Evolutionary Theory in the 1920s: The Nature of the "Synthesis"

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This paper analyzes the development of evolutionary theory in the period from 1918 to 1932. It argues that: (i) Fisher's work in 1918 constituted a not fully satisfactory reduction of biometry to Mendelism; (ii) there was a synthesis in the 1920s but that this synthesis was mainly one of classical genetics with population genetics, with Haldane's *The Causes of Evolution* being its founding document; (iii) the most important achievement of the models of theoretical population genetics was to show that natural selection sufficed as a mechanism for evolution; and (iv) Haldane formulated a prospective evolutionary theory in the 1920s whereas Fisher and Wright formulated retrospective theories of evolutionary history.

1. Introduction. This paper is about emergence of classical theoretical population genetics, 1918–1932, starting with Fisher's "The Correlation between Relatives on the Supposition of Mendelian Inheritance" (1918) and ending with Haldane's *The Causes of Evolution* (1932). This is well-worked territory by historians and philosophers of biology but this paper will challenge much of the received historiographies. At one extreme is that associated primarily with Mayr (e.g., 1980), which claims that the mathematical developments of the 1920s were irrelevant to the development of modern evolutionary theory; rather, the "synthetic" theory was due to the efforts of the "naturalists" such as Rensch, Mayr, and others in the late 1930s and 1940s. The arguments of this paper, which underscore the significance of the theoretical developments of the 1920s, will implicitly reject Mayr's historiography. At the other extreme is the historiography originally associated with Provine (1971) which holds: (i) that the devel-

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opments of the 1920s constituted a synthesis of biometry and Mendelism after a bitter dispute between their supporters from 1900 to about 1906, and (ii) that this synthesis was effected through the joint work of three figures, Fisher, Haldane, and Wright. Claim (ii) has a long pedigree within biology; usually it is taken to originate with Huxley (1942) but, as will be indicated below, it is of earlier vintage. More recently Provine has reinterpreted the developments of the 1920s as a "constriction" of permissible factors of evolutionary change (2001); Gould (2002) agrees with Provine on this point.

In what follows, each aspect of these interpretations will be implicitly challenged. The claims that will be explicitly defended are:

1. Conceptually there is no question of a synthesis of biometry and Mendelism. The appropriate philosophical description of the relation of biometry and Mendelism is reduction. This reduction was largely, though not fully satisfactorily, carried out by Fisher (1918)—see Section 2.
2. Nevertheless, there was an important synthesis, effected in the 1920s, of population genetics with classical genetics, chromosomal mechanics, cytology, biochemistry, and other biological subdisciplines. The founding document of this synthesis is Haldane's (1932) *The Causes of Evolution*—see Section 3.
3. The most important contribution of the models of population genetics was to show that natural selection alone sufficed to explain evolutionary change as recorded in geological history. The extent to which these developments also marked an evolutionary constriction is rather insignificant—see Section 4.
4. To the extent that an evolutionary *theory* was formulated in the 1920s, that theory was due to Haldane (1924). What Fisher (1930) and Wright (1931) formulated were theories of evolutionary history, though these are often incorrectly called evolutionary theories—see Section 5.

An implicit theme that will underlie all the discussions is that it was Haldane, rather than Fisher or Wright, who was most important for the evolutionary synthesis of the 1920s. This does not deny the importance of Fisher or Wright for theoretical population genetics. The concern here is with evolutionary theory, not merely population genetics.

2. The Reduction of Biometry to Mendelism.[1] Though philosophers have written much about unification and reduction in science, very little at-

1. For a more detailed discussion of most of the issues treated in this section (though not the explication of synthesis), see Sarkar 1998, 105–109.

tention has been given to "synthesis." Lack of space prevents any attempt at a general explication here; all that will be assumed is that: (i) a synthesis is a unification of originally disparate scientific structures (models, sets of models, theories, or even disciplines), and (ii) in the synthesized structure, there is *epistemic parity* between the structures so unified. Parity is being invoked to distinguish a synthesis from those forms of scientific change such as reduction in which one set of entities is presumed to have epistemic priority over others because its properties explain the properties of these others. Epistemic parity was lacking in the absorption of biometry into Mendelism.

