Evolutionary Theory in the 1920s: The Nature of the "Synthesis"[1]

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Abstract

This paper analyzes the development of evolutionary theory in the period from 1918 to 1932. It argues that: (i) Fisher's work in 1918 constitutes a not fully satisfactory reduction of biometry to Mendelism; (ii) that there was a synthesis in the 1920s but that this synthesis was mainly one of classical genetics with population genetics, with Haldane's *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; (iv) Haldane formulated a prospective evolutionary theory in the 1920s whereas Fisher and Wright formulated retrospective theories of evolutionary history; and (v) in the context of the history of evolutionary biology, the differences between Fisher, Haldane, and Wright are as important as their similarities.

Keywords: evolutionary theory, Fisher, Haldane, modern synthesis, population genetics, Wright.

1. **Introduction**.

This paper is about emergence of classical theoretical population genetics, 1918 –1932, starting with Fisher's (1918) "The Correlation between Relatives on the Supposition of Mendelian Inheritance" and ending with Haldane's (1932) *Causes of Evolution*. This is well-worked territory by historians and philosophers of biology but this paper will challenge much of the received historiographies about that period. At one extreme is the self-serving revisionist historiography, 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. Every argument of this paper, each of which underscores the significance of the theoretical developments of the 1920s, will implicitly reject Mayr's historiography. At the other, and much more interesting, extreme is the historiography originally associated with Provine (1971) which holds that: (i) the developments 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 much earlier vintage. More recently Provine (1989) has reinterpreted the developments of the 1920s as an "constriction" of permissible factors of evolutionary change; Gould (2002) agrees with Provine on this point. Both Provine and Gould continue to emphasize the similarity of the projects of Fisher, Haldane and Wright.

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

- 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;

- nevertheless, there was an important synthesis that was effected in the 1920s. This was the synthesis of classical genetics, chromosomal mechanics, cytology, biochemistry and other biological sub-disciplines with population genetics. The founding document of this synthesis is Haldane's (1932) *Causes of Evolution*—see Section 3;

- the most important role played by the development of 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;

- 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.

The differences in the projects of Fisher, Haldane, and Wright are as important as their similarities. Fisher's (1930) self-given task was the construction of a statistical theory of natural selection that came to be called Darwinian dynamics (Michod 1999); that it may have explanatory power in an evolutionary context was an added benefit. Haldane was obsessed with the problem of time, that there had been enough time for natural selection to have wrought the evolutionary changes seen in the geological record. For Haldane, this was important because religious opponents of evolution remained to be answered. Wright, at least, was concerned with macroevolution based on an appreciation of the physiological basis of evolutionary change. Lack of space will prevent further exploration of these themes here. However much of what is said in Sections 4 and 5 will underscore the differences between these three projects.

An implicit theme that will underlie all the discussions of this paper is that it was Haldane, rather than Fisher or Wright, who was most important for the evolutionary synthesis of the 1920s. This does not contradict any claim about the importance of Fisher or Wright for theoretical population genetics. The concern here is with evolutionary theory, not merely population genetics. Contemporary theoretical population geneticists often reconstruct the history of evolutionary theory as a grand battle between Fisher, Wright, and their respective followers, with no role for Haldane. Lately, historians and philosophers have begun rather abjectly to follow their lead; for purely professional reasons they would do better to study the details of the history they presume to interpret.

2. **The Reduction of Biometry to Mendelism**.[2]

Though philosophers have written much about unification and reduction in science very little attention 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 eventually 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. The only complete account is to be found in the second edition Pearson's (1900) philosophical tract, *The Grammar of Science*.

The striking difference between Mendelism and biometry was that, whereas the former studied discontinuous 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 claimed to have found 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 for many traits; 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 generation preceding the given one. Note that these rules do not say anything about individual inheritance and are thus potentially compatible with Mendel's laws.

