THE EVOLUTIONARY DYS-SYNTHESIS: WHICH BOTTLES FOR WHICH WINE?

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In 1942, that prolific philosopher, developmental biologist, and evolutionist par excellence Julian Huxley wrote a book entitled *Evolution: the modern synthesis*. It was a title that was to remain ingrained in our consciousness as a larger epigram for a viewpoint embodied in the works of other biologists of that decade. Of these, Simpson’s *Tempo and mode in evolution* (1944), Mayr’s *Systematics and the origin of species* (1942), and Dobzhansky’s *Genetics and the origin of species* (1937) are the most famous. Equally influential in their respective fields were Stebbins’ *Variation and evolution in plants* (1950), Darlington’s *The evolution of genetic systems* (1939), and White’s *Animal cytology and evolution* (1945). Other works, such as Schmalhausen’s *Factors of evolution* (published in Russian in 1946) and Rensch’s *Evolution above the species level* (published in German in 1947), are less well known but were influential in broadening the synthesis beyond English-speaking countries. This period around the 1940s has come to be known as the “evolutionary synthesis,” and it has been hailed as a major and revolutionary epoch in evolutionary biology (Mayr and Provine 1980). Here I reexamine and reevaluate what this period did and did not achieve. I will allude to its successes only briefly, not because they were meager and insubstantial but because they have been considered elsewhere at length and are well known to most evolutionary biologists. Instead, my emphasis is on what the Synthesis did not achieve; indeed, my thesis is that the Evolutionary Synthesis failed in many serious and insidious ways. I propose that the Synthesis had little direct effect on the progress of evolutionary biology as a discipline and that, at the conceptual level, it may even have hindered rather than furthered our understanding of evolution. Many of the negative effects of the Synthesis have lasted to this day in terms of the institutional and conceptual structure of the field. I suggest that it is probably time that, rather than trying to finish the Synthesis as Eldredge (1985) has exhorted, we instead earnestly work to dismantle it. I suggest that only by achieving a Dys-Synthesis can we free ourselves of many of the methodological, conceptual, and even socioreligious difficulties that plague evolutionary biology.

What did the Synthesis achieve? It primarily reaffirmed, following several decades of acrimonious debate, that the Darwinian view of evolution was tenable.
in the light of the findings of genetics. It also reconciled the Darwinian view with the accumulated knowledge in the fields of cytology, developmental biology, paleontology, and systematics. Thus, Huxley reassured us, "Biologists may with a good heart continue to be Darwinians and to employ the term Natural Selection, even if Darwin knew nothing of mendeling mutations" (1942, p. 28). The Synthesis was characterized by an overall uniformity of view, a uniformity that was explicitly noted at the Princeton conference in the late forties (see Mayr and Provine 1980, p. 42) and that persisted until the late sixties and early seventies. Natural selection could account for genetic change within populations, as well as for the origin of species and of higher taxa. Species were seen as biological entities, held together by gene flow and separated genetically from other species by suites of isolating mechanisms. Inherent in the Synthesis was a view of evolution as a gradual process, with natural selection as the driving force of continuous change; this was quite overtly a reaction against the mutationists of the early part of the century, who found it more parsimonious to imagine that random mutations leading to "hopeful monsters" were the lifeblood of evolution. Entwined with such gradualism was a continuing belief in natural selection as a creative progressive force. Thus, Huxley stated, "Neither mutation nor selection alone is creative of anything important in evolution; but the two in conjunction are creative. . . Their interplay is as indispensable to evolution as is that of hydrogen and oxygen to water." (1942, pp. 28, 29.)

These tides of generalization and synthesis were not confined to the scientific arena but extended into restatements of philosophy and world view. Indeed, the Evolutionary Synthesis was as notable for the idealism of its protagonists, for its Huxleys and Dobzhanskys, as for the idealism of its biology. These world views resulted from a resurgence of the materialism that emanated from the original Darwinism of the nineteenth century, combined with a liberalism that followed in the wake of the atrocities of the Second World War. The materialistic tremors that accompanied A book that shook the world (Huxley 1958) were revived in large part by the protagonist of the Synthesis, namely, Julian Huxley himself; much of that philosophy was expressed in a collection of his essays entitled New bottles for new wine (1957). In one of these essays ("Evolutionary humanism"), Huxley stated that "the monistic evolutionary hypothesis best meets the known facts. . . . In the light of such a view, religions like sciences or philosophies are creations of man, and gods are products of the human mind just as much as scientific 'laws of nature.' " (1957, p. 286.) Unlike other materialists, Huxley, in proposing this evolutionary monism, urged that rejection of a supernaturalistic view of the world be tempered by the realization that such supernaturalistic views may have valid origins and functions. He still saw the need for man "to understand, control, and utilize the forces of his own nature" (pp. 296–297), a need fulfilled in the past mainly by religions but one he saw being better fulfilled in the future by his evolutionary humanism.

