Journal of Genetics, Vol. 96, No. 5, November 2017, pp. 753–763
https://doi.org/10.1007/s12041-017-0840-5

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Haldane's *The causes of evolution* and the Modern Synthesis in evolutionary biology

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Abstract. This paper argues that Haldane's *The causes of evolution* was the most important founding document in the emergence of the received view of evolutionary theory which is typically referred to as the Modern Synthesis. Whether or not this historical development is characterized as a synthesis (which remains controversial), this paper argues the most important component of the emergence of the received view consisted of showing how the formal rules of Mendelian inheritance are based on (or emerge from) the material basis of heredity established by classical genetics primarily through the experimental work on *Drosophila* genetics of the Morgan school in the 1910s and 1920s. This is one of the most important achievements of Haldane's book. Thus this paper rejects both (i) the view that the synthesis was a unification of biometry and Mendelism and (ii) the claim that it arose from work primarily done in the late 1930s and 1940s by naturalists rather than theoretical population and classical experimental geneticists.

Keywords. *The causes of evolution*; modern synthesis; evolutionary biology; Haldane; Mendal.

Introduction

In 1942, in the middle of World War II, Huxley published a monograph, *Evolution: the modern synthesis* (Huxley 1942). Although the book's scope was ambitious and it attempted to survey all of evolutionary biology, while remaining accessible to a broad audience of biologists, the perspective was that of a 'new' systematics (Huxley 1940) that had been spawned with a more rigorous foundation than before by the emergence of a robust evolutionary theory based on Darwinian or, more accurately, neo-Darwinian or Weismannian principles. In this framework there was no room for the inheritance of acquired characters or for internal factors of evolution; rather, evolution was driven principally by natural selection acting on blind variation. As historians have noted over the years (e.g., Bowler 1992), this original Darwin–Wallace view of evolution by natural selection had come under serious challenge by the end of the nineteenth century, not because its critics denied evolution through common descent and modification, but because they had become skeptical that natural selection alone sufficed to account for all the changes seen in the historical record of the evolution of life on earth. Huxley's book marked the end of that challenge at least within evolutionary biology.

The central problem for a neo-Darwinian theory of evolution had been that of the available time. In the second half of the nineteenth century, the eminent physicist, Kelvin, and his students argued forcefully, on thermodynamic grounds, that the age of the earth was less than 100 million years (see Burchfield 1990). Both sides to the dispute agreed that this was far too short a span of time for evolution by natural selection alone to have effected all the changes seen in the fossil record. Darwin took this objection very seriously and modified his original theory to admit, in a Lamarckian move, environmentally induced directional change as well as the inheritance of acquired characters, both of which factors would enhance the speed of evolutionary change (Eiseley 1958). The physicists' arguments were based on the assumption that the source of the energy of the Sun was entirely from gravitation. Indeed, gravitation and electromagnetism were the only known fundamental forces (and sources of energy) and there was no reason to suggest that the latter played any role in generating the sun's heat; possible alternative sources of energy were only recognized after the discovery of radioactivity in the 1890s. It took a generation for physicists to work out its relevance to energy generation in the sun and, perhaps more importantly for the future of evolutionary biology, also to the question of the determination of the age of rocks and other pieces of matter through radioactive isotope dating.

By the time Huxley's book was written, the age of the earth problem had receded to the background and was largely accepted to be irrelevant for evolutionary biology; after 1900 there was ample physical reason not to trust the Kelvin school's thermodynamic arguments about that age. Meanwhile, the emergence of theoretical population genetics based on Mendelian principles and augmented by natural selection had provided quantitative estimates for the time likely to be taken for miscellaneous patterns of evolutionary change. The consensus was that natural selection could on occasion work much faster than what Darwin and his pre-Mendelian followers (i.e., those working on heredity before the recovery of Mendel's work around 1900) had ever conceived. Huxley went out of his way to emphasize the centrality of theoretical population genetics for evolutionary theory, in particular, because of the work of Haldane, Fisher and Wright. Further, a host of developments in the understanding of the material basis for heredity had mechanistically underpinned the formalism of Mendelian genetics (as modified by the theory of linkage) that theoretical population genetics had explored. The most influential work in this category was that of the Morgan school using the fruit fly, *Drosophila melanogaster*, as a model organism; this work led to what subsequently came to be called classical genetics. Strangely, these mechanistic developments largely escaped Huxley's attention though they had fully engaged Haldane (1932) 10 years earlier, in *The causes of evolution*, a fact that will be central to the arguments that follow. Working biologists embraced the Morgan school's tools and ideas starting in the 1920s (Kohler 1994); after 1925 when Morgan's *Evolution and genetics* was published, showing that Morgan was no longer skeptical of evolution by natural selection, the new framework for evolution based on theoretical population genetics came accompanied by the new experimental genetics. The publication of Haldane's *Causes* marked the maturation of this view of evolution and its first elaboration as an integrated theoretical framework. Thus, the relevant period is the 1920s.

