. (Kondrashov 2005, p. 1106)

While Kondrashov's fractured fairy tale approach is compelling, the challenge of neutrality to panselectionism warrants more careful scrutiny.

First, Kimura, King, and Jukes initially encouraged this idea of opposition. When King and Jukes titled their article "Non-Darwinian Evolution," they were deliberately trying to set their work apart from that of the neo-Darwinian synthesis. This oppositional approach certainly contributed to the polarization of the neutralist-selectionist controversy in the early 1970s. This sense of polarization extended beyond debates about the relative importance of drift and selection to the place of molecular evolution relative to evolutionary biology in general. While molecular biologists described evolutionary biology as old-fashioned and compared it to stamp collecting, evolutionary biologists attacked molecular biology as a fad and a bandwagon. Molecular evolution arose right in the middle of this larger turf war (Dietrich 1998; Hagen 1999). From the first conferences on molecular evolution in 1962, molecular evolutionists such as Emile Zuckerlandl had been clashing with architects of the synthesis, especially G. G. Simpson. Zuckerlandl was interested in using molecular comparisons to infer phylogenetic relationships. His advocacy with Linus Pauling of the molecular clock and his disagreement with Simpson's primate phylogeny drove a wedge between molecular and morphological approaches to evolution and systematics. When Kimura, Alan Wilson, and others began to argue that the apparent constancy of the molecular clock could be explained by the neutral theory, the clock controversies became enmeshed with the neutralist-selectionist controversies, and the split between neutrality and selection became identified with a split between evolution as it occurred at the molecular and morphological levels (Dietrich 1998).

One of the most important outcomes of these early controversies concerning molecular evolution was a division of the domain of evolutionary biology into molecular and morphological levels. Evolution at the molecular level is marked by a significant role for random drift but does not exclude natural selection. In contrast, evolution at the morphological level is marked by the predominance of natural selection. So in what sense did the rise of the neutral theory of molecular evolution contribute to the decline of panselectionism?

In order to answer this question, we need some analysis of what constitutes panselectionism. We propose a three-fold distinction that mirrors different forms of adaptationism proposed by Peter Godfrey Smith. Smith distin-

guished empirical, methodological, and explanatory senses of adaptationism in order to clarify both the claims and disputes swirling about adaptationist approaches to evolution. When applied to panselectionism, three kinds of panselectionist claims can be distinguished. First, empirical panselectionism would claim that “natural selection is a powerful and ubiquitous force, and there are few constraints, except general and obvious ones, on the biological variation that fuels it.” Second, methodological panselectionism would assert that “the best way for scientists to approach biological systems is to look for evidence of natural selection in some form.” Third, explanatory panselectionism would argue that explaining the effects of selection is “the core intellectual mission of evolutionary theory” (Godfrey Smith 2001, pp. 335–357).

With these distinctions in hand, we can now evaluate the extent to which they make sense of the impact of neutralism in evolutionary biology. The claim of empirical panselectionism in its strongest form of advocating that all molecular and morphological characters are the products of only selection was probably never held. That said, at the height of the neutralist-selectionist controversy, Christopher Wills mounted a defense of “naïve panselectionism,” where he argued that “virtually any change in amino acid composition of any protein molecule produces a molecule of slightly different properties and therefore of slightly different selective value from the original” (Wills 1973, p. 23). Wills’s defense of panselectionism did not extend to the DNA sequences, where synonymous mutations were held as strong evidence that some nucleotide substitutions were in fact neutral. As in many controversies in biology, the empirical extent of neutrality and selection is not an all-or-nothing affair but a matter of the relative frequencies of each (Beatty 1987, 1995, 1997; Dietrich 2006). If some cases of neutrality are accepted, then the strongest forms of empirical panselectionism can no longer be defended.

The most significant impact of neutralism, however, is methodological, not empirical. When Stephen Jay Gould and Richard Lewontin launched their now famous attack on adaptationism in “The Spandrels of San Marco and the Panglossian Paradigm,” they argued broadly against panselectionism (Gould and Lewontin 1979). In his response, Ernst Mayr defended adaptationism in methodological terms. For Mayr, seeking adaptations was the best method available because drift simply could not be detected (Mayr 1983). Undoubtedly, Mayr had in mind earlier debates over whether drift could be detected at the morphological level, while Gould and Lewontin were watching the rise of molecular evolution as well as that of sociobiology (Beatty 1987). While the early statistical tests of the neutral theory were plagued with problems of low statistical power, the introduction of DNA sequence information in the late

1980s led to a series of statistical tests that could reliably distinguish drift from selection at the molecular level (Kreitman 1983; Hudson et al. 1987; Kreitman 2000). Where selectionists’ hypotheses were once the starting point and ending point of the research for virtually all evolutionary biologists, by the 1990s the neutral theory had become established as a null model and a starting hypothesis for molecular evolution research (Crow 1987; Kreitman 2000). This represents a significant methodological reversal. Even for biologists predisposed to favor selectionists’ explanations, if they are using nucleotide sequence data, the neutral model is the starting place for their investigation. Methodological panselectionism, then, has been seriously undercut by the rise of neutral models and sequence data.

