The Modern Synthesis

Huxley coined the phrase, the "evolutionary synthesis" to refer to the acceptance by a vast majority of biologists in the mid-20th Century of a "synthetic" view of evolution. According to this view, natural selection acting on minor hereditary variation was the primary cause of both adaptive change within populations and major changes, such as speciation and the evolution of higher taxa, such as families and genera. This was, roughly, a synthesis of Mendelian genetics and Darwinian evolutionary theory; it was a demonstration that prior barriers to understanding between various subdisciplines in the life sciences could be removed. The relevance of different domains in biology to one another was established under a common research program. The evolutionary synthesis may be broken down into two periods, the "early" synthesis from 1918 through 1932, and what is more often called the "modern synthesis" from 1936-1947. The authors most commonly associated with the early synthesis are J.B.S. Haldane, R.A. Fisher, and S. Wright. These three figures authored a number of important synthetic advances; first, they demonstrated the compatibility of a Mendelian, particulate theory of inheritance with the results of Biometry, a study of the correlations of measures of traits between relatives. Second, they developed the theoretical framework for evolutionary biology, classical population genetics. This is a family of mathematical models representing evolution as change in genotype frequencies, from one generation to the next, as a product of selection, mutation, migration, and drift, or chance. Third, there was a broader synthesis of population genetics with cytology (cell biology), genetics, and biochemistry, as well as both empirical and mathematical demonstrations to the effect that very small selective forces acting over a relatively long time were able to generate substantial evolutionary change, a novel and surprising result to many skeptics of Darwinian gradualist views. The later "modern" synthesis is most often identified with the work of Mayr, Dobzhansky and Simpson. There was a major institutional change in biology at this stage, insofar as different subdisciplines formerly housed in different departments, and with different methodologies were united under the same institutional umbrella of "evolutionary biology." Mayr played an important role as a community architect, in founding the Society for the Study of Evolution, and the journal *Evolution*, which drew together work in systematics, biogeography, paleontology, and theoretical population genetics.

1. The Background to the Synthesis

In the late 19th and early 20th centuries, it was not uncommon for biologists to claim that "Darwinism is dead." By this was meant, not that Darwin's hypothesis of common descent was discredited, but rather that Darwin's preferred mechanism, selection, was neither the exclusive nor main cause of either adaptive differentiation or species forming.

In Kellogg's *Darwinism Today*, he claimed that "Darwinism… as the all-sufficient or even most important causo-mechanical factor in species forming and hence as the sufficient explanation of descent, is discredited and cast down." (Kellogg, 1907).

There were a number of competing theories on offer apart from Darwin's preferred selective explanation. More popular mechanisms for evolution were a variety of neo-Lamarckian theories, Orthogenesis (or inherent tendency toward "progress," understood as greater complexity of organization), and various saltationist or "mutationist" schools (where evolution proceeded by major mutations). Neo-Lamarckians accepted "soft" forms of inheritance, or direct influence of the environment on traits passed to offspring, also called the inheritance of acquired characters. DeVries, Johannsen and other "mutationists" argued exclusively for "hard inheritance," and argued on behalf of the view that mutation, not selection, was the engine of evolution.

This "eclipse of Darwinism" as it's been called (Huxley, 1942, Bowler, 1983), was, however, gradually reversed in the years of 1918-1930. A number of population geneticists demonstrated that the Mendelian, or "mutationist" theory, as it was then known, was compatible with a gradualist, Darwinian, and selective explanation of adaptive differentiation. This period has been called the early synthesis.

2. Early Synthesis: 1918-1932

The early synthesis may be broken down into three stages. First, there was a reconciliation of Biometry and Mendelism. Second, there was the development of a mathematical theory of evolution, classical population genetics, which delimited the major causal factors shaping populations over time. Third, there was a broader synthesis of population genetics, classical genetics, chromosomal mechanics, biochemistry, and cytology, in Haldane's (1932) *Causes of Evolution*. In this book, and earlier (1924), Haldane demonstrated the sufficiency of natural selection for both observed microevolutionary and significant macroevolutionary change. For some biologists, these texts served as a definitive answer to claims to the effect that "Darwinism is dead," by ruling out the necessity of appeal to mechanisms other than selection (such as Lamarckian or orthogenetic forces). However, for many biologists ("naturalists" such as systematists (those who classify species), the mathematical representations of evolution were too difficult to interpret, and thus unpersuasive. Another ten or fifteen years passed before these ideas were effectively communicated to a broader biological audience.