Huxley's book was so influential that the new framework for evolution, what I have elsewhere called (and, I hope, less contentiously) the 'received view' of evolution came to be called the Modern Synthesis or something related [e.g., 'evolutionary synthesis' (Mayr and Provine 1980) or 'synthetic theory of evolution' (Kimura 1983)] though there has never been any hint of consensus about what was being 'synthesized' (Smocovitis 1996; Sarkar 2004, 2007). (The 'received view' is supposed to be the version of evolutionary theory inherited from classical genetics and related fields by those working in evolutionary biology before the advent of molecular techniques challenged every aspect of that view, i.e., before the mid-1960s.) Nevertheless, with Provine (1971) and me (besides Huxley himself, given the title of his book) as exceptions, there has been historical consensus that this synthesis was a consequence of scientific developments from later decades, the 1930s, the 1940s, or perhaps even later, beginning only in the late 1940s. Let me quote Mayr (1980, p. 1):

> The term 'evolutionary synthesis' was introduced by Julian Huxley in *Evolution: the modern synthesis* (1942) to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ('mutation') and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms. The objective of this conference is to examine the rapid changes in evolutionary biology that occurred in the period of the synthesis (from approximately 1936 to 1947).

Provine (1971) originally held, along with Huxley, that the synthesis was accomplished between 1918 and 1932 by Haldane, Fisher and Wright. He also upheld a view that has had widespread historical prevalence within biology: that the synthesis was the unification of the work of the biometrical school of Pearson and Weldon with the work of the geneticists who elaborated and extended the Mendelian principles after their recovery around 1900. I have pointed out that the conceptual connection between these two bodies of work cannot in any reasonable construal be viewed as a 'synthesis' of different theories; rather it was a case of theory reduction (Sarkar 1998, 2004).

In later work on the development of evolutionary theory, summarized in his biography of Wright, Provine (1986) came to view the history of evolutionary theory as an epic struggle between Fisher and Wright, and their respective followers. Haldane falls out of the picture. In this work Provine, too, viewed the synthesis as a post-1930s development. Moreover, as I have pointed out in an earlier paper (Sarkar 2007), in a large number of historical works, Mayr (e.g. 1980, 1982, 1992) denied a central role not only for Haldane, but also for Fisher and Wright. Indeed, at times, emboldened perhaps by remarks originally made by Waddington (1953, 1957), Mayr denigrated the importance of all of theoretical population genetics for evolutionary theory. I have engaged with Waddington's claims in three earlier papers (Sarkar 2007, 2013, 2016) and will not consider them any further here: my assessment is that both Waddington and Mayr criticized what they did not understand, and Haldane 1964, in 'A defense of beanbag genetics', made the same assessment in the case of Mayr (see Haldane 1964).

This paper argues in favour of Huxley's and Provine's original timeline, i.e., that the emergence of the received view of evolutionary theory, in other words, the so-called synthesis, did take place between 1918 and 1932. Haldane's work was central to it, not only because of the models developed in his famous sequence of theoretical papers between 1924 and 1934 (all but one titled 'A mathematical theory of natural and artificial selection') and then summarized in the appendix of *Causes*, but because of the detailed discussion in that book of the material basis for evolution, i.e., the work of the Morgan school on *Drosophila* genetics. This founding role of *Causes* in the so-called synthesis has not been adequately appreciated by historians and other commentators before now; and the argument of this paper is new though Carson (1980) came close to making it earlier (and seems to have embraced the same assessment). In his words:

> Where else in that era [i.e., other than in *Causes* in the late 1920s and early 1930s] can we find integrated and facile discussions of the evolutionary implication of the *Drosophila* chromosome studies, allopolyploidy in *Primula,* and Darwinian fitness? Here 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 in to the argument. The synthesis had begun in earnest (Carson 1980, p. 89).

As Carson suggested, *Causes* did play a synthetic role insofar as it unified the material and formal study of heredity, that is classical and Mendelian genetics. However, contrary to Provine (who followed Huxley) it was not a synthesis of biometry and Mendelism. Strangely, as I will point out, in what I hope is an entertaining (but not *only* entertaining) end to this paper, that the mythology of a synthesis of these two disciplines also originates with Haldane though only in popular writing—there is ample reason not to treat it seriously for historiographic purposes.

Details of a few of the episodes and arguments discussed below are already in print (Sarkar 1998, 2004, 2007, 2013, 2016); the aim of this paper is to synthesize their implications in a more pointed way than I have done before.

Classical genetics and the mathematical theory

That Haldane would have appreciated the relevance of the Morgan school's work in genetics is not surprising once attention is directed to his personal history which Provine largely ignored even though Clark's (1969) biography has been available since 1969. Leaving aside the work of the Chetverikov school in the Soviet Union in the 1920s (Adams 1968), which is not really an exception either, Haldane was the only figure among the early population geneticists who seems to understood the evolutionary significance of the *Drosophila* work and followed it in detail. The contrast here is with both Fisher and Wright. On the former's part, there is no evidence of any serious interest in the material basis of heredity. Indeed in the 1920s, for Fisher, the locus of interest was the theory of natural selection itself. In *The genetical theory of natural selection*, Fisher (1930) makes an analogy between what that theory does for evolution and what statistical mechanics does for thermodynamics. For Fisher, just as statistical mechanics was interesting beyond its relevance to thermodynamics, natural selection was interesting in and of itself beyond the question of evolution. The material basis for heredity was peripheral to this perspective. In contrast, the question whether natural selection can account for the initial conditions embodied in evolutionary systems does emerge as a question of central interest: thus, by the early 1930s, Fisher (e.g., 1934) was occupied with constructing selectionist models for the origin of dominance.