The relevant developments are from the 1900–1918 period. Though the mathematical exploration of heredity began with Mendel's work in 1866, it remained entirely unknown until its recovery around 1900. Meanwhile, from entirely different assumptions, a mathematical theory that came to be called "biometry" was developed in the United Kingdom thanks largely to the work of Galton (1889) and Pearson (e.g., 1893, 1900). Classical biometry had a vigorous life of only about twenty years, from 1890 to 1910. It came under attack from the new Mendelians even before it matured, and its principles were never systematically enunciated.[2]

The striking difference between Mendelism and biometry was that, whereas the former studied discrete traits, the latter studied continuously varying traits. The biometricians did not generally doubt that Mendelism could explain the inheritance patterns of discrete traits to some extent; however, as they correctly noted, "pure" Mendelism (that is, with complete dominance and no linkage) was applicable only in rare cases. They doubted that the inheritance patterns of continuous traits, which for them comprised the vast majority of traits, could be given Mendelian explanations. For continuous traits, the biometricians produced three types of statistical rules: (i) extensive empirical investigation showed that these traits were normally distributed in a population; (ii) correlation coefficients between relatives could be computed and used for prediction; and (iii), most importantly, the "law of ancestral inheritance" described the contribution of each preceding generation to the distribution of traits in a given generation. Roughly, according to this law, that contribution decreased geometrically with each preceding generation. Note that these rules do not say anything about individual inheritance and are thus potentially compatible with Mendel's laws.

In 1904 Pearson attempted to derive these rules from Mendel's laws, but only halfheartedly, and concluded that they were inconsistent with those laws (1904a, 1904b). However, Yule (1902, 1906) and Weinberg

2. The only complete account is to be found in the 1900 edition of Pearson's philosophical tract, *The Grammar of Science.*

(1908) provided more optimistic assessments. What Fisher achieved in his 1918 paper was a resolution of this issue. Fisher's crucial assumption was that continuous traits were determined by a large number of Mendelian factors. This assumption seems innocuous but Fisher used it to argue that the distribution of the traits must be normal. In effect, what he assumed was that the number of factors is virtually infinite, each has very little effect, and each acts independently of the others. The asymptotic normality of the distribution is then a consequence of the central limit theorem for distributions.

Once the normality of the distributions was assured, Fisher calculated the various correlations between relatives to be expected under Mendelian inheritance and found them in approximate agreement with the measurements of the biometricians. Finally, he provided a putative derivation of the law of ancestral heredity (Fisher 1918, sect. 17). That derivation gave the required geometric decrease in generational contribution. However, there was no detailed agreement with the mathematical form of the law, a point that was ignored in the subsequent literature. In effect, to the extent that he was successful, Fisher provided an explanation of the biometrical regularities from Mendelian principles. There is no question of epistemic parity here; the latter were more fundamental.[3] For this reason, Fisher's work constituted a reduction of biometry to Mendelism. However, the success of this reduction is questionable on two grounds: (i) the failure to derive the exact form of the law of ancestral heredity (which is probably remediable but the details have never been worked out); and (ii) the assumptions introduced—an infinite number of independent factors, each of negligible effect—are counterfactual. (Later work in quantitative genetics has shown that these assumptions can be replaced by epistemically more palatable ones.)

3. The Synthesis of Classical and Population Genetics. Nevertheless, an important synthesis that resulted in the emergence of modern evolutionary theory did take place in the 1920s. Its founding document was Haldane's *The Causes of Evolution* from 1932. This synthesis was primarily between population genetics and classical genetics, systematically developed by the Morgan School and mechanistically interpreted through chromosomal mechanics and cytology. There was also a role for biochemistry. What most distinguished Haldane's *Causes* from Fisher's (1930) *The Genetical*

3. In Fisher's derivation, the Mendelian assumptions had epistemic primacy over the biometrical rules that were explained; the former formed the explanans, the latter the explananda. If the form of explanations is taken to be at least approximately captured by the covering law model, the relationship of epistemic primacy can equally well be captured as a logical relationship.

Theory of Natural Selection and Wright's (1931) "Evolution in Mendelian Populations" was that Haldane's concerns were much broader than population genetics even though the Appendix of *Causes* collected together almost all the mathematical models of population genetics that were then known. The text of *Causes* attempted to give a comprehensive account of all known mechanisms of evolution, interpreted, as far as possible, at the level of (classical) genetics and cellular mechanisms. The result is best called an evolutionary, rather than population, genetics. Neither Fisher nor Wright attempted such an integration—in this sense, at least, their work was not part of the synthesis of the 1920s.