The Evolutionary Synthesis, as its name implies, therefore embodied both a scientific and a philosophical monism, a monism that nonetheless had strength because it was supported by the essence of variation. Natural selection was the major force, but variation was the raw material on which it fed. If evolution was
"good," so was variation; a philosophy of individualism compatible with individual freedom resonated with a philosophy based on evolution. Not only was diversity tolerated, but singular superiority was seen as transient. I am reminded of the Taoist (or, perhaps, Red Queen) view:

Those who would take over the earth  
And shape it to their will  
Never, I notice, succeed.

For a time in the world some force themselves ahead  
And some are left behind,

For a time in the world some are puffed fat  
And some are kept hungry . . . .

(Laotzu, 29, trans. by Bynner, 1962, p. 43)

This philosophy was compatible not only with evolution but also with Western liberalism, which had been appalled by a Nazi racism that had fed its excesses on a belief in absolute superiority and by a Stalinism that had fed its excesses on a litany to uniformity. This view of the value of human diversity certainly found support from evolutionists. We see it in the works of Dobzhansky (1956, The biological basis of human freedom); we see it in the early UNESCO pronouncements on race in the 1950s (elegantly analyzed in Province 1986); and we see it in Lewontin’s (1972) article on "The apportionment of human diversity," where the evidence of genetic diversity is obliquely used to condemn racism.

The Evolutionary Synthesis therefore provided a unified view of evolution that was strengthened rather than weakened by the science of genetics and that was supported and nourished by other fields of biology; it also provided a philosophy reconciling individual liberty with a monistic, materialistic theology. Scientifically and philosophically, it seemed there were indeed new bottles for new wine.

It is now forty years since the Synthesis. It is a Synthesis that has pervaded our thoughts and is still the stuff of which introductory textbooks are made. But it is perhaps time also to reflect on this period and assess its consequences. I would like to do so from three perspectives. First, I take a personal view: I was very much a child of that Synthesis, being introduced to evolution through reading Huxley and Dobzhansky. Second, I want to concentrate on the conceptual properties of the Synthesis, emphasizing how our present views are radically different. Finally, I want to examine the institutional consequences of the Synthesis. Overall, my contention is that the subject of evolutionary biology, now in the 1980s, has in many ways returned to a pre-Synthesis state, a condition that I see as a symptom not of some malaise but of scientific vigor.

As a graduate student from 1963 to 1966, I remember the excitement and eagerness with which we studied natural selection. Much of this was due to the infectious enthusiasm of my mentor, Tony Bradshaw, and my fellow students Tom McNeilly, Peter Gregory, Roger Turner, and Phil Putwain. It was clear that on metal mines there had to be strong selection pressures favoring metal tolerance: I remember hauling Land-Rover-fuls of mine soil to set up experimental
plots on which to study natural selection. I remember helping to set up experimental wind tunnels, with sandpaper sides, to demonstrate that plants from sea cliffs were more resilient to wind action than plants from adjacent pasture populations. I remember snails eating (and not eating) cyanogenic clover in glass tanks. And I remember being abused by hordes of sea gulls on a trip to sample giant groundsel from an ammonia-soaked bird colony on Puffin Island, groundsel that indeed proved more tolerant of high nitrogen levels than its conspecific sand-dune counterpart. Although I remember the excitement of those times, I am now also appalled by it. Why on earth, a hundred years after Darwin and close to twenty years after the Synthesis, were we still excited by demonstrating natural selection?