Unlike Fisher, and more like Haldane, Wright was interested in the mechanisms underlying heredity and gene action, as indicated by his physiological theory of dominance (e.g., Wright 1934). However, for reasons that are not entirely clear, he did not follow the *Drosophila* work in the 1910s and 1920s or attempt to incorporate it into the statistical framework for population genetics that he was establishing through his work at the University of Chicago. Wright's two major publications from this period, a summary of his framework (Wright 1931), and on the adaptive landscape (Wright 1932), make no mention of the material basis for heredity. The latter is best viewed as a first statement of what later became the shifting balance theory of evolution which relied exhaustively on population-level processes and was neutral with respect to that basis.

Haldane's interest in genetics went back to his childhood, and he was one of the first to report linkage (though interpreted as 'reduplication') in vertebrates. This observation was made before World War I but the onset of the war, in which Haldane served with reckless bravery and distinction (Clark 1969), prevented publication until 1915 (Haldane *et al.* 1915). Moreover, his first scientific mentor was his father, the eminent physiologist John Scott Haldane, who was prone to philosophical reflection on his own scientific work. J. S. Haldane was a prominent critic of the theses of materialism and mechanism; J. B. S. Haldane largely followed him with respect to these philosophical views throughout his life (Sarkar 1992b). More importantly these philosophical theses are likely to have encouraged his engagement with the work on the material basis for heredity.

By the end of the war, Haldane had begun to follow the work of the Morgan school systematically; this interest precedes his interest in the mathematical theory of natural selection by at least five years. As he put it later, in an incomplete and unpublished autobiography written at the height of his involvement with the Communist Party, while recuperating from one of his war wounds in Delhi in 1918, he had done what he called 'a little rather second-rate theoretical work on genetics, working on results obtained by Morgan and his colleagues in New York', (Haldane *ca* 1942, chapter 2, pp. 1–2). This allegedly second-rate work, written up and published only after he began research at Oxford after the end of the war, was the derivation of what came to be known as the Haldane mapping function which computes the relative distances between loci in a linkage map of a chromosome from the observed recombination frequencies between alleles at these loci (Haldane 1919). Haldane even proposed a unit of measurement for distance between loci in a chromosome, as measured using crossover frequencies, the 'centimorgan' though the measure did not gain any traction until a generation later.

Wimsatt (1992) has analysed this episode in some detail. The Morgan group did not appreciate the relevance of Hadane's abstract formulation, preferring their own empirical maps constructed using laborious breeding experiments over a 15-year period. It was a classic confrontation between the theorist and the experimentalist, with the latter rejecting the abstractions of the former without full understanding of what they were trying to achieve (as has often been the case in the history of biology). There have since been many extensions and elaborations of Haldane's mapping functions (for instance, by Kosambi 1944) but it was never adopted by Morgan and his school.

However, the importance of the interaction between Haldane and the Morgan group lies elsewhere, in the Morgan school reciprocating Haldane's interest with respect to each other's work. Morgan and his students began to follow Haldane's work with some care. Starting in 1924, that work on the 'Mathematical theory' turned systematically to the question of not only what natural selection can do to a population given its mode of inheritance but, more importantly, to the question of how much time natural selection would take to effect each such changes. There is ample circumstantial evidence that suggests that Haldane was drawn to this question because of a challenge posed by Keith (1922a,b) that was motivated by religious critics of the theory of evolution who, in turn, were still influenced by Kelvin's nineteenth-century objections mentioned earlier (McOuat and Winsor 1995; Sarkar 2004). By this point Haldane had moved to Cambridge from Oxford to become Reader in Biochemistry in a new department that Hopkins had organized. He had become a resident of Trinity College where one of his colleagues was Norton, a mathematician who had collaborated with Punnett to produce a well-know table of the effects of selection on Mendelian populations (Provine 1971; Sarkar 2007).

Most of Norton's other results remained unpublished but Haldane learnt from him that not much more was known about the power—and limitations—of natural selection than what had been incorporated in his table. Haldane's 'Mathematical theory' sequence of papers between 1924 and 1934 changed that permanently. It was laborious work comprising a total of exactly 100 pages and analysing over 50 models. (The exact number depends on how these models are individuated.) How fast natural selection could act depended on the details of the system of reproduction in a population: inheritance patterns (e.g., haploidy, diploidy, or polyploidy, mating systems, and degree of dominance) besides the intensity of selection. Although natural selection could sometimes act very rapidly (and Haldane (1924a) famously analysed the transformation of a population of peppered moths in northern England within 50 years), there was no trivial path to speciation. In most circumstances, Haldane argued that reproductive isolation would be necessary for speciation. In the first two papers (e.g., Haldane 1924a,b), he seems to be bothered by the slow pace of changes induced by natural selection; after that he seems to have gradually realized that the number of generations involved was not high compared to the hundreds of millions of years that had been available to evolution. By the time that *Causes* was written, towards the end of this phase (and a first version of the conclusion of the book was published earlier as a paper in *The Rationalist Annual* from 1927 (Haldane 1927) where Keith had published one of his original challenges), Haldane had convinced himself that time was not a problem.