In 1926 Morgan published *The Theory of the Gene* summarizing fifteen years of breathtaking advances in classical genetics mainly through linkage analysis. After 1920 cytology began to be systematically integrated with this work. Biochemistry, with a focus on enzymes, also emerged as a recognizable subdiscipline during the 1920s. Haldane integrated all these developments in *Causes*: (i) genes were supposed to produce "a definite chemical effect" (115); (ii) in general, genetic differences between species were similar to those within species that had been discovered by the Morgan school and others; (iii) however, intraspecific differences were more often due to a few genes with large effects rather than chromosomal differences; and (iv) some forms of speciation were supposed to be explained by ploidy change—why selection encouraged, or at least tolerated, such changes merited much attention. Carson is the only commentator to recognize the important synthetic role played by *Causes:* "Haldane neatly conjoins Darwin and Mendel, Fisher and Wright, Newton and Kihara. In the evolutionary context, Haldane deals for the first time with inversions and translocations, polyploidy and hybridization. The paleontological record is woven into the argument" (1980, 89). Even a casual reading of *Causes* underscores this interpretation.

Note that there was epistemic parity at least between classical and population genetics, the two major components of the synthesis in Haldane's treatment. Mendel's laws, as modified by linkage relationships, were given a cytological interpretation from classical genetics. Thus, trivially, classical genetics could not be reduced to population genetics. However, the cytological interpretation of Mendel's laws raised the possibility that population genetics is being reduced to classical genetics. But the use of the concept of fitness, an essential ingredient in models of population genetics which incorporated selection, precluded such a reduction. There was parity between the parts synthesized, as required from the discussion of the last section.

4. Natural Selection and the Constriction of Evolutionary Mechanisms. Why did Haldane write *Causes*? In the absence of any explicit published or archival evidence, any answer must be partly speculative. Nevertheless, there is compelling circumstantial evidence that part of the answer lies in religious objections to evolution on the ground that natural selection is insufficient as a mechanism to account for all of the past evolutionary changes. The early 1920s witnessed a spirited public controversy between Wells and Belloc over Darwinism. Belloc's religiosity—he hated Wells' materialism—led to a rejection, not of evolution, but of natural selection. Meanwhile, Bateson's and other geneticists' continued doubts about natural selection, as well as efforts to ban the teaching of evolution in some U.S. states, generated ample public controversy about the status of that theory.[4] The paleontologist Keith (1922a, 1922b) stepped into the dispute. In the *Rationalist Annual* Keith exhorted fellow Darwinists to popularize their views. The "very fact that Mr. Chesterton and Mr. Hilaire Belloc could confidently assure readers of the Sunday Press that Darwin's theory was dead," Keith (1922b) argued, "showed that those who are studying the evidence of our origin, and who are Darwinists to a man, had lost touch with public intelligence." Five years later, Haldane rose to Keith's call and published a piece in the *Rationalist Annual* defending and explaining Darwinism.[5] *Causes* developed that argument in detail.

It is possible that Haldane's mathematical exploration of natural selection, starting 1924, was also a response to Keith's appeal. Between 1924 and 1934, Haldane published a series of ten papers establishing the basic results of the theory of natural selection. In the first paper of this series, their purpose was explicitly laid out: "A SATISFACTORY theory of natural selection must . . . show not only that it can cause a species to change, but that it can cause it to change at a rate which will account for present and past transmutations" (Haldane 1924, 19). Objections such as those of Belloc seem foremost on Haldane's mind. The papers in this series were spectacularly successful. As early as 1915 Norton had shown in the simplest of models (one locus, complete dominance, in a diploid panmictic population) that very weak selection could lead to unexpectedly rapid adaptive change.[6] Haldane's results showed that this conclusion held for a large range of one- and two-locus models. Moreover, in one case of industrial melanism in the peppered moth (*Biston betularia*) a retrospective use of a model showed that very intense selection might occur

4. See Belloc 1920a and 1920b, Bateson 1922, Huxley 1922, Keith 1922a, Livingstone 1922, and Robinson 1922.

5. See Haldane 1927. This interpretation of the history was originally put forward by McOuat and Winsor (1995). The extent to which natural selection had fallen into disrepute is emphasized by Bowler, who argues that the evolutionary synthesis should be regarded as a Mendelian rather than Darwinian revolution (1989).