Explanatory panselectionism may be the last refuge of the ardent panselectionist. In declaring what the explanatory agenda of evolutionary biology ought to be, explanatory panselectionists assert, as Richard Dawkins has, that adaptations constitute the business of evolutionary biologists (Dawkins 1983). While Dawkins may have empirical reasons for making this claim, it solves the problem of dealing with drift and neutrality only by dismissing it as a legitimate object of explanation. This strategy of narrowing the domain of evolution to include only the processes and products of selection would certainly preserve panselectionism, but at the cost of disregarding a significant portion of molecular evolution. As biology enters a postgenomic era, it is hard to imagine biologists embracing this alternative seriously.

The idyll of panselection has crumbled when given its strongest formulations, but selection remains the predominant cause invoked in most biological explanations. The inroads made against panselectionism are directed at molecular phenomena and techniques analyzing molecular data. Insofar as evolutionary biology wishes to include both molecular and morphological phenomena, it must recognize that the domain of evolutionary explanations has been significantly expanded with the advent of molecular biology. In his review of tests of neutrality and selection, Martin Kreitman claims that “Kimura’s theory of neutrally evolving mutations is the backbone for evolutionary analysis of DNA sequence variation and change” because a “substantial fraction” of the genome is best modeled as selectively neutral, because selective neutrality is a “useful null hypothesis,” and because “statistical analysis of (potentially) neutral variation in a gene (or other region of the genome) can be informative about selection acting at linked sites” (Kreitman 2000, pp. 541–542). The empirical and methodological prominence of neutrality and drift at the molecular level that Kreitman argues for indicates that the hardening of the evolutionary synthesis was short-lived and inadequate. While the neutralist and

selectionist positions have been refined into more nuanced and complicated models in light of new evidence and ongoing debate, neither the nearly neutral models articulated by Tomoko Ohta nor the fluctuating selection models articulated by John Gillespie, to cite just two examples, deny a role to either drift or selection (Gillespie 1991; Ohta 2002). Rather than seek a new unifying theory of evolution, however, current evolutionary biologists seem to accept multiple causal processes and types of explanations offered for evolutionary phenomena at the molecular and morphological levels. The result is explanatory and methodological pluralism in contemporary evolutionary biology.

Integrative Pluralism

As we have suggested, there is a long history of attempts to impose unity upon the diversity that is found in biology. It is our contention that though there is something to be learned by adopting these unificationist approaches, they do not account for the explanations that biologists seek. In place of unification, we counsel pluralism. At first blush, this would seem to invite disdain similar to Herschel's admonition of Darwin's *Origin of Species* as the "law of higgledy-piggledy" (Darwin letter to Lyell, 1837). But there are other varieties of pluralism. What we defend here is integrative pluralism, a view of the diversity of scientific explanations that endorses close study and modeling of different causes and different levels of organization but calls for integration of the multiple accounts in the explanation of concrete phenomena.

Some explanations offered for a given phenomenon are exclusive alternatives, of which at most one can be correct. Consider, for example, alternative hypotheses about the origin of an infectious disease that has been implicated in the recent amphibian decline. Some have suggested that the fungal pathogen *Batrachochytrium dendrobatidis* is endemic, while others say it is novel.

Emerging infectious diseases originate in two ways. The novel pathogen hypothesis states that the pathogen (or a newly evolved virulent strain of the pathogen) has recently spread into a new geographic area, encountering naive host individuals or species that are highly susceptible to infection (Alford 2001). The endemic pathogen hypothesis suggests that it has been present in the environment but has entered new host species or increased in pathogenicity because of environmental changes or, possibly, simply escaped previous human notice. Strategies for disease management will differ substantially, depending on which of these hypotheses is correct (CDC 1994). (Rachowitz et al. 2005, p. 1441)

It is clear that the logic of these hypotheses is one of exclusion. They could not both be correct for the same species or set of species at the same time. Only one can

capture the actual etiology, and tests to distinguish them are needed to determine which of them is, in fact, correct. Not only is our knowledge of population dynamics and selection regimes enhanced by understanding whether a pathogen is endemic or novel, but as the authors point out, the answer makes a difference to the conservation strategies that can successfully address the problem.