He had also convinced others. Until the early 1920s Morgan had been skeptical of the power of natural selection in effecting evolution. At one point he had adopted de Vries's theory of evolution being driven by large mutations (Allen 1978, 1980). Morgan (1916) had also published a critique of the theory of natural selection in 1916. Most of the rest of his group did not share this skepticism; in particular, Muller and Sturtevant engaged in systematic attempts to change Morgan's mind. What finally effected that change—at least in public—was Haldane's series of papers. Morgan was duly impressed by the mathematical analysis. As early as 1925 Morgan had capitulated; in *Evolution and genetics*, he cites Haldane's work from 1924 though he also notes, grudgingly, that what it had really shown was how difficult the problem of speciation was. (It is also likely, though there is no material evidence to the best of my knowledge, that Haldane's influence is seen in Morgan's general skepticism about the 'reality' of species as taxa, i.e., claims that species differences were more objective than differences between taxa at other levels of the taxonomic hierarchy. Allen (1978) criticizes this aspect of Morgan's evolutionary perspective but it had support from one of the foremost evolutionary biologists of that era, namely, Haldane.) Between 1924 and 1932, Haldane had published the most important papers of his 'Mathematical theory.' He had also written *Causes*, to which I will turn in the next section; its United States edition appeared almost simultaneously with the Sixth International Congress of Genetics at Ithaca, New York in 1932 which Haldane attended. Morgan was ensconced as President of the Congress and attended the session that included Haldane, Fisher and Wright. Haldane's presentation summarized the argument of the book and much of it, as we shall see, had to do with interpreting the work of the Morgan school in the context of evolution by natural selection.

Subsequent to the Cornell meeting, Haldane was a guest at Morgan's house in Woods Hole (Allen 1978, pp. 18–19). (There is no evidence of direct interaction between Haldane and Morgan either earlier or later.) Any personal disagreements over the Haldane mapping function (on this, see Wimsatt 1992) seem to have been forgotten. The Morgan school's increasing influence on biology in the United States is likely to have helped the spread of theoretical population genetics in the United States, particularly after the addition of Dobzhansky who brought with him the focus on natural populations pioneered by the Soviet school of population genetics in the 1920s. Muller went on to make many theoretical (though not mathematical) contributions to the emerging field. If Haldane had only built theoretical models for routes to speciation by 1932, Dobzhansky's 1937 book, *Genetics and the origin of species*, summarized the experimental situation. Dobzhansky emphasized the role of isolation even more than Haldane but, by and large, his book underscored the importance of the same processes that Haldane had analysed. From the perspective of this paper, if its argument is sound, these post-1932 works added detail and important corroboration to a framework that had already been constructed and sufficiently demonstrated before that date, most importantly, in Haldane's *Causes*. I will turn next to that book to show how it provided a unifying evolutionary interpretation of the details of heredity elucidated within classical genetics; as Carson pointed out, Haldane also attempted to incorporate insights from all the other fields that had evolutionarily relevant data.

The causes of evolution

In January 1931 Haldane delivered a series of lectures at the Prifysgol Cymru at Aberystwyth, Wales, entitled 'A re-examination of Darwinism.' The text of these, along with a technical appendix, became Haldane's best-known book (to which I have referred several times), *The causes of evolution*. One indication of its central role in the history of twentieth-century evolutionary biology is the discussion it continued to inspire a half-century after original publication. First published in 1932 in both the United Kingdom and the United States (with a second edition in 1935), a new reprint edition appeared in 1966 from Cornell University Press. Princeton University Press brought out a new edition in 1990 with extensive annotations, particularly on the mathematical appendix, by Leigh (1990). Mayr (1992) published a 60-year reappraisal in 1992, largely critical but not as unsympathetic as in his writings on Fisher and Wright. There was little agreement between Leigh's and Mayr's assessments. Both Leigh and Mayr approached the book as biologists; *Causes* has continued to be relevant beyond its historical role as adumbrated in this paper. Among other things, Mayr argued, with no evidence, that *Causes* was neither widely available nor widely read. (Fisher's 1930, *Genetical theory of natural selection* has also continued to be discussed throughout this period but by a much narrower audience of mathematically minded selectionists.)

In *Causes*, Haldane started with what he took to be the unquestionable fact of evolution, 'the descent from living beings in the past of other widely different living beings' (Haldane 1932, p. 4). What remained debatable was its possible causes. That was the goal of the lectures. Haldane's arguments will be reconstructed in some detail here because, in spite of its reputation for being well-written (see, e.g., Carson 1980), *Causes* is hard to follow. Arguments are often imprecise and the narrative disjointed, as Fisher observed in an review of the book that remained unpublished till 1983 (see Sarkar 2004). The book reads like a transcript of lectures that could have profited from more careful editing. (Perhaps the most humorous editorial lapse occurs in the list of references where all of Haldane's works are attributed to his wife, Charlotte.)