6. Norton's results were published as a table in Punnett 1915.

in nature (Haldane 1924). Whether or not it was responsible for the evolutionary changes in past history, there could no longer be any question that natural selection alone sufficed as a mechanism for evolutionary change. The context of debate about the status of evolution was permanently changed; arguably, at least, this change was already complete by 1927 when Haldane published the outline of the argument of *Causes*. This was Haldane's primary contribution to evolutionary theory. Fisher (1922) participated in the process only to the extent that he attempted to refute a claim by Hagedoorn and Hagedoorn-Vorstheuvel la Brand (1921) that random survival maintained variability within populations.

One consequence of the proof of the sufficiency of natural selection was that speculative evolutionary mechanisms dreamed of by biologists outside the evolutionary mainstream became unnecessary. In *Causes*, Haldane quantitatively explained away putative cases of orthogenesis by selection (1932, 197–198). The inheritance of acquired characters was similarly discredited. It is true that these moves amounted to an exclusion of some possible mechanisms of evolutionary change. Nevertheless, it seems idiosyncratic to interpret the developments of the 1920s as the exclusion of these mechanisms rather than the positive accomplishment of establishing the sufficiency of natural selection. Even at the height of their popularity the other mechanisms had very few adherents. It is more important to note that the sufficiency of natural selection led to a rejection of other mechanisms because a traditional principle of parsimony was being implicitly invoked. Provine and Gould's interpretation puts the emphasis on the less important point.

5. Prospective and Retrospective Theories. It will be assumed here that scientific theorizing consists of the construction of models for various purposes including, but not limited to, prediction of testable results. From this perspective, theories are more general structures used as recipes for the construction of these models. Haldane had precisely this view of theory and model in mind when he began:

> A SATISFACTORY theory of natural selection must be quantitative. In order to establish the view that natural selection is capable of accounting for the known facts of evolution we must show not only that it can cause a species to change, but that it can cause it to change at a rate which will account for present and past transmutations. In any given case we must specify:
>
> (1) The mode of inheritance of the character considered,
> (2) The system of breeding in the group of organisms studied,
> (3) The intensity of selection,

> (4) Its incidence (e.g., on both sexes or only one), and
> (5) The rate at which the proportion of organisms showing the character increases or diminishes.
>
> It should then be possible to obtain an equation connecting (3) and (5). (1924, 19)

From this explicit recipe, Haldane constructed thirteen models in the first paper (1924) and about thirty more in the next nine.

In the early 1920s, Wright used a similar strategy though it was not explicitly stated. In 1921 Wright published a set of five papers, "Systems of Mating." Working with one- and two-locus models, Wright first worked out several of the correlation coefficients for populations at equilibrium (1921a)—these were special cases of Fisher's (1918) treatment. Wright gave a systematic treatment of inbreeding (1921b) and assortative mating (1921c). However, his analysis of selection (1921d) was superficial. When only one locus was involved, he rederived older results of Jennings (1916) and Wentworth and Remick (1916). Results such as these showed the extent to which population genetics was being systematically developed independent of Fisher, Haldane, and Wright. This critical point has not received due historical attention. For two loci, Wright's results amounted to little more than a demonstration that selection decreased the variability within a population.[7] Thus, though Wright's theoretical strategy in these papers was similar to Haldane's, they did not provide a theory of evolution.

In the early 1920s, Wright developed quantitative models of selection. A manuscript reporting this work remained unpublished as Wright coped with heavy teaching responsibilities at the University of Chicago (Provine 1986). A large portion of it became obsolete as, starting in 1924, Haldane published his series of ten papers. The rest of Wright's manuscript, after significant development, became Wright's classic, "Evolution in Mendelian Populations." However, by then Wright's concerns had largely shifted: What he was groping for was a theory that accounted for the patterns of change in evolutionary history. The result was the "shifting balance theory of evolution" (1931). Fisher's interest was also in the reconstruction of the historical course of evolution and, more importantly, in the theory of natural selection independent of its role in evolution (1930).