My research interests centered on speciation. Having spent my final year as an undergraduate studying genetics at Cambridge in the department of John Thoday, I was naturally intrigued by his studies of *Drosophila*, which had shown that disruptive selection could lead to divergence and even to genetic isolation. This finding seemed to fly in the face of the dogma of the time, namely, that gene flow was a major cohesive force that would prevent population divergence and speciation. I was eager to pursue this in graduate school, perhaps even to demonstrate that a mode of speciation other than the allopatric one (in which isolation was a prerequisite of divergence) could be valid in nature. Thoday suggested I consider looking at the curious example being studied by Bradshaw, in which metal tolerance could evolve in wind-pollinated grasses even though a few meters away nontolerant plants of the same species were growing on normal pasture. I still remember taking visitors to the sharp boundary at Trelorgan mine, straddling the stone wall, and watching their disbelief and skepticism on being told that if they leaned one way they could sample a tolerant population, whereas if they leaned the other way the plants would be nontolerant. It is again appalling in retrospect to think that such a monistic view of speciation events prevailed that even to suggest an alternative mode was to be somewhat heretical, to be believed only because the data were incontestable.

But of course, the data were contested. At the informal Ecological Genetics Group meetings, the counterargument was proposed that since we were dealing with perennial grasses, perhaps the evolutionary situation was not very dynamic: a tolerant mutant arose, was selected, and then, being perennial, persisted on the mine as did its tolerant progeny. There was thus a steady accretion of tolerance, a process on which gene flow had little impact. Since I had failed to produce an adequate counterargument, it became obvious that my casual observation of dying plants required precise documentation. I therefore began mapping individuals on the mine to demonstrate that they did indeed die (far more quickly than I thought, with a half-life of two years or so). After three years, when I was ready to abandon the tedium (and cold) of mapping, I was urged to continue by John Harper, who pointed out to me that my data were close to unique, that only a handful of studies had been made on the lives and deaths of individual plants (one of those by Darwin; see Harper 1967). Again, in retrospect, one can only be aghast that precise quantification of individuals’ lives and deaths had received so little empirical study when the entire theory of natural selection was based on such processes.
Most, if not all, of the methodologies we used were simple and universally accessible. They were not predicated on the existence of the electron microscope, X-ray crystallography, monoclonal antibodies, or high-speed computers. Given the lack of technical impediments to progress in the empirical study of evolution, the absence and poor state of development of such studies must surely be attributed to conceptual roadblocks, or more likely to an absence of a realization that "something is rotten in the state of Denmark" (Shakespeare, *Hamlet*, I, 4, 90).

From a conceptual standpoint, where did the Synthesis fail? I think the synthesis failed in numerous ways.

1. It did not demand the measurement and quantification of selection processes; it simply reaffirmed what has come to be known as the "adaptationist program." Morgan pleaded in 1909: "The neo-Darwinians seem less concerned with the advancement of the study of evolution than with expounding Darwinism as a dogma. . . . To imagine a use for an organ is for them equivalent to explaining its origin by natural selection without further inquiry." (Pp. 373–374.) It was a plea that had to be reiterated eloquently by Gould and Lewontin (1979), almost as though no methodological lessons had been learned in the intervening years. Certainly the Synthesis had little effect. Endler (1986) recently summarized studies of natural selection in the wild. Retabulating his charts by date, we see that the real burst in the study of natural selection occurred not after the Synthesis, but in the late sixties and seventies (table 1). The United States was the source of many of the major writings for the Synthesis; yet in the decade following the Synthesis, Endler listed only one study from the United States (on water snakes; Camin and Ehrlich 1958) that was concerned with actually demonstrating natural selection.

2. The Synthesis emphasized the "progressive" nature of evolutionary events. It focused on the achievements of natural selection rather than on its failures. Selection limits, constraints, failures of adaptation, and extinction were processes laid out for all to see by the authors of the Synthesis but then somehow swept under the carpet by the accompanying surge of optimistic adaptationism. It thus became commonplace—if not in evolutionary biology per se, then in related disciplines—to show how organisms are adapted to their environment. In fact, it has become so commonplace that when I suggest to students in our "Evolutionary mechanisms" class that on their way back from class they look for ten ways in
which the organisms they see are not adapted to their environment (why don’t birds have arms as well as wings?), I am met with quizzical stares about the seriousness of my suggestion.