The first chapter considered five potential causes of evolution that had been suggested historically 'for the deeper transformations of the geological record' (Haldane 1932, p. 11): (i) random inheritable variation; (ii) environmentally induced inheritable variation; (iii) variation due to 'internal causes'; (iv) variation due to hybridization; and (v) selection. Although Darwin (in later editions of the *Origin*) had coupled selection with both random and acquired inheritable variation, Haldane argued that experimental evidence had largely ruled out the latter. Those who believed in natural selection as a major cause of evolution were thus left with selection acting solely on random (or blind) inheritable variation. Haldane's 'Mathematical theory' series of papers had provided a quantitative basis for neo-Darwinism. The problem of *Causes* was to provide a full biological interpretation of the new theory, to show how the new material genetics permitted the construction of a complete theory of evolution from only causes (i) and (v). The success in this enterprise was the major contribution of *Causes*. If this full interpretation was supposed to play a unifying role for biology, which Haldane's discussion strongly suggests (but does not explicitly claim), then this is how the work becomes 'synthetic.' (It is also hard not to draw a comparison to Darwin's project in the *Origin*; each of these books consist of one long argument.)

By the late 1920s, at the time when Haldane's mature views were being formed, the so-called Lamarckists who advocated the inheritance of acquired characters were rare. In *Causes*, as noted earlier, this type of Lamarckism was peremptorily dismissed on experimental grounds: there was no credible evidence (Haldane 1932, pp. 130–138). The other alternatives to neo-Darwinism such as saltationism and orthogenesis (both due to internal factors, i.e., cause [iii] in the schematism above) continued to merit more attention. In the 1920s, saltationism came with an illustrious pedigree, at least among some geneticists. (Recall the earlier discussion of Morgan's endorsement of large mutations.) Though Haldane emphasized neo-Darwinism, he remained ambivalent about saltationism and regarded it as a live possibility at that time, at least for plant speciation, e.g., through ploidy change.

In the case of orthogenesis, invoking selection to explain the usual cases of evolutionary progress through adaptation was straightforward and less vacuous than invoking orthogenesis dependent on experimentally unknown mechanisms. However, Haldane also deployed an additional argument against orthogenesis which is interesting because it captures the subtlety of his view of evolution. He denied the ubiquity of evolutionary progress and, thus, the possibility of there being operative any inner perfecting principle in evolution (as orthogenesis and similar proposals required): According to him:

> Degeneration is a far commoner phenomenon than progress. It was less striking because a progressive type, such as the first bird, has left many different species as progeny, while degeneration often leads to extinction, and rarely to a widespread production of new forms. Just the same is true with plants. …Certainly the study of evolution does not point to any general tendency of a species to progress. The animal and plant community as a whole does show such a tendency, but this is because every now and then an evolutionary advance is rewarded by a very large increase in numbers, rather than because such advances are common. But if we consider any given evolutionary level we generally find one or two lines leading up to it, and dozens leading down (Haldane 1932, p. 153).

Haldane went on to argue that all talk of progress represents rather a tendency of man to pat himself on the back[;] . . . [t]he change from monkey to man might well seem a change for the worse to a monkey (p. 153). In contrast to almost all evolutionists of the time and since, Haldane did not see evolution through natural selection as necessarily implying progress. There were just too many ways in which selection could act, be constrained, and result in evolution. This is the type of thinking that prevented him from ever proposing grand narratives for the course of evolutionary history on Earth along the lines of Fisher and Wright.

Chapter II began the systematic engagement with the material basis of heredity that, as I have been arguing, sets Haldane's project apart from all others in the population genetics (and, more generally, evolutionary theory) of that time. This chapter summarized what was then known about intraspecific variation at the levels of both genes and chromosomes, i.e., primarily due to the work of the Morgan school, which was thus given an evolutionary interpretation. Differences within species were differences between alleles at individual loci and, in some cases, the arrangement of such loci on chromosomes. Haldane duly noted the many complexities of chromosomal (what would now be called genomic) organization that the Morgan school had demonstrated.

Chapter III then turned to variation between species, now focussing somewhat more on British work on plants than on *Drosophila* genetics. What intrigued Haldane was that species could differ by ploidy, i.e., entire sets of chromosomes. This automatically suggested speciation through hybridization and allopolyploidy, and Haldane provided the example of *Primula floribunda* and *P. verticillata* hybridizing to form *P. kewensis* (Haldane 1932, pp. 67–69). Allopolyploidy was common among plants, though, according to Haldane, rare among animals if it occurred at all. Ultimately, Haldane concluded:

> [I]nterspecific differences are of the same nature as intervarietal. But the latter are generally due to a few genes with relatively large effects, and rarely to differences involving whole chromosomes or large parts of them. The reverse is true of differences between species. The number of genes involved is often great, and cytologically observable differences common. It is largely these latter which are the causes of interspecific sterility, (Haldane 1932, p. 82).

The conclusion harked back to Darwin and Wallace: varieties were incipient species. According to Haldane (and, as noted earlier, Morgan apparently agreed with him on species' differences to the extent that he appreciated the relevant evolutionary issues), the material basis for heredity as explicated by classical genetics corroborated the original insight of Darwin and Wallace.