In 1904 Pearson (1904a, b) attempted to derive these rules from Mendel's laws, but only half-heartedly, and concluded that they were inconsistent with those laws

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[2] For a more detailed discussion of most of the issues treated in this section (though not the explication of synthesis), see Sarkar (1998), pp. 105 −109.

though Yule (1902, 1906) and Weinberg (1908) provided more optimistic assessments. What Fisher achieved in his path-breaking 1918 paper was a complete 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, but each has very little effect, and acts independently of the others—the asymptotic normality of the distribution is then a consequence of (one version 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 claimed to provide a derivation of the law of ancestral heredity (Fisher 1918, § 17). That derivation does give the geometric decrease in generational contribution mentioned above. However, there was no detailed agreement with the mathematical form of the law, a point that was ignored in the subsequent literature in which it was assumed that, after Fisher's paper, there was no issue to be resolved between biometry and Mendelism. 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 are more fundamental.[3] For this reason, Fisher's work constitutes 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 has never been worked out; and (ii) the assumptions introduced—an infinite number of factors, each factor having the same negligible effect, and each acting independently of the others—are counterfactual. Later work in quantitative genetics has shown that these assumptions can be replaced by more epistemically palatable ones.

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[3] In other words, in Fisher's derivation, the Mendelian assumptions had epistmic primacy over the biometrical rules that were explained; the former formed the eplanans, the latter the explananda. If the form of explanations are 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 with the explanas forming part of the antecedent and the explananda the consequent of a true (material) conditional.

3. **The Synthesis of Classical and Population Genetics**.

   Nevertheless, an important synthesis that was critically responsible for the emergence of modern evolutionally theory did take place in the 1920s. Its founding document is Haldane's *Causes of Evolution* from 1932. This synthesis was between population genetics and classical genetics, primarily developed by the Morgan School, and mechanistically interpreted through chromosomal mechanics and cytology. What most distinguishes Haldane's *Causes* from Fisher's *Genetical Theory of Natural Selection* and Wright's "Evolution in Mendelian Populations" is that Haldane's concerns were much broader than population genetics even though the justly famous Appendix of *Causes* collects 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 may best be 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 first edition of *The Theory of the Gene* summarizing fifteen years of breathtaking advances in classical genetics mainly through the use of linkage analysis. After 1920 cytology began to be systematically integrated with the new genetics. Biochemistry, with a focus on enzymes, also emerged as a distinct recognizable sub-discipline during the 1920s.[4] Haldane integrated all these developments in *Causes*: genes, for instance, are supposed to produce "a definite chemical effect (Haldane 1932, p. 115)." In general, genetic differences between species were similar to those within species that has been discovered by the Morgan school and others. However, intra-specific differences were more often due to a few genes with large effects rather than chromosomal differences. In particular, some forms of speciation were supposed to be explained by ploidy change (a view that is largely rejected today). Why selection encouraged, or at least tolerated such changes, merited much attention. Carson (1980, p. 89) seems to have been the only commentator to recognize the important role played by *Causes* in synthesizing the various biological sub-disciplines: "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." Even a casual reading of *Causes* underscores this interpretation.

   Note that there is epistemic parity between classical and population genetics, the two major components of the synthesis in Haldane's treatment. Mendel's laws, as modified by linkage relationships, is given the standard cytological interpretation from classical genetics. Thus, trivially, classical genetics cannot be reduced to population genetics. However, the cytological interpretation of Mendel's laws raises the possibility that population genetics is being reduced to classical genetics. However, the use of the

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[4] By profession, Haldane was a biochemist during this decade. See Haldane (1930).

concept of fitness, an essential ingredient in models of population genetics which incorporate selection, precludes such a reduction. There is 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 evidence in the published record or in archival sources, 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 1920's witnessed a spirited public controversy between H. G. Wells and Hilaire Belloc over Darwinism. Belloc's Catholic predispositions—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 US states, generated ample public controversy about the status of that theory.[5] The paleontologist, Keith (1922a, b) 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, in an outline of the argument of *Causes*, Haldane rose to Keith's call and published a piece defending and explaining Darwinism in the *Rationalist Annual*.[6] *Causes* developed that argument in detail.

It is even 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 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 (Haldane 1924, p. 19)." Objections such as those of Belloc seem foremost on Haldane's mind. The papers in this series (all but one called "A Mathematical Theory of Natural and Artificial Selection") 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 can lead to unexpectedly rapid adaptive change.[7] Haldane's results showed that this conclusion held for a huge variety of one and two locus models. Moreover, in the case of industrial melanism in one population of the peppered moth

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[5] See, for example, Belloc (1920a, b), Bateson (1922), Huxley (1922), Keith (1922a), Livingstone (1922), and Robinson (1922).

[6] 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 was emphasized by Bowler (1983, 1988, 1989) who correctly notes that the evolutionary synthesis should be regarded as a Mendelian rather than Darwinian revolution.