3. By emphasizing the continuity between past and present evolutionary events, the Synthesis failed to emphasize the methodological dichotomy between reconstructing past evolutionary events and studying present-day evolutionary mechanisms. This has led to an uncritical application of the comparative method for testing evolutionary ideas and to a lack of confidence in (and respect for) the methodologies of evolutionary science. I will return to this point later.

4. The Synthesis failed to recognize the multiplicity of speciation processes, and thereby failed to devise rigorous criteria for studying these events. Such was the prevailing monism of the allopatric model of speciation that other rampant exceptions (polyploidy) were reduced to special cases (plants don’t count) and contradictory evidence was passed over. Thus, despite an early demonstration that, theoretically at least, speciation could occur without spatial separation of populations (Ludwig 1950), this finding was ignored in later treatises on speciation, even though other concepts from that same paper (e.g., “annidation”) were freely mentioned (Mayr 1963).

5. Following the Synthesis, the study of evolution remained thoroughly wedded to systematics and the comparative approach. Although in and of itself this approach can be powerful, there was a corresponding lack of emphasis on the need for a rigorous testing of hypotheses by experiment and for methodologies relating to rigorous evolutionary inference. It also failed to emphasize the value of in-depth analysis of a few organisms and their evolution as model systems (Raven 1979), thus equating almost any comparative biology, no matter how cursory or superficial, with evolutionary biology.

In summary, the Synthesis placed restrictive notions on the conceptual richness and depth of evolutionary biology as a science. It also failed to establish appropriate methodologies with which to explore this richness. The presentation of a confirmed theory of such broad scope led to a complacent acceptance and reduced evolutionary biology to everybody’s toy and plaything. The ability to generate a simplistic speculation about some putative past selection process seemed to qualify anyone as an evolutionary biologist and, perhaps worse, led others to imagine that this is what professional evolutionary biologists do. Someone, and I regret I cannot remember who, referred to “the evolutionary playground.” From eight o’clock to ten o’clock real biologists work collecting data and doing science, but then for relaxation they run to the evolutionary playground, only to return, fortified and reenergized (perhaps relieved) by the gay abandon of speculation, to the stuff of which science and technology are really made.

In pinpointing the weaknesses of the Synthesis in such an ex post facto way, I have not meant to condemn it. The historian of biology, rather than my personal hindsight, will provide a final, more-balanced judgment. My main purpose is to reexamine this period more critically in order that we may understand how we are influenced unknowingly by it. Reexamination may also help us understand the institutions and scientific support structures that surround evolutionary biology today.
With regard to scientific journals, the Synthesis was accompanied by one major event, the founding of the Society for the Study of Evolution in 1946, followed by the publication of the journal *Evolution*. This was a remarkable achievement, particularly notable since in spite of all the discussion and controversy about evolution, no one since Darwin had seen fit to devote a scientific journal exclusively to its study. The spirit of the Synthesis rings true in the foreword to the journal by Mayr: "The deeper insight into the factors and processes of evolution gained through the accumulation of facts by representatives of the various fields clearly brought out that the differences of opinion (characterizing the early decades of this century) were spurious. This coming together of evolutionists from all fields has initiated a new era in evolutionary research." (1947, p. i.) Unfortunately, this new era proves elusive, and its coming has been delayed by perhaps another few decades. Certainly, no other evolutionary journals appeared until the seventies.

We fail to find evidence of this new era in a number of realms. With regard to textbooks, there was no flood of standard works clearly stating the principles, methodologies, and major insights of evolutionary biology. The original works of the Synthesis were not texts, but expository writings that marshaled information supporting their respective theses. A few other similar works ensued, such as Waddington's *The strategy of the genes* (1957). There were also short, summary books, such as Sheppard's *Natural selection and heredity* (1958) and Maynard Smith's *The theory of evolution* (1958), but textbooks were absent. In the sixties, I can think of only Ehrlich and Holm's *The process of evolution* (1963) falling into this category. The same is true of works on population genetics. Li's *Population genetics* (1955) is an early text, but the surge of texts in population genetics did not occur until the late seventies. Even now it is hard to find a good text on evolutionary biology (I think of Futuyma 1979 as an exception).