The conflict between the Mendelian and Biometrical schools took place roughly from 1900-1918, largely in the UK. The divide was over whether gradual selection on "quantitative" or continuously varying traits, was sufficient for the transformation of species and higher taxa. For instance, can slight variations in such things as leg length or girth be added up in such a way that new species can be created, or whole new phyla? On the one hand, Weldon, Pearson, Mendola, and Poulton argued that evolution was largely a gradual process. On the other hand, Bateson, DeVries, and Johannsen argued that major mutations were the driving force of evolution; evolution proceeded by "macro-mutations." Members of both groups were concerned with the nature of inheritance. Biometricians took a descriptive, statistical approach, measuring phenotypic variation and relations of these measurements within and between parent and offspring populations. This data was used to found investigations into the role of natural selection in shaping the distribution of continuous traits in populations from one generation to the next. Weldon, for instance, was one of the first biologists to conduct statistical inquiry into a case of selection in the wild.

After the rediscovery of Mendel's 1865 paper in 1900, Bateson, DeVries, and others claimed Mendel as their predecessor, and thus came to be called the "Mendelian" school. DeVries claimed to have found evidence that evolution proceeded via selection on major mutations, or "discontinuous" variation. The Mendelians posited a particulate theory of inheritance; they held that variation was of two sorts, "fluctuating" and "discontinuous," and that it was the latter that was important to evolution. Evolution must ultimately rely on mutation as the source of new variation, where by mutation they meant new genetic factors that caused genuinely novel characters, or major morphological shifts.

The first stage of the early synthesis was a resolution of a conflict between these two schools of thought. Fisher's 1918 paper, "On the Correlation Between Relatives on the Supposition of Mendelian Inheritance," demonstrates how a multifactorial theory of inheritance can serve to underpin observed correlations between relatives discovered through biometrical methods. While Fisher's demonstration has some of the characteristics of a reduction – one that involved a number of simplifications – it nonetheless failed to convince many biologists, for at least another ten years, of the compatibility of a Darwinian, gradualist view of evolution, and a Mendelian, particulate theory of inheritance.

The second stage of the synthesis built upon this early synthesis. Haldane, Fisher and Wright represented evolution as change in genotype frequency in a population from one generation to the next. At this stage, roughly from 1922-1930, this family of models effectively served as a "how possibly" demonstration of how a Darwinian view of evolution could be modeled mathematically, assuming a particulate theory of inheritance. These authors placed emphases on different factors – selection, mutation, migration, and, what was at first called "inbreeding effect," now known as random genetic drift (or, the notion that chance factors, such as the random sampling of alleles due to meiosis and recombination from one generation to the next could change the distribution of allele frequencies). In addition to demonstrating not only how it was possible for evolution to proceed along these lines, these three authors also engaged in empirical work, attempting to test various theories concerning the effects of selection in the wild, for instance, in the evolution of dominance.

More importantly, at least for many skeptics of Darwinism at this point, was Haldane's demonstration that a very small selection coefficient over a relatively short amount of 'geological time,' might effect vast changes in populations. An empirical case study of the same was the case of *Biston betularia*, the famous peppered moth population in Manchester, which, over a relatively small amount of time changed their distribution of the "carbonaria" gene – or, from a primarily white phenotype to a dusky color, due (it was then argued) to predation of white moths on polluted trees (Haldane, 1924). (The pollution leads to death of light coloured lichens, thereby exposing the darker bark.) This case of industrial melanism was one of several studies of both artificial selection, in the lab, in agricultural contexts, and selection in the wild in the 1910s through the 30s (Castle and Philips, 1914; Sturtevant, 1918; Payne, 1920; Sturtevant and Dobzhansky, 1938). The accumulated evidence for gradual selection on Mendelian traits, however, took some time to find their way into mainstream evolutionary biology.

3. The Modern Synthesis: 1932-1942

The modern synthesis of the 1930's and 40's did not consist in the development of a new theory of evolution, nor did it consist in a unification or reduction of two previously distinct theories. Rather, this later synthesis had two components, a "negative" as well as "positive." The "negative" component was a removal of misunderstandings between different fields in biology about the major causes of evolution, and the "positive" component was the advance of a new research program (Mayr and Provine, 1980).