[7] Norton's results were published as a table in Punnett (1915).

(*Biston betularia*) a retrospective use of one of the models showed that very intense selection might occur in nature (Haldane 1924). (This story has also come under question in recent years.) Whether or not it was responsible for the evolutionary changes in past history, there could no longer be any question that natural selection sufficed as a mechanism for evolutionary change. The context of disputes 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 fully developed in *Causes*. This change was Haldane's primary contribution to evolutionary theory. Fisher (1922) participated in the process only to the extent that he attempted to refute the claim by Hagedoorn and Hagedoorn-Vorstheuvel la Brand (1921) that random survival maintained variability within populations. Wright, in a rather different context in the US, played no role.

One consequence of the proof or the sufficiency of natural selection was that speculative evolutionary mechanisms dreamed of by biologists outside the evolutionary mainstream became unnecessary. In *Causes*, Haldane (1932, pp. 197 −198) quantitatively explained away putative cases of orthogenesis by selection. 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 more positive accomplishment of establishing of the sufficiency of natural selection for evolution. 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 these other mechanisms because a traditional principle of parsimony was being implicitly invoked. Since natural selection, the operation of which was taken to be well-established, sufficed to save the phenomena, other mechanisms became unacceptable.

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 point of view, theories are more general structures used as recipes for the construction of these models. Haldane (1924, p. 19) had precisely this view of theory and model in mind when he began his explorations of population genetics.

> "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:
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> > (1) The mode of inheritance of the character considered,
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> > (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 of diminishes.
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> It should then be possible to obtain an equation connecting (3) and (5)."

From this explicit recipe, Haldane (1924) constructed thirteen models in the first paper 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 (1921a) first worked out several of the correlation coefficients for populations at equilibrium—these were only special cases of Fisher's more general 1918 treatment. Wright gave a general and systematic treatment of inbreeding (1921b) and assortative mating (1921c). However, his analysis of selection was superficial. When only one locus was involved, he rederived older results of Jennings and Wentworth and Remick from 1916.[8] For two loci, his results amounted to little more than a demonstration that selection decreased the variability within a population.[9] Thus, though Wright's theoretical strategy is similar to Haldane's these papers do not constitute a theory of evolution.

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[8] Jennings (1916); Wentworth and Remick (1916). Results such as these show the extent to which population genetics was being systematically developed independent of Fisher, Haldane and Wright. This point has not received due historical attention to date.

[9] 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.

In the early 1920s, Wright developed quantitative models of selection. A long manuscript reporting this work remained unpublished, as Wright dealt with his heavy teaching responsibilities at the University of Chicago (Provine 1986). A large portion of it became obsolete as, starting in 1924, Haldane began publishing his series of ten papers. The rest of Wright's manuscript, after significant development, became Wright's (1931) classic, "Evolution in Mendelian Populations." However, by now Wright's concerns had largely changed: 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." To the extent that Fisher (1930) was interested in evolution, his interest was also in the reconstruction of the course that evolution had historically taken to generate the patterns seen today.

Ewens (1979, 1990) has usefully distinguished between prospective and retrospective theories in evolutionary biology: the former predict processes forward in time, the latter are designed to infer processes in the past. This distinction reflects the explicit purpose for which a theory is crafted; obviously, prospective theories 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. 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. To the extent that an evolutionary *theory* should be one that attempts prediction forward in time, 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 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 captures all of the evolutionary changes of the past.

6. **Further Discussion**.

The claims defended 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 is the source of both of Provine's (1971) claims that turn out to be incorrect. 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 (p. 33)." Later, in the chapter on Natural Selection (Chapter IV), 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 (p. 96)." And, again: "The theory of selection in Mendelian populations is mainly due to R. A. Fisher, S. Wright, and myself."[10] 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.[11] Fisher objected on three grounds: "(i) 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, pp. 289 –290)." What was said in this paper supports Fisher's appraisal of the situation in points (ii) and (iii).

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

> "[The biometricians, Pearson and Weldon] saw quire 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

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[10] Haldane (1932), p. 172; here, at least, Haldane does explicitly note that there were other important papers by Kemp, Warren, and Newton.

[11] 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.)

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], pp. 232 –233)."

The last sentence is the only one that suggests 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 is misleading. What was retained from Pearson were certain statistical techniques. If this suffices 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 comes to be viewed in the framework of the Hegelian thesis, anti-thesis and, of course, synthesis.

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