This structure of competing explanations driven from exclusive hypotheses is common currency in the philosophy of science. Indeed, in an early articulation of scientific method, Francis Bacon ([1620] 1902) explored the idea of an *experimentum crucis* where mutually exclusive alternatives are set up, to be decided by experiment and observation, and then as the finger post points in the direction of the truth, the scientist follows, leaving behind the defeated hypothesis and moving on to suggest further alternatives among which tests of nature will decide.

It is well known that this type of inductive inference is inconclusive, given that there are bound to be more alternative hypotheses than the two posed to be tested. Thus, while one of the two posed may be logically refuted by the observational evidence, the one left standing is not thereby proven to be true. It may account for the test case at hand but later be defeated in another bout with a third alternative hypothesis. Indeed, the assumptions and interpretations required to generate observable tests of exclusive hypotheses themselves are implicated in the "refutation" of the losing side, and hence there is no guarantee that the one inconsistent with a current observational test might not be revived to fight again with the help of other auxiliary assumptions. Thus, modern versions of the structure of competing explanations in science are more modest in the conclusions that can be drawn by any experimental test. They nevertheless account for alternative approaches and explanations in terms of their competitive relation and look into the future for the resolution to a single true account. Take, for example, Kitcher's (1990) endorsement of a plurality of explanations in science. He argues that because of our fallibility in determining which hypothesis is true based on finite observational evidence, it is rational to keep alternative competing accounts around. The aim, though, is to ultimately resolve the conflict, or, in his words, "the community goal is to arrive at universal acceptance of the true theory" (Kitcher 1990, p. 19). Thus, while pluralism is acknowledged and even defended on this approach, it is only as a means to a unified end.

While testing competing hypotheses does account for some of the pluralism characterizing biological explanations, not all explanations compete. In the case of the decline of amphibians, scientists have collectively explored a number of possible alternative causes, including habitat destruction, climate change, increasing levels of ultraviolet radiation, environmental contamination, disease, and the

introduction of nonnative species. Blaustein and Kiesecker (2002) present the case that ecosystem complexity is responsible for the failure of consensus on which of these is the cause or the most significant cause. They give evidence that multiple factors in interaction are responsible for amphibian decline. Additionally, they claim that different constellations of causes in different contexts are generating this effect. Thus, not only is it unlikely that one cause is responsible for global decline, it is unlikely that the same collection of causes is responsible for every case of decline.

Thus, pluralism in the explanations of some feature of the biological world might refer to competing hypotheses (endemic vs. novel in a particular population) or multiple contributing causes (climate change and disease acting jointly) or multiple constellations of causes (climate change and disease in one population and disease and nonnative species in another) acting in different contexts or at different times. There is little evidence to suggest that any single causal factor typically accounts for the total effect or that any successful causal explanation appealing to one or many causal factors will account for all cases in all contexts. Thus, any simple hypothesis will fail to generalize and thus fail to adequately explain similar effects in all situations. Distinguishing among this plurality of pluralisms, that is, competing hypotheses, partial causes, and contingent causes, aids in determining where real conflict exists among different explanatory models and where compatibility lies and integration is possible.

This situation is typical of evolved, dynamically robust biological systems. The different hypotheses that scientists propose to identify causes of an effect of interest are more probably not solely determinant but rather contribute in context-dependent ways to bring about the effect. But how does one then study complex causality? A successful methodology has been decomposition (see Bechtel and Richardson 1992). That is, take a complex system, and investigate the subsystems that constitute it. Take the set of potential causes, and investigate what power each of them has individually in generating the effect. Thus, the nature of the complexity of the systems studied by biology in conjunction with a decomposition methodology necessitates a plurality of causal hypotheses that are not competing but compatible.

Biologists have long recognized the existence of compatible alternative explanations, and there have been attempts to partition the plurality in ways that locate areas of compatibility and areas of competition. Tinbergen (1963), in an influential article, outlined a four-part classification of questions one might ask of a biological phenomenon. More recently, Sherman (1988; see also Reeve and Sherman 1993) revived this classification and dubbed it "levels of analysis." Biological questions are stratified

into levels of evolutionary origin, current reproductive function, ontogeny, and mechanism. Naturally, questions at different levels require different answers. In some sense, the questions are not addressing the same problem, and hence, the answers given cannot be taken as competing. As Sherman put it, "every hypothesis within biology is subsumed within this framework; competition between alternatives appropriately occurs within and not among levels" (Sherman 1988, p. 616). But is this erotetic stratigraphy the right way to describe the relations among the plurality of compatible explanations? Different levels of analysis might target different partial causes, but will there be no competition between levels? Different constellations of partial causes at different levels may represent compatible harmony, but how on this framework does one account for context contingency?