Coincidentally, there was a substantial institutional change in biology at this time. Indeed, in order to understand the character of the synthesis, it is important to describe some institutional features of biological study prior to the 1930's and 40's. The study of evolution was not a recognized discipline; rather, there were zoologists, botanists, paleontologists, systematists, cytologists, embryologists, and (at that time, a relatively new field), geneticists. Participants in these different fields were divided on questions about scientific methodology, and on substantive issues about major patterns and processes of evolutionary change. One of the great advances of the synthesis was that these separate fields of investigation came into communication, sharing evidence, methods, and theoretical frameworks, as well as a forming of consensus concerning the major mechanisms of evolution.

What was required for such consensus building were "bridge builders" – not only in the sense of those willing to learn new fields of biology and entertain novel views, but individuals willing to organize conferences, journals, and institutional settings where experts in these initially distinct fields could communicate (See Cain, 1993). One such bridge builder was Ernst Mayr, who, along with Dobzhansky, Simpson, and Huxley, published a series of books in the 1930's and 40's with broadly "synthetic" themes

(Mayr, 1942; Dozhansky,1937; Simpson, 1944; Huxley, 1942) . These books surveyed their respective fields (systematics, genetics, speciation, paleontology) and argued that the observations of these diverse fields were compatible with the new science of genetics, according to which heredity was particulate and broadly Mendelian. Moreover, all these books argued for a Darwinian view of evolution, according to which microevolution, or change within populations, was not distinct in kind, but only in degree from macroevolution. The genetic differences within species were the same as those between species; and, given sufficient time and the appropriate conditions, selection could yield genuine evolutionary novelty. Over the course of ten years, from the 1930s to the 1940s, selection was gradually accepted as the major if not exclusive cause of evolution (see, Gould, 1983). Thus, the synthesis was effectively a "constriction" of mechanisms – appeal to neo-Lamarckian and orthogenetic causes was no longer regarded as necessary or appropriate. Further, Mayr, along with collaborators such as Dobzhansky, Jepsen and Simpson, organized the Society for the Study of Evolution, founded the journal, *Evolution*.

What enabled this synthetic view? There were several components. First, the theoretical framework was put in place by population geneticists in the 1920s and 30s. In addition, there was cytological and experimental work that strongly supported a Mendelian view of genetics, as well as the effectiveness of selection in experimental and wild populations. Sutton and Bovari advanced the chromosomal theory of inheritance, Morgan and Muller did important work on patterns of inheritance using *Drosophila*, experimental work by Castle, East, Dobzhansky, Wright, and others on selection in the laboratory, and, Jordon's, Grinnell's, and Mayr's extensive surveys of biogeography and work on speciation demonstrated that geographical isolation played an important rule in speciation. Finally, Simpson's (1944) survey of the paleontological literature demonstrated a consistency with a range of Darwinian genetics models.

In addition to these empirical advances, there was a bridging of "divide" between experimentalists and naturalists. Some (Mayr, 1980, Allen, 1979) have argued that the most substantial divide between biologists in the late 19th and early 20th Centuries was that between proponents of a "descriptive," "classificationist" and "naturalist" approach and an "analytic," "experimental" approach. Allen (1979) documented the different fields of expertise, training, views on mechanisms of inheritance and genetics of a wide variety of biologists at the turn of the century and confirmed this divide. On the one hand, those in the "new" experimental fields of genetics, experimental embryology, physiology, or cytology, for instance, tended to be strong Mendelians, and skeptical of gradualist, Darwinian views. On the other hand, those trained in geology, paleontology, systematics, zoology or botany, were largely skeptical of or indifferent to Mendelian genetics, and were more likely to be pro-Darwinian, or Lamarckians. Allen discusses how naturalists and experimentalists disagreed, not only on questions of how to do science, but also on the question of whether Mendelian genetics was relevant to, in opposition to, or consistent with a Darwinian view of evolution. It took roughly 30 years for biologists to become convinced that the isolated, experimental conditions under which the principles of genetics were discovered and studied, could be relevant to evolutionary processes occurring in the wild and over the very long term.