Having thus integrated the experimental results of genetics into the framework of evolution, chapter IV finally turned to the analysis of selection. It provides a systematic biological interpretation of the 'Mathematical theory,' pooling together the implications of the more important examples that were scattered through its 10 parts. But, more importantly, it revealed a more sophisticated view of natural selection than found in that sequence of papers. In particular, in both this chapter and chapter V, Haldane's biochemical expertise (recall that, professionally, he was still a biochemist at Cambridge) was brought to bear on genetics to an extent that neither he, nor anyone else, had ever attempted before. For instance, when he noted the possibility of epistasis saying '[i]t is important to realise that the combination of several genes may give a result quite unlike the mere summation of their effects one at a time,' (Haldane 1932, p. 96), he immediately proceeded to suggest a biochemical basis: '[epistasis] is obviously to be expected if genes act chemically,' (Haldane 1932,

p. 96). The context makes it clear that the hypothetical is purely rhetorical: for Haldane, genes obviously acted chemically.

Primula sinensis provided an example: in it, 'a dark stem (recessive) is associated with no great change in colour of acid-sapped (red and purple) flowers. But blue (recessive) flowers, which have a neutral sap, when growing on a dark stem are mottled. The same recessive dark stem genes, along with genes for a green stem, give plants which will not set seed, though they give good pollen' (Haldane 1932, p. 96). The Morgan school also believed in the relevance of chemical action emanating from the gene though they were careful to acknowledge that their results could also be interpreted formally and did not necessitate any specific chemical (or material) interpretation of the gene (see Allen 1978 and Sarkar 1998). But Haldane, around this time, had also begun thinking of a programme in chemical genetics (which came to fruition during the next decade at the John Innes Horticultural Institution (for detail see Sarkar 1992a). He was thus willing to take more intellectual risks in following genes down their chemical pathways.

The question of time remained a central issue. Haldane commented on the possibilities of pleiotropy and neutral or nearly-neutral genes. With respect to pleiotropy, '[o]ccasionally a single gene might produce simultaneous and harmonious changes in many [characters] at one, but this is not generally the case with new mutants, though some such genes, being almost harmless, are not eliminated, and account for much of the variation in natural populations,' (Haldane 1932, p. 103). He was keenly aware of how this affected the rate of evolution: 'Evolution must have involved the simultaneous change in many genes, which doubtless accounts for its slowness' (Haldane 1932, p. 103). However, neutral or nearly neutral mutations may have enabled rapid evolutionary change. 'If the only available genes produce large changes, disadvantageous one at a time,' Haldane argued,

> then it seems to me probable that evolution will not occur in a random mating population. In a self-fertilized or highly inbred species it may do so if several mutations useful in conjunction, but separately harmful, occur simultaneously. …But when natural selection slackens, new forms may arise which would not survive under more rigid competition, and many ultimately hardy combinations will thus have a chance of arising. …This seems to have happened on several occasions when a successful evolutionary step rendered a new type of organism possible, and the pressure of natural selection was temporarily slackened (Haldane 1932, pp. 104–105).

Hybridization was another possible source of rapid evolutionary change. The chapter ends with a discussion of the relative importance of mutation and selection. About mutation as a source of evolutionary change, Haldane's final conclusion is negative: 'we cannot regard mutation as a cause likely by itself to cause large changes in a species,' (Haldane 1932, p. 110).

The most innovative discussion in chapter V were of altruism and of the conflict between competition and selection (and these discussion went way beyond anything in the 'Mathematical theory'). Both were motivated in part by political concerns of the time and, because of that, they will be briefly elaborated here even though they are not central to the argument of this paper. Haldane was deeply concerned to expose the 'poisonous nonsense which has been written on ethics in Darwin's name,' (Haldane 1932, p. 119). These writings were based on a

> fallacy …that natural selection will always make an organism fitter in its struggle with the environment. This is clearly true when we consider the members of a rare and scattered species. It is only engaged in competing with other species, and in defending itself against inorganic nature. But as soon as a species becomes fairly dense matters are entirely different. Its members inevitably begin to compete with one another. …And the results could be biologically advantageous for the individual, but ultimately disastrous for the species. The geological record is full of cases where the development of enormous horns and spines (sometimes in the male sex only) has been the prelude to extinction. It seems probable that in some of these cases the species literally sank under the weight of its own armaments (Haldane 1932, pp. 119–120).

In passing, note how there is a clear recognition of the potential conflict between various levels of selection in this passage. (Mayr (1992) has read this passage to indicate that Haldane, allegedly like many others in the 1920s, was assuming that selection acts for the benefit of the species rather than the individual. This reading is at best uncharitable: what Haldane seems to be saying is that individual selection relative to other individuals in a population need not give any indication of the rate of change of the population size, an important point that still deserves emphasis. Another way of putting it is that Haldane, having explicitly recognized the difference between absolute and relative fitness, was noting how the use of the former alone can be misleading about evolutionary consequences.)