For example, explaining ontogenetically how a vertebrate limb develops by detailing the cell-cell interactions that determine the axes upon which the limb is patterned does not immediately implicate the fitness consequences or the hormonal or genetic triggers for cell differentiation and thus is in a sense autonomous from selectionist or mechanism explanations. Yet, especially salient with the increasing interest in evolutionary-developmental biology, the relationship between evolutionary questions and developmental questions and the answers to them can no longer be left in oblivious isolation. Answers to questions posed at the different levels of analysis cannot be satisfactorily answered without consideration of the other levels. Evolution without development is empty, and development without evolution is blind (to butcher an old Kantian chestnut). The pluralism of levels of analysis identifies strata in which explanations do not directly compete with each other; however, an isolationist stance with regard to these levels would be mistaken.

Competition does occur between hypotheses within a level, but not only within those confines. Developmental explanations suggest limits to the range of variability that is and might have been available for selection to have acted on. Fitness consequences of early developmental alternatives might constrain the range of subsequent developmental processes that are accessible. The relationship among *prima facie* compatible alternative explanations posed at different levels of analysis should be one not of isolation but of integration. A consequence of such an integrative strategy is the recognition of a new location for competition among hypotheses. Which collection of causal processes at all levels characterizes the etiology of a targeted effect? What contribution does each potentially contributing cause make? In different particular cases, there will be different answers, but in any given case only one answer will map onto the actual processes that brought about the trait (Mitchell 2002, 2003). A "levels of analysis"

framework recognizes the plurality of partial causes but obscures rather than highlights the means of integrating them.

Complexity, we have claimed, invokes multiple levels of organization and multiple causal factors in generating an effect. Evolved complexity introduces historical contingency, and ecological complexity introduces distributional contingency into the mix. That is, how a complex organism develops is in part a result of the particular evolutionary trajectory its lineage traversed. There are alternative developmental schemas; which one is present in which individual may not result from physical or chemical necessity but rather from its evolution. There are multiple mechanical triggers for behavior for a complex system. Which ones are present and active may well be a function of the ecological context in which the system is located. Explaining complex, evolved biological systems is not a "one-size-fits-all" enterprise.

Consider again the case of multiple causal contributors to generating a complex effect. In the example of amphibian decline, the increase in UV radiation has been implicated as a cause by means of its effect on hatching success. Of course, it may be that the competing hypothesis, that UV radiation plays no role in amphibian decline, may turn out to be correct. However, even if UV radiation does causally contribute to amphibian decline, its effect is not consistent across all species or taxa. Some populations show marked decrease in hatchlings in the presence of increased UV, but others show no decrease. When and why does the effect vary? One suggestion (Blaustein and Kiesecker 2002) is that UV radiation has different effects when combined with other factors in a complex causal network. It may, for example, be destructive only when interacting with effects of acid rain or with other environmental pollutants. It may interact with biotic factors such as the presence of other species that might participate as disease vectors for the amphibian population.

By modeling each individual causal factor, one can discover its possible contribution to a complex effect. But only by integrating multiple causes in multiple combinations can one begin to detect the actual causal history leading to the decline of, say, western toads in Oregon as compared with toads occurring in Colorado (Blaustein et al. 1998). The developmental variations among amphibians may determine how various causal factors can interfere with phenotypic factors that contribute to fitness differences. At the molecular level of developmental regimes, at the behavioral level sensitive to external context, various causal processes are likely to be interacting to generate variant fitness. A unified theory would promise that a single type of causal factor (drift or selection) or at least a single model of multiple causal factors (UV radiation plus introduced species) would explain all the biological

phenomena we investigate. But contingency, context sensitivity, and nonlinear interaction among contributing causes preclude the success of these types of unification. The "levels of analysis" framework describes the territory of pluralistic investigations, but it is only by integration of the multiple levels and multiple causes, including attention to the diverse contexts in which they occur, that satisfactory explanations can be generated.

Conclusion

The lure of a general and unified theory of evolutionary biology was powerfully appealing to the founders of neo-Darwinism. While we do not deny the appeal of this vision, the expanding domain of evolutionary biology has complicated this supposed selectionist unification. Finding ways to integrate molecular and phenotypic (i.e., morphological, physiological, and behavioral) levels represents a new challenge for contemporary evolutionary biologists. It is our contention that explanations of complex phenomena in biology regularly integrate phenomena across levels. These integrative explanations result in a type of pluralism that does not require general unification and that explains why innovative and productive explanations are possible in the absence of a unified theoretical framework.

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