4. Philosophical Issues: Unification, Reduction, Synthesis, or "Constriction"?

The import and character of the modern synthesis has been controversial (see Smokovites, 1996). Nonetheless, a unification of sorts was accomplished in the sense that participants in the synthesis agreed on a number of substantive and methodological issues. First, neo-Lamarckian, orthogenetic and mutationist forces of evolution were no longer considered important factors in evolution. Second, the Mendelian, particulate view was established as the exclusive model of inheritance. Third, one could represent the major factors of evolution – selection, mutation, migration, and drift – in a suite of mathematical models. Fourth, micro- and macro-evolution were viewed as continuous, rather than distinct kinds of evolutionary change, requiring radically different mechanisms or explanatory resources. Finally, there was consensus that the methods and aims of the different fields of biology – zoology, botany, genetics, systematics, paleontology, etc. – were not in tension, but could be reconciled, and that evidence from these disparate fields could be shared with the common aim of understanding the pattern and process of evolution. Granting all these claims, there are many open questions about what sort of "synthesis" the modern synthesis was, how it was distinct from other kinds of scientific change, and whether the synthesis underwent a "hardening" or constriction, which left out significant advances, in particular, in developmental biology.

Was the synthesis a "reduction" or "unification" in philosophers' senses of the terms? There are stages of the synthesis that approximate but still fall short of these notions. Fisher's (1918) demonstration of the compatibility of biometric correlations with particulate inheritance was, while not a reduction of one theory to another in the most restrictive sense of a deductive derivation from sets of laws and bridging principles, a reduction in the most permissive possible sense (Sarkar, 1998). Fisher made a number of idealizing assumptions that departed from Mendelism (e.g. no dominance), which permitted the correlations discovered by biometers to be derived from a particulate model of inheritance.

Also, the development of theoretical population genetics in the early period was unifying in that it provided a mathematical model, and thus explanatory framework, for how evolution was possible on a Mendelian theory of inheritance. Such a framework permitted the development of quantitative tests of evolutionary change in the laboratory and field. This account is captured to some extent by Glymour's (1980) account of unification, according to which unified theories demonstrate how diverse phenomena are of a kind or exhibit a common pattern. Likewise, Morrison (2000) argues that unified theories "embody a mathematical structure or mathematization of the phenomena that furnishes an abstract, general framework capable of unifying diverse phenomena under a single theory." These characterizations capture some aspect of what was accomplished in the early synthesis. For, Fisher, Haldane and Wright did demonstrate how diverse phenomena are of a kind, and the same patterns of inference and argument would be used to predict evolutionary change using these models.

The later synthesis (1936-1947) was, however, not so much a unification in the classical sense of reduction, as a removal of barriers to understanding and a reconciliation of views and sharing of evidence across previously distinct fields of study. The synthetic theory is better understood as the advance of a Darwinian research program, one that involved thinking about data in new terms, developing a new vocabulary, and sharing of methods and evidence. Shapere (1980) has argued along these lines that the modern synthesis was more in the way of developing a policy or creed than a theory. He compares the synthesis to Oersted's experiment relating electricity and magnetism, and Sutton's demonstration of a correlation between Mendelian genes, and cytological data concerning chromosomes. Both demonstrations provided a strong reason for thinking that a unified explanation of the two domains could be expected. In other words, the evolutionary synthesis had more of the character of a demonstration of what is possible and likely, than the notion of a "deductive," or "logical" syntheses, where facts to be explained could be deduced from a set of laws and principles.

One issue that has persisted as controversial concerns what the synthesis "left out"; in particular, some have argued that innovations in developmental biology and embryology were not incorporated into the synthesis (Waddington, 1957). Further, Gould (1986) has argued that over the course of approximately 10 years (1930's- 40's) a neo-Darwinian view came to predominate in the synthesis, according to which adaptation became the central problem of evolutionary studies, and cumulative, gradual selection on minor, mutations the exclusive cause and adequate explanation of the diversity of life. There is no doubt that there is some truth to both claims. However, there is some explanation for this. First, as Hamburger (1980) has pointed out, the synthesis of genetics and development was in its early stages in the early 20th Century. Genetics was a relatively new field, and very little was known about the relationship between genetics and development; or, at least, there were very few biologists at the time with familiarity with both evolutionary theory generally and developmental genetics in particular. Thus, the process of development was more or less treated as a "black box" for most evolutionists participating in the synthesis. Though, Huxley (1942), who himself did research in embryology and one of the most popular authors of the synthesis, referred to developmental biology and embryology as contributing to the synthesis, he did not discuss how at much length. As Hamburger asserts "it has always been a legitimate and sound research strategy to relegate to a "black box," at least temporarily, wide areas that although pertinent would distract from the main thrust. No great discoveries or conceptual advances are made without this expediency."(Hamburger, in Provine and Mayr, 1980, pp. 99-100) In other words, at this stage, what first required reconciliation were the new science of genetics and the broad sweep of evolutionary change over time. Only recently has a new synthesis of evolutionary developmental biology and genetics been possible (Raff, 1996).