A less explicit but eventually more influential recognition of different levels of selection is to be found in the other major innovation of this chapter, the account of altruism:

> It can be shown mathematically that in general qualities which are valuable to society but usually shorten the live of their individual possessors tend to be extinguished by natural selection in large societies unless these

> possess the type of reproductive specialisation found in social insects. This goes a long way to account for the much completer subordination of the individual to society which characterises insect as compared to mammalian communities (Haldane 1932, p. 130).

Haldane's conclusion was that: while he 'doubt[ed] if man contains many genes making for altruism of a general kind, …we do probably possess an innate predisposition for family life. …For in so far as it makes for the survival of one's descendants and near relations, altruistic behaviour is a kind of Darwinian fitness, and be expected to spread through natural selection' (Haldane 1932, p. 131).

Despite the spirited defense of natural selection, at the end of the book, Haldane remained cautious about its power. He argued that two other factors must be included in a general account of evolution: (i) discontinuous changes (for instance through hybridization); and (ii) the mutations to generate the necessary variation. As he put it:

> if we come to the conclusion that natural selection is probably the main cause of change in a population, we certainly need not go back completely to Darwin's point of view [though without cause (b) in the schematism at the beginning of this section]. In the first place we do have reason to believe that new species may arise quite suddenly, sometimes through hybridisation, sometimes perhaps by other means. Such species do not arise, as Darwin thought, by natural selection. When they have arisen they must justify their existence before the tribunal of natural selection, but that is a very different matter. …
>
> Secondly, natural selection can only act on the variations available, and these are not, as Darwin thought, in every direction. In the first place, most mutations lead to a loss of complexity. …This is probably the reason for the at first sight paradoxical fact that …most evolutionary change has been degenerative. But further, …mutations only seem to occur along certain lines, which are very similar in closely related species, but differ in more distant species (Haldane 1932, pp. 138–140).

For the next generation of population geneticists, the mathematical appendix of *Causes* was at least as important as the text. There, Haldane summarized the mathematical results obtained by Fisher, Wright and himself. Given that Fisher (1930) had uncharitably altogether ignored both Haldane's and Wright's work in *The genetical theory of natural selection*, and Wright did not write a general review or book during this period, this Appendix became the only compendium of mathematical population genetics for that generation.

Interpretation and influence

In retrospect, in emphasizing the mathematical work on natural selection, and the connections between his own work and that of Fisher and Wright, Haldane inadvertently did *Causes* a disservice. However, this emphasis was present only in the appendix. Nevertheless, it was routinely promoted in the subsequent decades. What seems to have helped promote this interpretation of *Causes* is that this appendix was the major resource for theoretical population geneticists for the next generation (as Crow (1992) emphasized in his centenary assessment of Haldane). The importance of Haldane's work on mathematical models of population genetics should not be under-emphasized and I have previously argued that this work, because of its connection with empirical data, is as (if not more) important for evolutionary theory than the grand theories about evolutionary history pushed by Fisher and Wright (Sarkar 2007). Leigh (1990) made a related point in his reassessment of *Causes*, particularly its mathematical appendix, in 1990. He emphasized the extent to which Haldane's models continued to be a resource for further inquiry even then. That situation has not changed.

However, my concern in this paper is not even with evolutionary theory in general let alone with grand narratives such as those constructed by Fisher and Wright; rather, it is with the historical emergence of what I have been calling the received view of evolutionary theory or the synthesis. It does not seem to me that much depends on whether the term 'synthesis' continues to be used to describe this development. As others have pointed out earlier (e.g., Smocovitis 1996), the use of 'synthesis' is problematic for multiple reasons and likely never did no work other than rhetorically announce the triumphant emergence of a successful, mature, neo-Darwininan evolutionary framework. What may be more historically (and philosophically) interesting is the question whether there is any intellectually respectable construal under which what emerged as the received view can be viewed as a synthesis of biometry and Mendelism—I have been suggesting otherwise.

At the very least, talk of a synthesis does imply some sense of two (or more) conceptually (better yet, logically) independent strands of conceptual thinking being brought together in such a way as they reinforce each other in an integrated framework. What is critical to the emergence of the received view is this is what happened in the late 1920s as, first, consistency was established between the material basis of heredity explicated mainly by the Morgan school and the formal theory of heredity as embodied in Mendel's rules (as modified by linkage). Without the mechanistic (material) interpretation, Mendel's rules would not have continued to serve as a resource for further development of evolutionary theory. But Mendel's rules came riddled with exceptions—linkage and incomplete dominance being the ones to be first recognized but being followed also by inversions, ploidy changes, and many others. That the

Mendelian framework was not heading to a future filled with iterated epicycles only became clear because of the elaboration of the material models of heredity. Thus, and this is the second aspect of this synthesis, this material basis provided a description (if not yet an explanation) of how and why these exceptions and complications occurred. At the same time, these material models explained the remarkable extent to which these models approximated (or, for philosophers 'saved') the phenomena. Potentially these developments laid the stage for further theoretical innovation after the emergence of molecular biology: unification of the independent conceptual strands in this unification progressed to the molecular explanation of the Mendelian principles, i.e., what philosophers have called the reduction of classical genetics (or Mendelian genetics) to molecular biology (or, more accurately, macromolecular biophysics) (Sarkar 1998). (Note that the question of reductionism, like many others in philosophy, continues to be controversial—see Brigandt and Love 2017.)