Given that most people would credit evolutionary events as playing a central role in biology, it is also remarkable that evolutionary biology is rarely thought of as a discipline in its own right. An international congress devoted to evolution was not started until the seventies, but when it was, it became The International Congress of Systematics and Evolution. There are few departments, subdepartments, or programs in evolution at our universities. Where they do exist, they always have company: Ecology and Evolution (Stony Brook), Ecology and Evolutionary Biology (Tucson), Evolutionary Ecology and Behavior (Iowa). Or the subject is tacitly submerged in titles of the nature of Environmental, Population, or Organismal Biology (God forbid that evolution should be associated with less than organismal-level processes studied by molecular biologists and biochemists). I can think of only one institutional organization with the singular purpose of studying evolutionary biology, the Committee on Evolutionary Biology at the University of Chicago. And even though its origins can be traced to an earlier date, this program's title was not created until the late sixties.

The lack of recognition of evolutionary biology as a science in its own right is nowhere more transparent than in funding. I still remember my surprise at finding that my first National Science Foundation grant proposal to study the evolution of life history traits was to be considered by the systematics panel—and this was in
the early seventies. On delving a bit further, I was told that the genetics panel "could not properly evaluate" proposals dealing with evolution (this was nearly thirty years after the "synthesis" of genetics and evolution). Instead, the genetics panel deemed such proposals more appropriate for systematics. Even now a proposal in evolutionary biology receives strange treatment. If comparative in nature, it is still thought fit company for systematics; yet if, curiously, it considers a single system, it is deserving of an unobtrusive place before the panel on population biology and physiological ecology, itself the prodigal son of other unresponsive parental panels. Even though evolutionary biology is the pure-science counterpart of much of plant and animal breeding, it has not attained any respectability even among those in the U.S. Department of Agriculture that can persuade the behemoth to throw a few crumbs, a few hush puppies, to competitively funded research.

My institutional analysis is a kind of glib historiography; yet even in its superficiality one cannot escape the conclusion that evolutionary biology has lacked a respectability and an acceptance afforded other areas of biology. It is as if evolution has been everyone's and no one's subject. Whether the acceptability that it has attained is a latent result of the Synthesis, or whether the Synthesis in fact retarded the development of the subject, I leave for others to decide. Certainly, the Synthesis did not generate this respectability and acceptance in any immediate sense.

Where are we now? It is my contention that evolutionary biology is returning to a kind of pre-Synthesis condition: the philosophical monism and the unitary schemes are being dismantled, and many old conceptual habits are being broken and replaced. We are in a period of Dys-Synthesis, with conflicts, controversies, and new discoveries. These conflicts are being incorporated into a rich theoretical tapestry based on empirical evidence. This evidence is being garnered by a revival of experimentation, by a demand for quantification, by the development of rigorous methods of phylogeny reconstruction. It is also being enriched by the discoveries of molecular biology. This Dys-Synthesis should be recognized and encouraged, since at the intellectual level, it is infusing evolutionary biology with vigor and excitement.

Doubts about natural selection as a major causative force have again arisen, particularly with regard to changes at the molecular level, but also with regard to its being an instigating force in speciation events and macroevolution. Even Lamarckian concepts are starting to achieve a qualified cogency as stress-induced DNA changes are no longer mere inferences from genetic experiments but have been demonstrated in molecular reality. Genetic transmission processes are seen both as causes of genetic change and as objects of natural selection. Many of the principles governing genetic variation in natural populations are understood, but the reality of its origins and maintenance remains elusive. At last, methods are being developed for measuring selection intensities, and students of natural populations have also become experimentalists. There is a disenchantment with adaptationist paradigms; yet it is not clear whether our models should optimize, maximize, satisfy, or simply prevent invasion by mutants that otherwise obey the rules of the game. There is a disbelief in the unitary nature of speciation processes, and a surge of theoretical and experimental studies on speciation
modes. There is an increased level of operationalization and impatience with nonoperational emotive words. If an organism is adapted to its environment, is it 10% adapted or 90% adapted? For a gene complex to be coadapted, how many genes with how many kilobases need to be how epistatic at what map distance? And though I know that a Waddington would be an excellent term for a unit of developmental constraint, we still seek the parameters of this unit.