Ewens has usefully distinguished between prospective and retrospective theories in evolutionary biology: The former predict processes in the future, the latter are designed primarily to infer processes in the past. This

7. The real contribution of this set of papers was the first systematic presentation of his method of path coefficients, his novel—and peculiar—method for calculating the correlations between variables.

distinction reflects the explicit purpose for which a theory is crafted; obviously, prospective theories (provided that they are sufficiently deterministic) can be used to retrodict past events and thus used for a retrospective purpose. Ewens uses this distinction to distinguish between the older (pre-1970) and more modern periods of the history of theoretical population genetics (1979, 1990). However, the distinction is relevant even to the 1920s and 1930s. Fisher's and Wright's theories were retrospective in intent; Haldane's was purely prospective though it allowed retrodiction. To the extent that an *evolutionary theory* should be one that attempts future prediction, only Haldane's work qualifies. From this perspective, Fisher's and Wright's projects were to formulate retrospective *theories of evolutionary history*. Where they disagreed was the appropriate model for past evolutionary change. Fisher suggested that evolution had taken place by weak selection on many genes with very small individual effects in large panmictic populations; Wright argued for a balance of factors, including selection and random genetic drift, in highly structured populations. In this dispute Haldane maintained a pluralist attitude arguing that no single model captured all of the evolutionary changes of the past.

6. Further Discussion. The claims made in this paper emphasize Haldane's role in the emergence of modern evolutionary theory and strongly suggest that his work has not received the historical and philosophical attention it deserves. It is, therefore, ironic that he was the source of both of Provine's questionable claims (1971). In *Causes* Haldane created the mythology of the holy trinity: In the Introduction he claimed, "I can write of natural selection with authority because I am one of the three people who know most about its mathematical theory" (33). Later, he went on to say, "The mathematical theory of natural selection where inheritance is Mendelian has been mainly developed by R. A. Fisher, S. Wright, and myself" (96). And, again, "The theory of selection in Mendelian populations is mainly due to R. A. Fisher, S. Wright, and myself."[8] Huxley, in 1942, took this assessment at face value, canonizing the mythology of the trinity.

In a caustic review of *Causes,* unfortunately unpublished at the time, Fisher took exception to this claim.[9] Fisher objected on three grounds:

8. Here, at least, Haldane did explicitly note that there were other important papers by Kemp, Warren, and Newton (Haldane 1932, 172).

9. Perhaps it was fortunate for Fisher that the review remained unpublished. Haldane was instrumental in acquiring a Professorship at University College, London, for the inadequately employed Fisher in 1933. (It is doubtful though that a caustic review would have prevented Haldane, one of the fairest of individuals, from supporting Fisher's candidacy.)

> The probability that some 300 readers or more have probably assimilated everything of value that [the three] have written, and may well know more about the mathematical theory than any of the three writers named. (ii) That the points in which these writers have agreed have so far consisted chiefly in clearing the ground of the *debris* of anti-Darwinian criticism. . . . (iii) The third criticism, therefore, of the theory of the 'three authorities' is that they show wide disagreement in questions of interpretation, such as the evolutionary modification of dominance, and the existence of selection in species showing a stable polymorphism. Professor Haldane evidently disagrees largely, or entirely, from the reviewer's opinions on these points, and it follows unmistakably either that Professor Haldane, or that I, would be a less satisfactory guide than any judicious reader who had formed a just view of the state of the evidence. (Fisher [1932] 1983, 289–290)

What was said in this paper supports Fisher's appraisal of the situation, especially in points (ii) and (iii).

It was Haldane in 1938, again before Huxley (1942), who suggested that biometry was being synthesized with Mendelism. However, except in one sentence, he interpreted the "synthesis" methodologically:

> [The biometricians] saw quite correctly that the early Mendelian theory was too crude and simple, and they gave particularly effective criticism to some of the early attempts to apply Mendelism to man. The present situation is, I think, as follows: in spite of the biometricians Mendelism is accepted by a vast majority of biologists, but if we want to discover whether a particular Mendelian hypothesis will explain a set of facts we are forced to use the methodological criteria invented by Pearson. If we want the best examples showing Mendelian inheritance in man we have to turn to the Treasury of Human Inheritance started by Pearson, perhaps in the hope of disproving Mendelism. The synthesis between these two opposing schools has very largely been due to R. A. Fisher. (Haldane 1938, 232–233).

The last sentence was the only one that suggested that the synthesis was more than methodological; it was pointed out in Section 2 that Fisher's seminal work is best interpreted as a reduction.

Even in the methodological context, Haldane's claim was misleading. What were retained from Pearson were certain statistical techniques. If this sufficed for a synthesis, biometry was synthesized with every discipline employing statistics. Why did Haldane make such a claim? The best answer seems to lie in the fact that Haldane was then undergoing a Marxist conversion (Haldane 1937, 1939). And, thus, the development of evolutionary theory came to be viewed in the framework of the Hegelian thesis, antithesis and, of course, synthesis.

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