The first work that established this unificatory codependence of the formal and material accounts of heredity was *Causes*; the first person to realize that this was possible was probably Haldane and probably very early in the 1920s. (But Haldane did more than that in *Causes*, incorporating into the general framework the facts of evolutionary history as found in the palaeontological record—Carson's (1980) insight into this achievement deserves recognition and reiteration.) If the conclusions of this paper are correct, then the historiography of evolutionary theory not only must move beyond the infatuation with Fisher and Wright, and Mayr and the other contributors late in the game after 1940, but should go back to the Morgan school and the early classical geneticists, perhaps to the dialectic between Haldane's theorizing and Muller's resistance that Wimsatt (1992) analysed. *Causes* is the most important founding document in the emergence of the received view evolutionary theory.

Final remarks: why 'synthesis'?

Finally, let me return to the potentially puzzling question of where all this talk of a 'synthesis' between biometry and Mendelism began. Strangely enough, it also goes back to Haldane, to a (perhaps justly) forgotten popular paper from 1938. This is where, to the best of my knowledge, the idea of a 'synthesis' between biometry and Mendelism is first suggested. However, Haldane's interpretation of 'synthesis' was not substantive but methodological except for one recalcitrant sentence (see below):

> [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; emphasis added).

Only the last sentence is more than methodological; here, Haldane was referring to Fisher's (1918) seminal paper from 1918 which, as I have argued in detail in an earlier book (Sarkar 1998), established the reduction of biometry to Mendelian genetics rather than a synthesis. However, turning to the rest of this quotation, even in a methodological context, Haldane's claim was misleading. All that was retained from Pearson in the context of population genetics was a class of statistical techniques which were not uniquely applicable to biometry and population genetics. Indeed, if the satisfaction of this criterion alone suffices for a 'synthesis', biometry had been synthesized with every discipline employing statistics.

Given these problems, of which Haldane would have been aware if this forgotten paper was playing some tangible intellectual role in the development of his theoretical work, why did Haldane make such a claim, i.e., why did he invoke the term 'synthesis' in this context? The most plausible answer turns to what, in the twentyfirst century, probably appears to be an idiosyncratic turn in Haldane's thought but, at the time when that paper was written, was critically important to him. At that time Haldane was undergoing a Marxist conversion and the paper was written at the height of his newfound enthusiasm for the Hegelian dialectic that Marx had famously inverted by giving it a materialist interpretation (Haldane 1937, 1939; Sarkar 2004). And, thus, Haldane came to interpret the development of evolutionary theory through the framework of the Hegelian triad of thesis, antithesis and, of course, synthesis. As demanded by the logic of Hegel and Marx, and exemplified in the quoted passage, both the thesis and the antithesis were crude compared to the synthesis.

It should be emphasized that the paper from which this quotation is taken (entitled 'Forty years of genetics') was not intended as anything more than popular anecdotal history of science; for historians, it should never have been the basis for any historiographic tradition and, in a sense, has not directly played any such role. However, it is highly likely that, given the continuous interactions between Haldane and Huxley at the time, Huxley would have known the volume in which this paper had appeared. Presumably that is where he acquired 'synthesis' from for the title of his highly popular book which was composed soon afterwards. As I noted at the beginning of this paper, and as Mayr (1980) has insisted in his remarks quoted there, Huxley's influence was largely responsible for the historiographic tradition to which I am responding. Nevertheless, the irony of this odd Marxist origin of the evolutionary 'synthesis' should also not be entirely forgotten. Most importantly, Haldane's turn to Marxism deserves more than ironic attention. Those were the years when western Europe had capitulated to Hitler; the communists were the only political party willing (at least until the Hitler–Stalin pact of 1939) to provide principled resistance to the Nazis. Distraught liberal intellectuals, some of whom had fought on the losing side in the Spanish civil war earlier in the decade (as had Haldane, in an advisory capacity), routinely turned to the Communist Party. As he explicitly mentioned in his unpublished biography, resistance to Nazism was the motivation for Haldane becoming a 'cooperator' (Haldane *ca*. 1942). Haldane took his new ideology seriously. The Hegelian dialectic came as part of the package.

Acknowledgements

My interest in Haldane and in the history of evolutionary theory dates back to the late 1980s. Many people have contributed to the development of the ideas expressed here and in earlier work, and have provided help at various stages while a scientific biography of Haldane is very slowly being composed. Not all of them will be mentioned here because the list would be far too large. However, the following individuals have influenced and helped me most: among those since deceased are James F. Crow, Joshua Lederberg, John Maynard Smith, Ernst Mayr, and William B. Provine; the others remain Anthony W. F. Edwards, Warren Ewens, Raphael Falk, Vidyanand Nanjundiah, John Stachel, and William C. Wimsatt. Thanks are also due to Nanjundiah for comments on an earlier draft of this paper. Finally thanks are due to the ever-patient archivists at the John Innes Institute, the National Library of Scotland, and University College London.

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