I think that one of the most important components of the Dys-Synthesis is the recognition that evolution, as a science, consists of two quite disparate disciplines, an inference of past events and the study of present-day processes. I have tried, but failed, to coin separate terms for these disciplines. None of the existing terms quite captures the difference: the study of past events has usually come under the rubric of phylogeny reconstruction or cladistics, and the study of present-day processes has been termed population or ecological genetics. But these terms have other, more specialized (and, for some, discomforting) associations. A major contribution to the Dys-Synthesis has been the rise of modern cladistics, which sees each phylogeny as a hypothesis constructed by explicit methods and based on stated assumptions, rather than as a personal declaration of opinion (whose force used to depend more on the status of the investigator than on any objective criterion). Although hypotheses about the past may not be amenable to experimental test, they are nonetheless valid scientific inferences whose strength can be assessed as more lines of evidence become available. Methodologies for the study of past processes contrast with those used to study present-day processes; these can be studied by the formulation of experimentally testable hypotheses, in a manner identical to that used in other areas of experimental science. This recognition of two major subdisciplines, each with its own distinctive goals and methodologies, enables us to use their interaction constructively, rather than confusing them and being accused of that sin of sins, "weak inference." Thus, it becomes clear than an observation about past relationships can suggest a mechanism of evolution but cannot itself be an independent test of such a mechanism. Similarly, an experiment or observation involving a present-day character tells us about the forces now acting on the population, but nothing per se about the forces that acted during the trait's earlier evolution or about the historical pathway of such evolution. Similarly, in order to invoke the comparative method as a test of an evolutionary hypothesis, it is essential to know the phylogeny of the organisms being used in the comparison. As Felsenstein (1985) elegantly pointed out, only in this way can one know how many independent evolutionary events were involved and therefore what degrees of freedom to assign to any test of a prediction.

There are many other ways in which we could benefit from a Dys-Synthesis. For example, paleontologists today seem to be schizophrenic in relationship to the Synthesis. When championing punctuated modes of evolution, they want nothing of the Synthesis; yet at other times, under the guise of species selectionists, they wish to embrace the Synthesis. I imagine that more progress would be made if they expended less effort in convincing and integrating the population geneticist but instead interacted with the community ecologist. After all, community ecologists have been studying species selection for many years under the guise of theories of species replacement.
In summary, it is only recently, so long after Darwin, that evolutionary biology is becoming a discipline in its own right. It is as if, from the beginning, evolutionary theory has been embodied in that mythical animal, the unicorn. This unicorn remained a distant but highly visible, highly controversial animal that nonetheless redirected a simplistic mythology based on God's design to a mythology based on a faith in natural selection. However, it was a unicorn that no one was able or willing to catch (Meagher 1979). The Synthesis was a bold attempt to understand the unicorn. In retrospect, perhaps chauvinistic retrospect, we see that although the unicorn was indeed captured, it was then merely washed off, dressed up, and again released for all to admire. The myth remained. It is only in the past decade or so that we have caught the animal and are willing to dissect it rigorously and objectively. It has taken over a hundred years to do this. It has often puzzled me why evolutionary theory should have had such a remarkable impact on our cosmic view, when the more decisive, remarkable discoveries of, say, molecular biology, which are of great social consequence, seemingly have so few philosophical implications. Similarly, it has been unclear to me why the evolutionary biologist has to bear the tedium of the creationist debate, when creationism flies in the face of physics, plant physiology, biochemistry, immunology, and indeed every other science imaginable. I suspect it is not because, as Huxley would have had us believe, evolutionary biology provides us with particular socioreligious insights, but because it has been a muddled simplistic science willing to stay at the periphery of its own concepts. When evolutionary processes are seen as mechanistic events with precise causes and effects, when questions are posited as clear hypotheses amenable to empirical test, and when quantities are no longer created that cannot be measured, then and only then will we be able to trap Darwin's unicorn and truly demonstrate that there are indeed many different bottles for much good wine.

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LITERATURE CITED

THE EVOLUTIONARY DYS-SYNTHESIS

Oxford University Press, Oxford.
Ludwig, W. 1950. Zur Theorie der Konkurrenz: die Annihilation (Einnischung) als funfter Evolu-
Mayr, E., and W. B. Provine. 1980. The evolutionary synthesis: perspectives on the unification of
Meagher, L. R. 1979. The influence of Darwinian theory upon biological research of the late nineteenth
Press, New York.
phia.