5. The Synthesis and Biology Today

Is the synthetic view representative of what biologists today view as the central commitments of their field? Biologists today would agree with many of the tenets of the synthesis described above. First, they would agree that neo-Lamarckian, orthogenetic and mutationist forces of evolution are not factors in evolution. Second, the Mendelian model of inheritance is still central to genetics, though of course it has been vastly elaborated upon with modern quantitative genetics, molecular biology, and genomics. Third, population genetics is still used today to address a variety of questions about microevolutionary change. Though, of course, these models have been advanced upon. With advances in molecular biology, population geneticists now understand far more about the nature of genetic variation and its history. Population genetic theory is both "backward" and "forward-looking." While early population genetics theory concerned itself only with immediate future generations, today, using coalescent theory, biologists can determine the time to most recent common ancestor of distantly related species.

Fourth, while many biologists would agree that micro- and macro-evolution are not distinct kinds of evolutionary change, there are some who would forcefully disagree. Gould (2002) and others have championed the view that explaining major transitions in evolution requires different explanatory resources than those available in traditional microevolutionary theory. That is, changes over vast stretches of evolutionary time may exhibit unique patterns, and be subject to processes at higher levels of organization than mutation, migration, drift, and natural selection between individuals. Fifth, that evidence from different fields of biology can be shared with the common aim of understanding the pattern and process of evolution is certainly not in question; indeed, there have been even greater cross-disciplinary advances in the last fifty years. Molecular biologists, systematists, population geneticists, developmental biologists, and ecologists, all draw upon one anothers' work with the shared aim of understanding the patterns and processes of evolutionary change.

Admittedly, the synthesis has been subject to some "bashing" by biologists on a variety of grounds. First, Lewontin and Gould (1979) famously criticized what they took to be the "adaptationist" bent inherited from the authors of the latter synthesis. In their view, the "hardening" of the synthesis led biologists to too frequently assume that each and every trait could be "atomized" and understood as a product of selection. They unhesitatingly ruled out the role of developmental constraints and chance factors in evolution. In this same vein, some biologists argue that a "new synthesis" of evolutionary theory with developmental biology is ongoing. "Evo-Devo" acknowledges the role(s) of development in shaping the tree of life, as well as the vast importance of plasticity in development to evolution (West-Eberhard, 2003). Finally, the rapid advances in genetics and molecular biology in the past 25 years in particular has dramatically changed not only the conceptual, but also the institutional character of biology since the synthesis. More funding is available into research in molecular biology, and with the genomes and related projects, ever more funding supplied to work with potential medical applications. Much more funding goes into molecular biology than field work. Thus, (and rightly so), many biologists bemoan the loss of the "naturalist" – ecologists, systematists, and field biologists who can identify species in the wild and do their main experimental work in the field, and not merely the laboratory. This loss may have unfortunate implications for the future of conservation biology.

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Recommended Readings:

Allen's (1979) "Naturalists and Experimentalists: The Genotype and the Phenotype," as well as his (1978) biography, *Thomas Hunt Morgan: The Man and His Science*, are classic intellectual histories of the period immediately preceding the synthesis.

Mayr and Provine's (1980) *The Evolutionary Synthesis: Perspectives on the Unification of Biology* is an excellent overview of the synthesis, addressing the synthesis in the U. S. and abroad, both substantive and philosophical issues.

Provine, W. B. 1971. *Origins of Theoretical Population Genetics*, as well as his 1986. *Sewall Wright and Evolutionary Biology* are also excellent introductions to the early synthesis and the period immediately proceeding.

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